

A TEST OF THE VARIABLE NATURE OF
DENSITY-DEPENDENT MORTALITY IN
FISH POPULATIONS,

by

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Dissertation submitted to the Graduate Faculty of the
Virginia Polytechnic Institute and State University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

Fisheries and Wildlife Science

(Fisheries Science Option)

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ACKNOWLEDGEMENTS

I would like to thank the members of my advisory committee, Drs. Marvin Lentner, John Ney, Garland Pardue, and Jackson Webster, for their efforts in improving this work. I am appreciative of help given by Drs. Robert Lackey and Larry Nielsen in reviewing this dissertation and in locating data from Oneida Lake, respectively. I am grateful to Dr. Philip Goodyear and the Fish and Wildlife Service for financially supporting this work. Finally, many thanks must go to Dr. Alan Tipton for his patience and his influence on the quality of this research.

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INTRODUCTION

Assessment of environmental impacts has greatly increased in the past several years. As a consequence of numerous pieces of legislation, notably the National Environmental Policy Act of 1969 and Amendments to the Federal Water Quality Control Act of 1972, industry and government have placed increased emphasis on assessment of impacts of their actions on stream and lake biota. The resultant mixture of biology and law has spawned much controversy. The number of litigations concerning aquatic biota, industry, government, and/or other groups has increased dramatically (Wallace 1975, McFadden 1977, Swartzmann, Deriso, and Cowan 1977, Van Winkle 1977).

One reason for so many legal battles is that biologists are often working near the frontiers of knowledge in their discipline. In these gray areas, different theories are proposed to explain the same or similar phenomena. Often the theory of one group contradicts the theory of another. The subsequent schools of thought may be debated in a court of law, especially if there is a large social or economic consequence hinging on resolution of the conflict.

One such controversy surrounds operation of power plants with once-through cooling systems. These power

plants have the potential to destroy large numbers of small fish by pulling them into and through cooling systems (Coutant 1974, Hanson, White, and Li 1977). Larger fish are impinged on intake screens and other structures where abrasion, impalement, and dessication may cause great mortality. Smaller fish pass through screens and are entrained into cooling systems where algacides and rapid changes in water temperature and pressure cause large losses. The fact that large numbers of fish are killed through impingement and entrainment is generally not disputed; what is in dispute is the impact of the loss of these fish to the dynamics of their populations (Goldstein and Hamilton 1977).

The significance of losses of small and larval fish is dependent upon the manner in which populations respond to reduction in numbers. There are three possible responses: the population "compensates" for these losses by absorbing them, "decompensates" by magnifying them, or neither compensates nor decompensates but simply adds these losses to those incurred naturally. All of these responses are based on the relationship between mortality and abundance.

The first use of terms similar to those of "compensation" and "decompensation" in the literature of fisheries science was by Neave (1953). This paper dealt

with the dynamics of populations of pink and chum salmon (Oncorhynchus gorbuscha and O. keta, respectively). In his abstract, Neave stated that:

"Population levels and changes are determined by the combined effects of three types of mortality: (a) mortality which becomes relatively heavier as populations increase in density (compensatory); (b) mortality that becomes relatively heavier as populations decrease in density (depensatory); (c) mortality which is independent of density (extrapensatory)¹."

Compensatory dynamics occur when the probability of an individual dying is directly related to the abundance of its peers; depensatory dynamics occur when the probability of death for an individual is inversely related to abundance; and density-independent dynamics occur when the probability of an individual dying is unrelated to abundance.

Past studies have not clearly shown which of the three kinds of mortality most commonly occurs in fish populations. McFadden (1977) listed 17 examples of compensation as an argument for its predominance. Yet in probably the most

¹This nomenclature was adopted for subsequent use in this thesis with one exception. "Density-independent" was substituted for "extrapensatory" to conform with convention.

documented and thoroughly investigated instance, compensatory and density-independent mortality have been observed in various age groups of yellow perch (Perca flavescens) in Oneida Lake, New York (Forney 1971, Tarby 1974).

Results summarized by Tanner (1966) are indicative of other papers on this subject. Tanner correlated estimated rates of survival and abundance calculated from catch statistics for 7 fish populations. All correlations were negative (compensatory dynamics) except for that of a population of lake trout (Salvelinus namaycush). None of the correlations were large ($r < .5$), and when these correlations were tested for deviations from zero, many had high probabilities of a Type I error.

This ambiguity in the literature can be explained with a relatively simple hypothesis. Neither compensatory, compensatory, nor density-independent mortality is consistently more prevalent than the others, but each is dominant as warranted by temporally variable conditions. One feature of most studies addressing this problem is the low value of correlation coefficients. These coefficients are usually based on mortality and abundance as measured over a number of years. If the hypothesis is true, temporally variable conditions would alter measured relationships from year to year. In cases where

significantly influential, but yearly variable factors are present, effects of density-dependent mortality would be masked by effects of these factors. Indeed, if conditions warranted, relationships between abundance and mortality could change; under one set of circumstances, mortality in a fish population could be compensatory, while mortality for the same population could be density-independent or compensatory in another year under different circumstances.

A new procedure for "measuring" relationships between abundance and mortality in fish populations is needed. If the aforementioned hypothesis is true, present procedures based on correlation coefficients are not dependable. Only when abiotic and biotic environmental factors exert a constant influence on relationships between abundance and mortality over a number of years are such procedures reliable. What is needed for such a measurement is a situation where potentially variable factors are either stable or controlled.

A simulation model based on a given fish population or populations could present the opportunity of controlled experimentation. By using a model, variables can be changed at will with all others held constant; effects of single factors and their interactions can be separated and tested. To ensure close similarity between dynamics of real and

hypothetical populations, such a simulation model must include all those factors that significantly affect population dynamics of modeled fishes and be rigorously validated².

Beyond the natural changes in mortality, this simulation model could be used to measure effects of impingement and entrainment on small fish in the context of many simulated abiotic and biotic factors.

Simulation models have been used in this manner before. Drawing largely from the literature on exploitation of commercial fisheries and concepts of maximum-sustained yield, most of these models are based on the population as a single unit. Calculations and processes concerned fish as a group, and their parameters described a direct relationship between mortality and abundance. These empirical models require a priori knowledge on the kind of mortality at work, whether compensatory, depensatory, or density-independent. Indeed, the major difference between some of these models is their assumptions concerning mortality and its relation to abundance (Swartzmann, Deriso, and Cowan 1977).

If my hypothesis is true and relationships between mortality and abundance are based on temporally variable

²See Appendix A for an explanation of "validation".

circumstances, all models based on such a priori assumptions about these relationships are unrealistic. Such assumptions would only be valid under uniform circumstances; any variability in significant abiotic and biotic factors would render them highly inaccurate.

To circumvent this need of making a priori assumptions about mortality, the dynamics indigenous to a population of fish must be modeled as a consequence of their biology. Mortality is the result of actions taken by those killed and by those doing the killing. For instance, a particular fish is a better predator than its competitor because it can see further, swim faster at less energetic cost, and digest more efficiently. Whether mortality is related to density is a result of intra- and inter-specific relationships such as these. Only when these processes are addressed can population dynamics be treated as results rather than assumptions. This philosophy has been stated by C. S. Holling in his various works concerning predator-prey relationships and is summarized in the following abstract concerning the philosophy of a model of predation:

"A different type of model concerning predation was therefore developed by ignoring the need for simplicity and emphasizing the need for reality. The model was developed from an approach that used extensive experimentation to suggest and test possible explanations for the action of each component of the process so that it evolved in

gradual steps to include one component after another." (Holling 1962)

The goal of my project was to create such a model and use it to test the effects of impingement and entrainment on the dynamics of small fishes in a selected fish community. Objectives to be achieved in attaining this goal were to:

- 1) select a fish community to serve as a focal point for the study,
- 2) construct and document a simulation model based on the philosophy that population dynamics are results of the biology of individuals,
- 3) validate this model with data from the selected fish community, and
- 4) conduct several experiments with the validated model.

Walleye (Stizostedion vitreum vitreum) and yellow perch in Oneida Lake, New York, were chosen as populations upon which validation and subsequent experimentation could be based. This fish community provided several advantages for validation:

- 1) Oneida Lake and its fishery have been extensively studied for many years (Clady 1976a),
- 2) dominant fishes in Oneida Lake are usually limited to walleye and yellow perch (Forney 1976), thereby limiting the scope of the modeling effort to these species,

3) dominant fishes in Oneida Lake have been relatively well-studied throughout their range,

4) walleye and yellow perch are relatively important sport fisheries wherever found, and

5) walleye and yellow perch are not major influences on the dynamics of invertebrate populations in Oneida Lake (Noble 1975), thereby limiting the scope of the modeling effort mainly to fishes.

Model experiments were analogous to controlled experiments; certain variables were altered, and subsequent results were analyzed. Experiments were conducted to:

1) measure effects of impingement and entrainment on annual rates of fry survival,

2) measure effects of certain abiotic and biotic factors and their significant interactions with impingement and entrainment on fry survival, and

3) identify those mechanisms behind simulated fry dynamics.

METHODS

Validation

The model was constructed of various representations of fish behavior and fish biology as observed in populations of walleye and yellow perch in Oneida Lake (Appendix B). Emphasis was placed on documenting each equation describing modeled phenomena.

Validation of the model was conducted with data collected on populations of walleye and yellow perch in Oneida Lake, New York. Chronological limits for all simulations were May 20, 1972, to May 19, 1973. Iterations were made weekly, except from early April to May 19, 1973, when time steps were two days. Each species was divided into nine life stages roughly corresponding to age groups, and three life stages were reserved for nonpiscine taxa (Table 1). Initial conditions and chronological estimates of dependent variables³ were obtained or calculated from various reports (Table 2). Initial estimates of parameters

³Dependent variables in the model were numbers, current median weight, mean length, weight of stomach contents, limits of the size distribution, and maximum median weight of organisms within each life stage. Initial conditions were the values of these variables in mid May, 1972, at the start of each simulation.

Table 1. Assignment of age groups of walleye, yellow perch, and nonpiscine organisms to life stages for validation and model experiments.

Life stage	Age group
1	0+ yellow perch (limnetic)
2	0+ yellow perch (benthic)
3	I+ yellow perch
4	II+ yellow perch
5	III+ yellow perch
6	IV+ yellow perch
7	V+ yellow perch
8	VI+ yellow perch
9	VII+ and older yellow perch
10	0+ walleye (limnetic)
11	0+ walleye (benthic)
12	I+ walleye
13	II+ walleye
14	III+ walleye
15	IV+ walleye
16	V+ walleye
17	VI+ walleye
18	VII+ and older walleye
19	Nauplii larvae
20	Remaining zooplankton
21	Benthos

Table 2. Sources of all estimates of initial conditions for dependent variables. All estimates were obtained outright or were calculated from cited reports.

Life stage	Variables		
	Number	Total length	Maximum ¹ median weight
1	Clady 1973 Clady 1974b	Clady 1973 Clady 1974b	
2 ²			
3	Forney 1973a Forney 1973b	Nielsen ³	
4	Clady 1973	Nielsen	
5	Clady 1973	Nielsen	
6	Clady 1973	Nielsen	
7	Clady 1973	Nielsen	
8	Clady 1973	Nielsen	
9	Clady 1973	Nielsen	
10	Forney 1977b	Forney 1973b	
11 ²			
12	Forney 1977b	Nielsen	

¹ When no citation is present, weights were calculated from length-weight relationships described by el-Zarka (1958), Fortin and Magnin (1972), and Carlander and Payne (1977).

² No benthic fry of either species are normally present in Oneida Lake on May 20.

³ Larry A. Nielsen 1973 (unpublished data).

Table 2. Sources of all estimates of initial conditions for dependent variables. All estimates were obtained outright or were calculated from cited reports (continued).

Life stage	Variables		
	Number	Total length	Maximum median weight
13	Forney 1977b	Nielsen	
14	Forney 1977b	Nielsen	
15	Forney 1977b	Nielsen	
16	Forney 1977b	Nielsen	
17	Forney 1977b	Nielsen	
18	Forney 1977b	Nielsen	
19	Clady 1974b	Clady 1974b	Clady 1974b
20	Tarby 1973 Forney 1973c	Clady 1974b	Clady 1974b
21	Forney 1973c	Clady 1974b	Clady 1974b

for the functional relationships within the model were collected or calculated from published literature (Table 3).

Validation of the model was conducted as specified in Appendix A. Initial values of parameters were altered until deviations between measurements of dependent variables from Oneida Lake and predictions made by the model were minimized.

Limited information on dependent variables of a few life stages was available for validation. Sequential data on lengths, weights, and numbers of 0+ yellow perch and weights of II+ walleye during the growing season in 1972 (Tarby 1973, Forney 1973a) were all that were directly usable. No itemized data on other age groups were found. When no such data were available, values of dependent variables for each life stage on May 20, 1972, were assumed indicative of those same variables one year later and were used as observations for this later date during validation.

Information on independent variables* was also incomplete. Water temperatures at readings of 2 and 10 m were given in Forney (1973b) and Clady (1974a) for ice-free months in 1972 and 1973. Median estimates for each time

*Independent variables in the model were mean water temperature, mean turbidity, mean wind velocity, and mean angling mortality (instantaneous rates) over each iteration during each simulation.

Table 3. List of parameters, switches, and their sources from which their initial values were drawn prior to validation. Values for some parameters were used as found in the literature; others were calculated from published data. Definitions for parameters and switches are in Tables I and II of Appendix B.

Name of variable (identifier)	Citations
PACTVE	Fry 1957
PARC	Nakamura 1968, Kerr 1971
PBURST	Bainbridge 1960, Houde 1969
PCRUIS	Hergenrader and Hasler 1967, Kerr 1971, Kelso 1976
PDIGST	Kelso 1972
PESCAP	Nursall 1973
PEVACT	Brett and Higgs 1970, Schneider 1973a, 1973b, Swenson and Smith 1973
PFAST	Bilton and Robins 1973
PPECND	Priegel 1969, Wolfert 1969, Clady 1976b
PFRY	Norden 1961, Mansueti 1964
PGRAM	Wissing and Hasler 1971, Kelso 1973
PHATCH	Hurley 1972, Hokanson 1977
PJTU	Vinyard and O'Brien 1976
PLOG	Clady 1974a, 1974b

Table 3. List of parameters, switches, and sources from which their initial values were drawn prior to validation. Values for some parameters were used as found in the literature; others were calculated from published data. Definitions of parameters and switches are in Tables I and II in Appendix B. (continued).

Name of variable (identifier)	Citation
PLOVE	Forney 1965, Clady 1976b
PLWREG	el-Zarka 1958, Fortin and Magnin 1972, Carlander and Payne 1977
PMOUTH	Wong and Ward 1972
PNUTRN	Beamish 1974
POVA	Mansueti 1964, Wolfert 1969
PPREF	Cuff 1977
PSSIZE	Hasler and Bardach 1949, Hergenrader and Hasler 1968
PRDMIN	Hasler and Bardach 1949, Hasler and Villemonte 1953, Hergenrader and Hasler 1968
PSDA	Beamish 1974
PSEX	Forney 1965, Clady 1976b
PSM	Winberg 1956, Beamish 1964, Paloheimo and Dickie 1966
PSTOM	Brett 1971
PSTRES	Clady 1973, Forney 1975

Table 3. List of parameters, switches, and sources from which their initial values were drawn prior to validation. Values for some parameters were used as found in the literature; others were calculated from published data. Definitions of parameters and switches are in Tables I and II in Appendix B. (continued).

Name of variable (identifier)	Citation
PTHRM	Clady 1974a, 1974b, Huh, Calbert, and Stuiber 1976, Hokanson 1977
PWIND	Clady 1976b
PDIMEN	Clady and Hutchinson 1975
PPHOTO	U. S. Weather Service
SETHBT	Marshall 1977, Thorpe 1977
SHABIT	Hergenrader and Hasler 1966, Houde 1969, Marshall 1977, Thorpe 1977
SLOVE	Forney 1965, Clady 1976b
SPROWL	Hergenrader and Hasler 1966, Houde 1969, Forney 1973b, Marshall 1977, Thorpe 1977
SSCHOL	Marshall 1977, Thorpe 1977
STRANS	Faber 1967, Houde 1969, Marshall 1977, Thorpe 1977

step were calculated using both depths and both years. Temperatures in winter months in late 1972 and early 1973 were estimated with a trigonometric equation that had been fitted to available data from summer months in both years. Secchi disc readings were obtained from Forney (1973b). These depths were first transformed into percent transmittance of light by using the standard equation for decreasing light intensity with depth of the water column and the expected percentage of light absorbed at a Secchi depth (Hutchinson 1957). Percent transmittance was transformed into Formazin Turbidity Units from standard charts in EPA (1975). Wind velocities were taken from Clady (1974b). Fishing mortality was given as 50 percent per annum for adult walleye, approximately 80 percent of all mortality (Forney 1977b). Annual mortality in adult yellow perch was 35 percent (Clady 1973), and angling was assumed to account for 80 percent of this loss. All angling mortality was assumed to occur from mid May to November for adult walleyes and from mid May to mid April for adult yellow perch; no information was available on actual dates when angling occurred. All mortality rates were transformed into instantaneous rates conforming to lengths of accompanying time steps. Since no information on catches of fry and juveniles (II+ and younger) of both species was

available, fishing mortality on these groups was assumed to be insignificant.

During validation, simulated and observed dynamics of yellow perch fry and walleye fry were compared. Eight simulations with eight different values for abundance of yellow perch fry on May 20, 1972, were run with all simulations covering the period of mid May, 1972, to mid May, 1973. All values of abundance were within limits typical of natural variation in year-class strengths (Clady 1974b). Annual rates of survival were calculated for both yellow perch fry and walleye fry over the period for each of the eight simulations. Correlation coefficients between these rates and their associated abundance of yellow perch fry in mid May, 1972, were calculated.

During validation, observed and simulated food habits of fish in certain life stages were compared. Simulated values of daily rations were obtained from temporary variables⁵. Frequencies of dietary constituents were summed over each simulated day. When observed rations from Oneida Lake were composites of several age groups, simulated frequencies were averaged over several life stages with the

⁵Temporary variables were results of calculations within each simulation and were destroyed after each iteration. Definitions of all temporary variables were given in Appendix B.

average weighted by the numbers in each life stage.

Model Experiments

Length-conditional Mortality

Mortality due to impingement and entrainment was represented as a function of fish length. As fish grow and their swimming prowess increases, they became more apt to survive this type of mortality (Hanson, White, and Li 1977). Code in the model was reworked to apply this mortality as a density-independent factor for all life stages of fish. Rates of survival against impingement and entrainment as the sole source of mortality were assumed asymptotic (Fig. 1). Three levels of length-conditional mortality (impingement and entrainment) were chosen: 0, 5, and 10 percent annual mortality for fish 10 mm long. Annual survival rates from length-conditional mortality for yellow perch fry and walleye fry were calculated by integrating the asymptotic equations from length at the start of the simulation to that at the end and dividing the result by the difference in lengths. Expected reductions in total fry survival were differences between these average rates and unity.

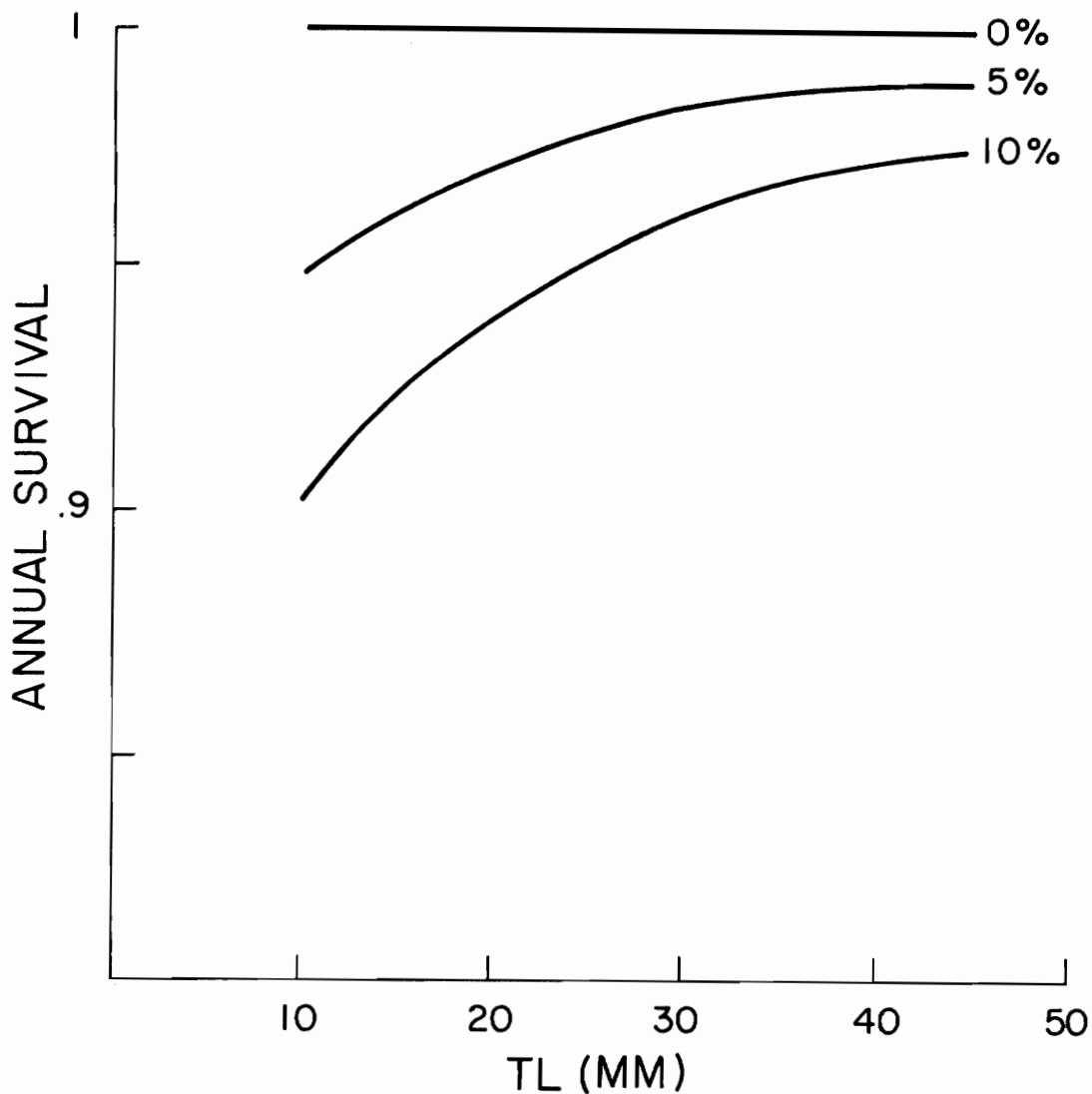


Fig. 1. Asymptotic relationship between length and annual survival rate of fish from impingement and entrainment acting as sole source of mortality. Intensity of length-conditional mortality was 0, 5, and 10 percent as measured as an annual rate of mortality for fish 10 mm long.

Analysis of Variance

Effects of certain abiotic and biotic factors on survival of 0+ yellow perch and 0+ walleye were estimated by using analysis of variance. An experimental design with five factors of three levels each was implemented by varying levels of factors in the model. These factors were chosen for their influence on dependent variables as determined in the preliminary stages of validation. These factors were abundances of yellow perch fry and walleye fry in mid May, 1972, turbidity, water temperature, and length-conditional mortality (Table 4). All levels except those for impingement and entrainment were selected as to be representative of natural variation as observed in Oneida Lake. One level of each factor had the same value as that factor in the validated model. Two hundred forty-three simulations corresponding to all possible combinations of levels for each factor were conducted; each simulation covered the period May 20, 1972, to May 19, 1973. Output from each simulation consisted of annual rates of survival for 0+ yellow perch and 0+ walleye. In each analysis of variance, only main effects and two- and three-factor interactions were tested; all other interactions were returned to the error sums of squares.

Table 4. Factors used in the experimental design investigating those phenomena influencing the annual survival rates of 0+ yellow perch and 0+ walleye in Oneida Lake, New York.

Factor	Levels		
0+ Yellow perch abundance	4.6•10 ⁹	5.5•10 ⁹	6.4•10 ⁹
0+ Walleye abundance	30.•10 ⁸	40.•10 ⁸	50.•10 ⁸
Turbidity (FTU's)	1	5	10
Water temperature (percent of observed)	-5	0	+5
Length-conditional mortality (percent annual mortality for fish 10 mm long)	0	5	10

Mechanisms

A search was conducted to identify those biological and behavioral mechanisms that determined the outcome of model experiments. During simulations, temporary variables representing interim calculations within the model were printed. Values of these variables were compared among different levels of turbidity, length-conditional mortality, and abundance. By comparing values of dependent and temporary variables, cause and effect were separated to explain the reasons behind the results of different model experiments.

RESULTS

Validation

Simulated and observed values of abundance of 0+ yellow perch were more similar when these fish were limnetic than when benthic (Fig. 2). Little deviation occurred until mid June when simulated values became higher than observed values for the month. During August, simulated and observed values began to converge.

Simulated and observed growth in 0+ yellow perch were more divergent than values of abundance. Transfer from limnetic to benthic habitats by young perch was made by mid June in Oneida Lake (Clady 1973) and in the validation. Since body length was used to trigger this transfer in simulations and actual fry became benthic at a relatively constant length in Oneida Lake, proximity in dates indicated a close similarity between simulated and observed growth during limnetic habitation (Fig. 3). After this transfer, simulated growth in perch slowed in comparison to that observed in Oneida Lake. By August and September, simulated rate of growth was greater than observed, and simulated sizes of young perch surpassed those observed in Oneida Lake (Fig. 4).

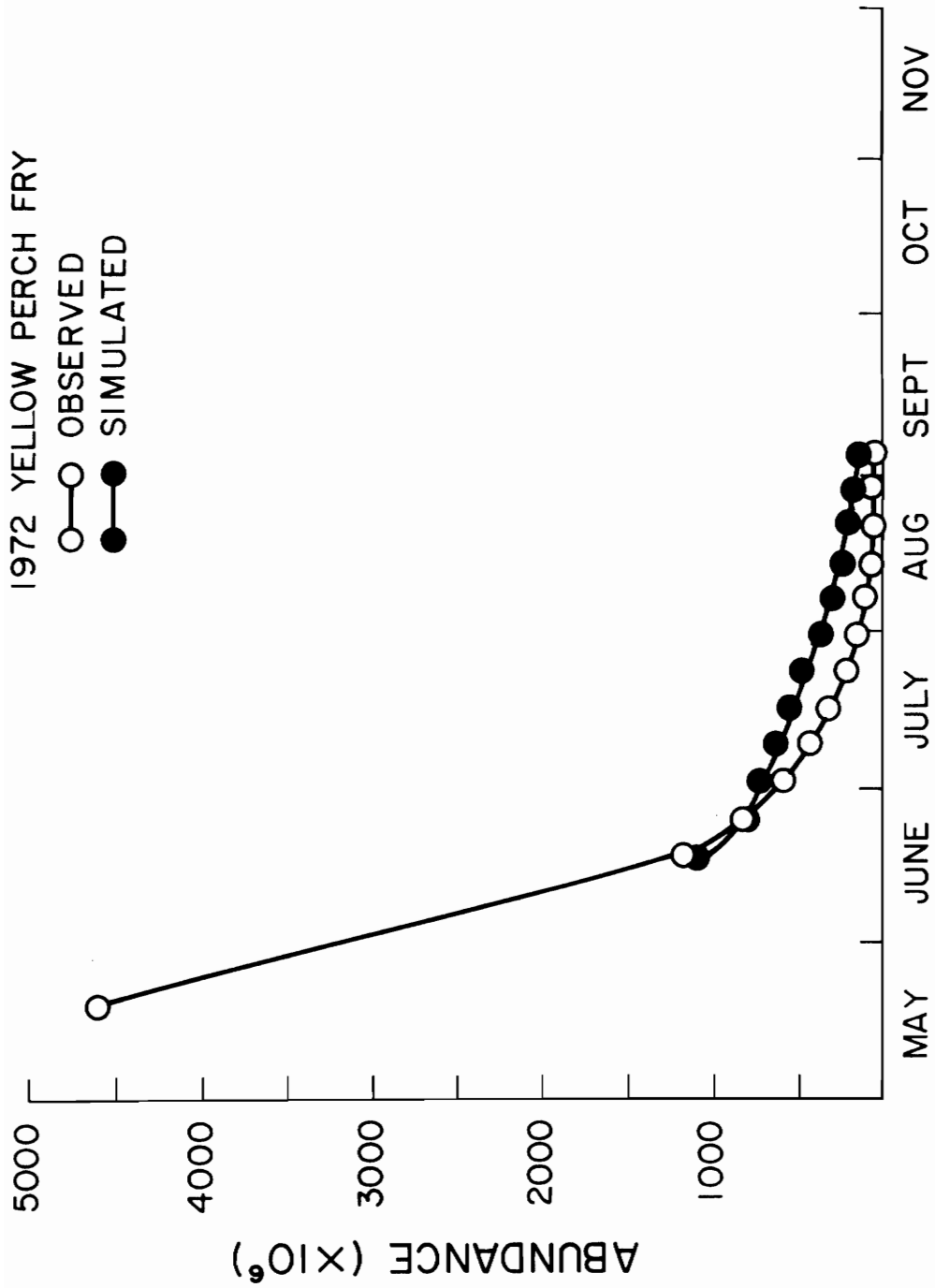


Fig. 2. Comparison between observed and simulated abundance of 0+ yellow perch in Oneida Lake, New York, during 1972.

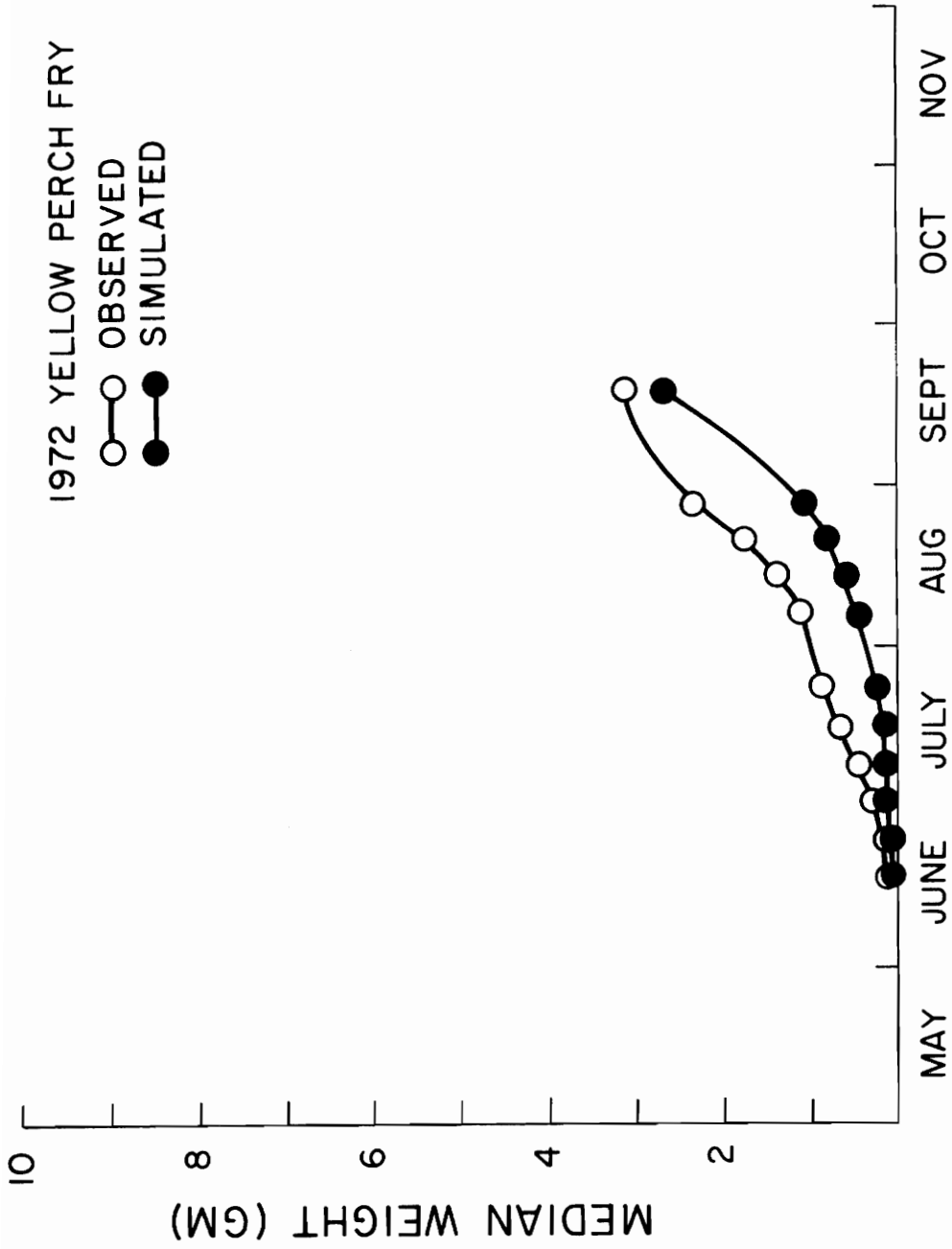


Fig. 3. Comparison between observed and simulated median weights of 0+ yellow perch in Oneida Lake, New York, during 1972.

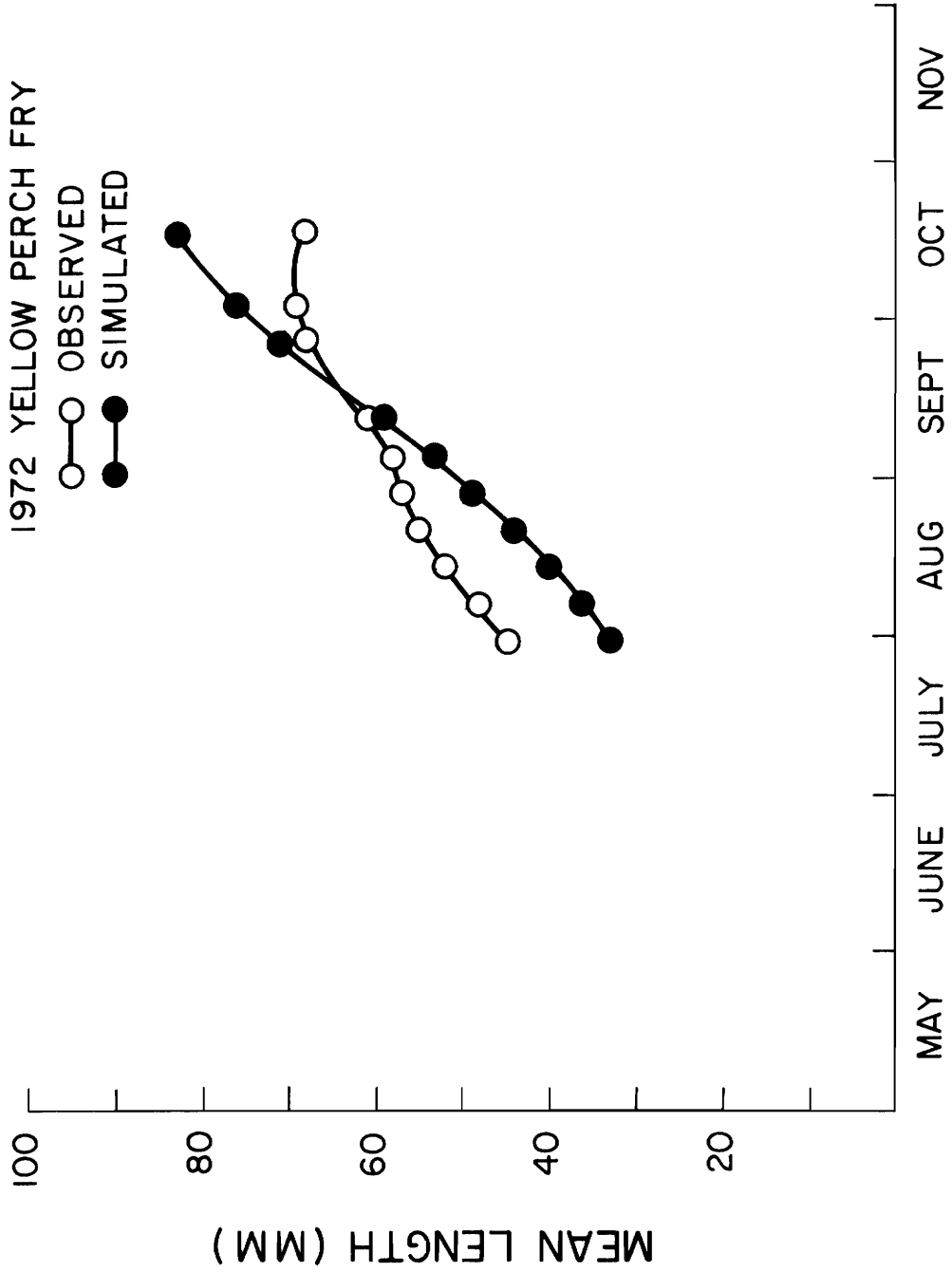


Fig. 4. Comparison between observed and simulated mean lengths of 0+ yellow perch in Oneida Lake, New York, during 1972.

Simulated and observed growth in II+ walleyes were more similar than for young perch (Fig. 5). Simulated values were consistently lower, but never more than 9 percent.

Simulated estimates of abundance of yellow perch other than fry were near to those observed in Oneida Lake in April, 1973, but were generally smaller (Table 5). For all yellow perch four years and older, simulated estimates were within reported 95 percent confidence intervals. Over all, simulated estimates for yellow perch three years and older were 23 percent lower than those observed from Oneida Lake. Simulated abundance of yearling yellow perch was 5.36 million. Abundance as estimated from catch/effort data and area swept by trawls was .83 million (Forney 1973b). No estimate from Oneida Lake for II+ yellow perch was available, and no comparison could be made.

No estimates of abundance of walleyes older than fry were available for mid May, 1973, and no comparison with simulated values was possible. However, a comparison of simulated versus observed annual rates of mortality revealed that modeled rates were slightly higher for the 1967 through 1971 year classes. The simulated annual rate of survival was .69; the observed rate was .62 (Forney 1977b).

Simulated dynamics of young perch and young walleye were much like those observed in Oneida Lake. Forney (1971)

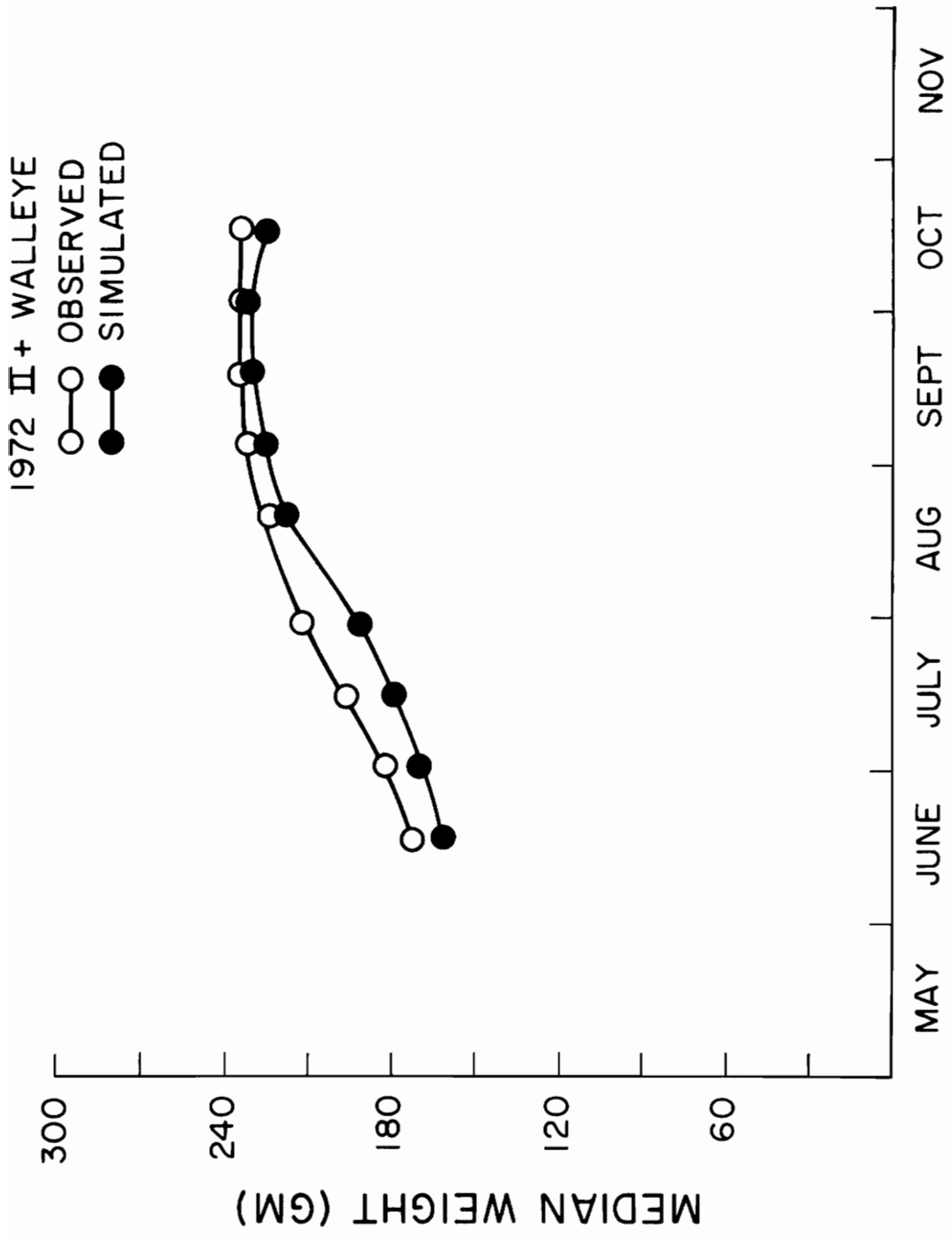


Fig. 5. Comparison between observed and simulated median weights of II+ walleye in Oneida Lake, New York, during 1972.

Table 5. Simulated and observed estimates of abundance for yellow perch three years and older in mid May, 1973, in Oneida Lake, New York. Observations were taken from Table 7 in Forney (1973b). Limits below are 95 percent confidence limits.

Age	Simulated	Observed	Upper Limits	Lower Limits
III+	2,124,000	2,837,000	3,372,000	2,301,000
IV+	35,000	62,000	108,000	16,000
V+	152,000	189,000	270,000	108,000
VI+	395,000	407,000	507,000	306,000
VII++	338,000	447,000	621,000 ¹	271,000 ¹

¹ Limits were reported for VII+ and VIII++ yellow perch. Limits presented here are sums of limits for each of these groups.

showed an inverse correlation between abundance of yellow perch fry and their instantaneous rates of mortality based on catch/effort data from trawls (Pearson's $r = -.67$); the correlation coefficient between simulated abundance of yellow perch and their simulated annual rates of survival was positive (Pearson's $r = .94$). Since instantaneous rates of mortality are negatives of the natural logarithms of survival rates correlations based on observed and simulated data both prove mortality of yellow perch fry as compensatory. Forney (1974, 1976) found that when abundant, yellow perch fry acted as a buffer against cannibalism of walleye fry. Annual rates of survival of walleye fry were directly correlated with abundance of yellow perch fry based on both catch/effort data and estimated abundance (Pearson's $r = .86$ and $.53$, respectively); the correlation coefficient between simulated abundance of yellow perch fry and simulated annual rates of survival for walleye fry was also positive (Pearson's $r = .95$).

Observed and simulated diets were similar for 0+ and adult yellow perch (Table 6). Both observed and simulated cannibalism subsided by September, but the latter more slowly. Consumption of Daphnia sp. by 0+ yellow perch as observed in Oneida Lake was slightly lower than simulated values after mid July, but simulated consumption slowly

Table 6. Comparison of observed (O) and simulated (S) diets of 0+ and adult yellow perch from Oneida Lake, New York, in 1972. Adults are fish IV+ and older. Diets are numbers of organisms per perch per day.

Date	0+ perch ¹ eaten by adult perch		<u>Daphnia</u> sp. ² eaten by 0+ perch		<u>Daphnia</u> sp. ² eaten by adult perch	
	O	S	O	S	O	S
Jun 6	.21	1.46			86	768
13	.06	1.50	16	131	127	884
20	.17	.36			190	1747
27	2.43	1.71	85	3	91	2524
Jul 4	2.27	2.26	92	4	0	3044
11	.52	1.20	191	4	140	2870
18	.96	1.27	128	10	21	4070
25	.41	1.13	50	12	6	3790
Aug 1	.08	.90	50	25	685	5295
8	.09	.91	94	20	478	4595
15	.08	.73	10	48	655	5109
22	.08	.73	414	55	655	4379
29	0	.46	16	103		
Sep 5	0	.32			745	4367
12	0	.32			932	4883

¹ Observed values were taken from Tarby (1975).

² Observed values were taken from Tarby (1973).

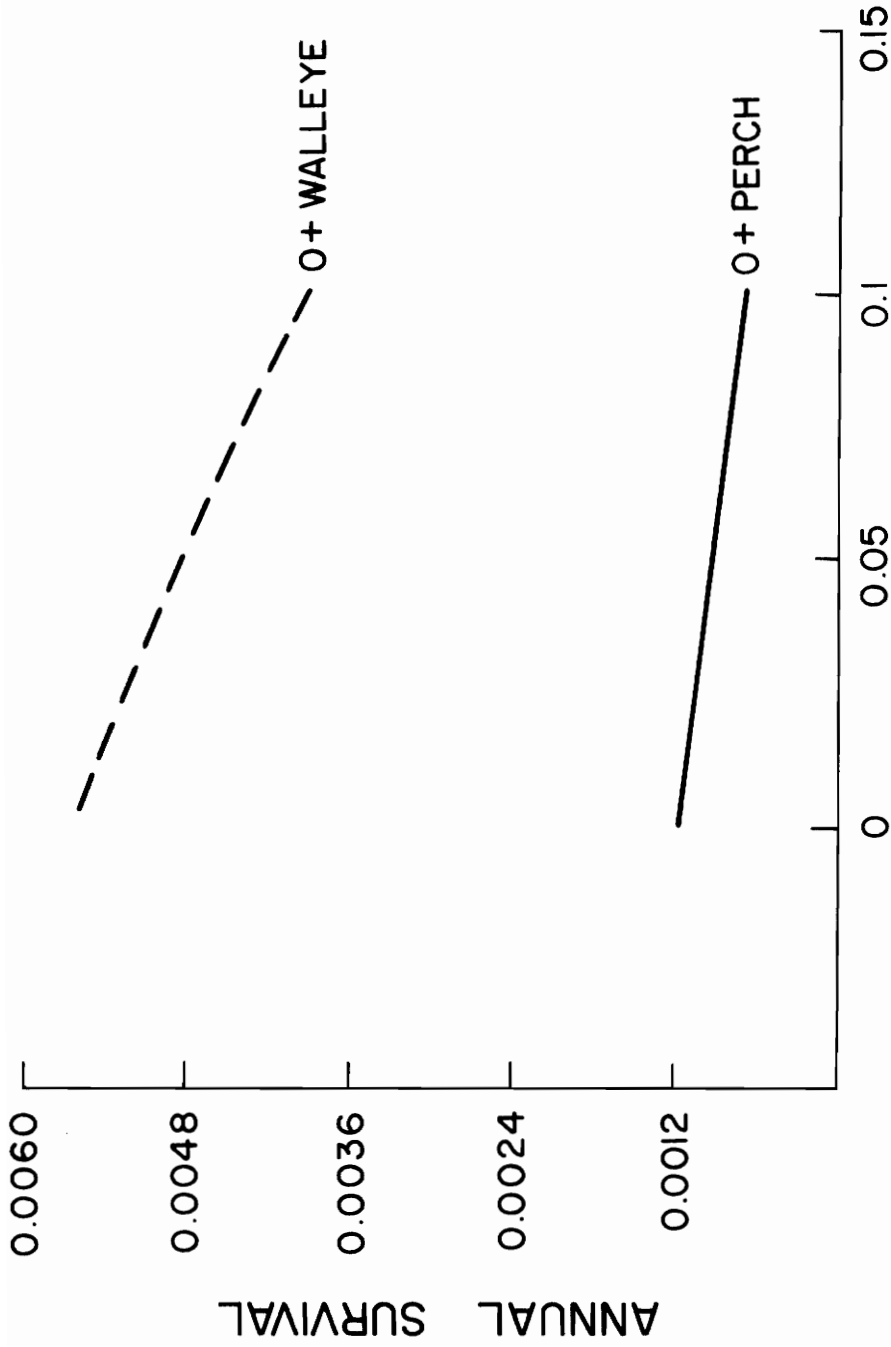
Simulated values are for all zooplankton except nauplii larvae.

converged on observed values thereafter. Simulated consumption of zooplankton by adults was almost an order of magnitude higher than that observed for Daphnia sp. alone. No observed values of consumption by walleyes were found for 1972, and no comparison was made.

Model Experiments

Length-conditional Mortality

Survival of fry of both species was adversely affected by length-conditional mortality (Fig. 6). Annual rates of survival for yellow perch fry and walleye fry without length-conditional mortality were .0012 and .0056, respectively. With length-conditional mortality of 10 percent added, these rates were .00068 and .0039. These decreases were 43 percent for yellow perch and 30 percent for walleye. By integrating the asymptotic formulation in Fig. 1 between initial and final lengths of fry, their annual rates of survival from length-conditional mortality during the simulations were calculated; expected losses from this additional density-independent mortality were 3 percent for yellow perch fry and 2 percent for walleye fry.



ANNUAL L/C MORTALITY FOR FISH 10 MM LONG

Fig. 6. Simulated annual survival rate of young perch and young walleye versus length-conditional mortality (L/C) as simulated at intensities of 0, 5, and 10 percent annual mortality for fish 10 mm long.

Analysis of Variance

Analysis of variance showed that all factors influenced survival of 0+ yellow perch in 1972 (Table 7). All five main effects were statistically significant ($P < .01$) with turbidity the most influential. Survival rate of perch fry rose from .0012 to .14 as turbidity increased from 1 to 10 FTU (Fig. 7). Survival of young perch was also directly related to their initial abundance and that of walleye fry (Fig. 8 and 9). Water temperatures had a different kind of effect on perch survival; increases and decreases in temperatures from those used during validation caused increases in annual rates of survival (Fig. 10).

For young perch, many two- and three-factor interactions were statistically significant ($P < .01$). When turbidity was 1 FTU, survival rate of 0+ yellow perch was decreased 43 percent by length-conditional mortality (Fig. 6); but when turbidity was 10 FTU, this drop was only 5 percent, very close to the expected density-independent mortality of 3 percent (Fig. 11). Another important interaction was initial abundance of perch fry and turbidity. As initial abundance of 0+ yellow perch increased, survival rate of 0+ yellow perch increased 5200 percent from .0012 to .061 when turbidity was 1 FTU; when

Table 7. Analysis of variance used to investigate effects of abundance of yellow perch fry (0+ PERCH), abundance of walleye fry (0+ WALLEYE), turbidity (TURB), water temperature (TEMP), and length-conditional mortality (L/C) on survival of yellow perch fry. Only significant (probability of larger F less than .05) main effects and interactions are listed.

Factors	Degress of freedom	Sums of squares
TURB	2	1.06573
0+ PERCH	2	.28452
0+ WALLEYE	2	.00011
TEMP	2	.02270
L/C	2	.00110
(0+ PERCH) * (TURB)	4	.01101
(0+ PERCH) * (TEMP)	4	.00770
(0+ PERCH) * (TURB) * (TEMP)	8	.00533
(TURB) * (TEMP)	4	.00363
(TURB) * (L/C)	4	.00029
(0+ PERCH) * (L/C)	4	.00006
ERROR	112	.00011
CORRECTED TOTAL	243	1.40221

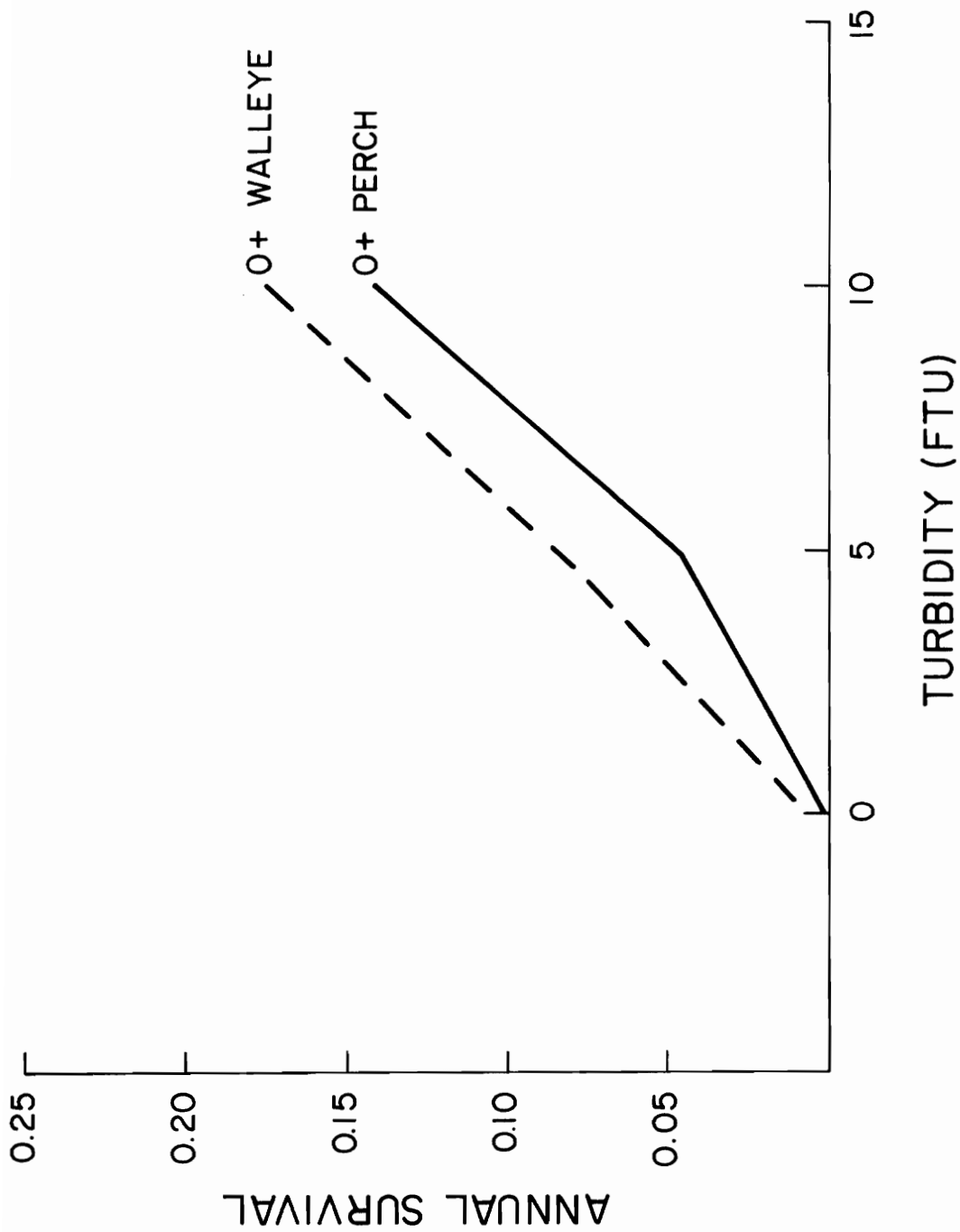


Fig. 7. Simulated annual survival rate of young perch and young walleye from May 20, 1972, to May 19, 1973, versus three levels of turbidity.

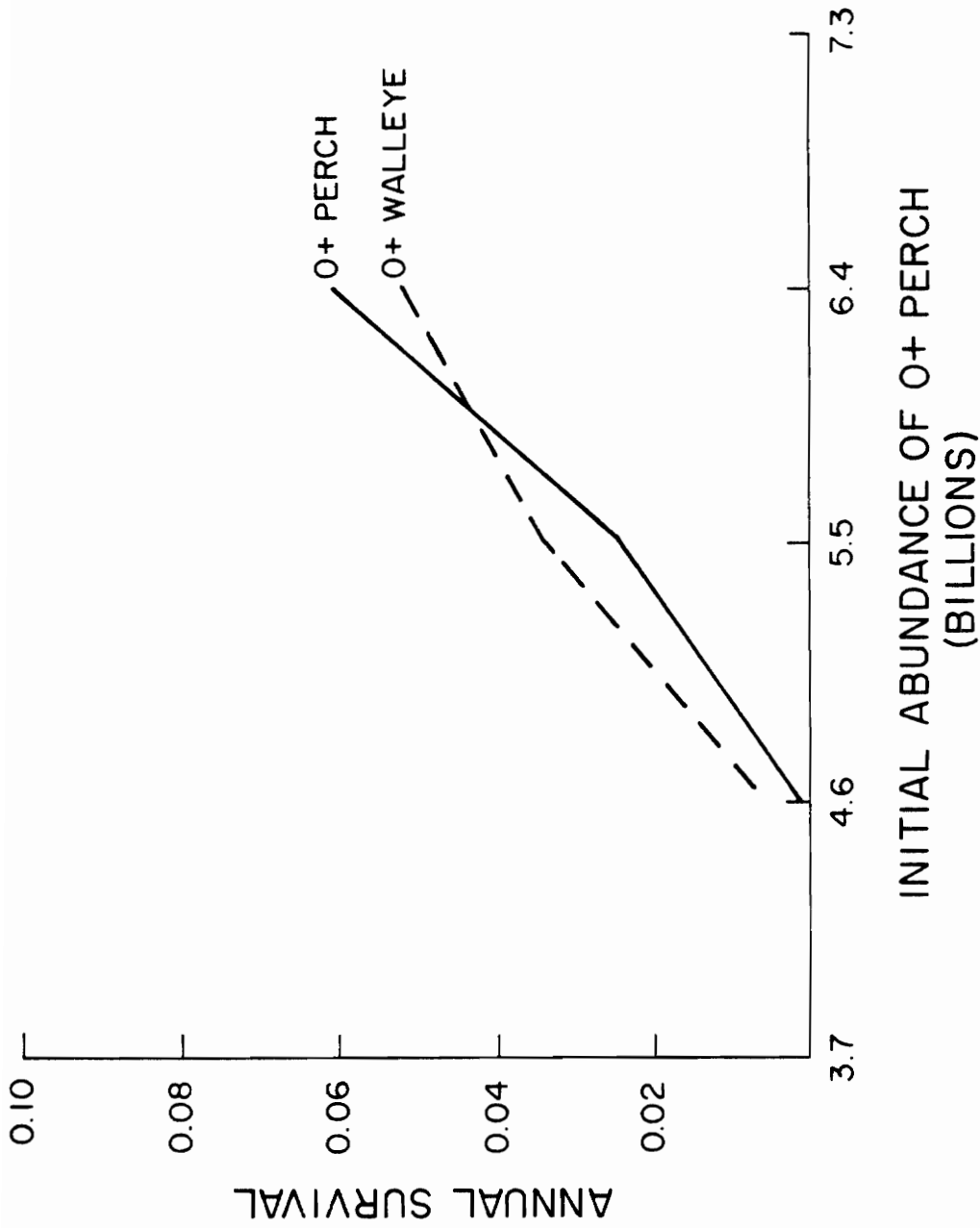


Fig. 8. Simulated annual survival rate of young perch and young walleye from May 20, 1972, to May 19, 1973, versus abundance of young perch on the former date.

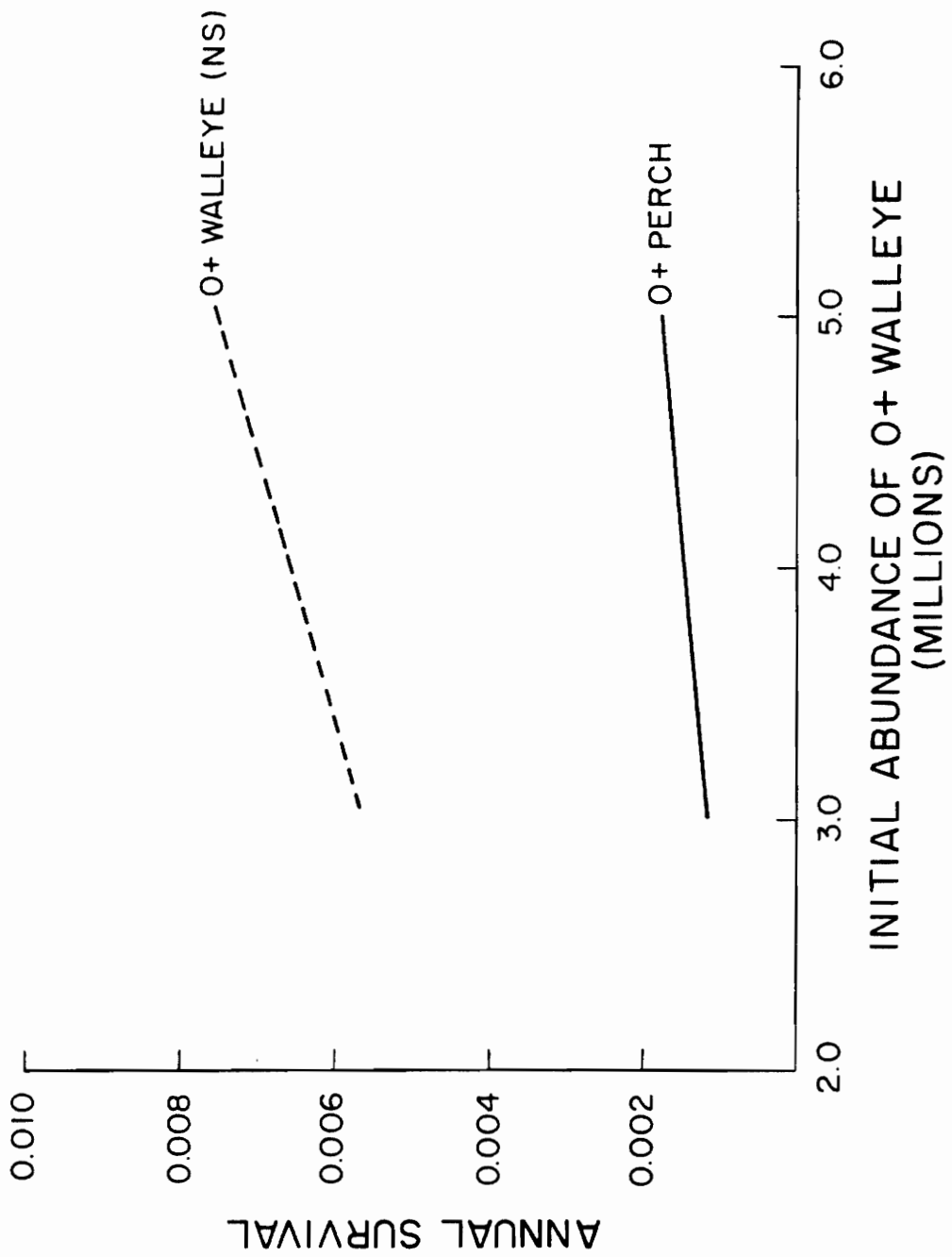


Fig. 9. Simulated annual survival rate of young perch and young walleye from May 20, 1972, to May 19, 1973, versus abundance of young walleye on the former date. NS denotes a statistically non-significant relationship ($P > .05$).

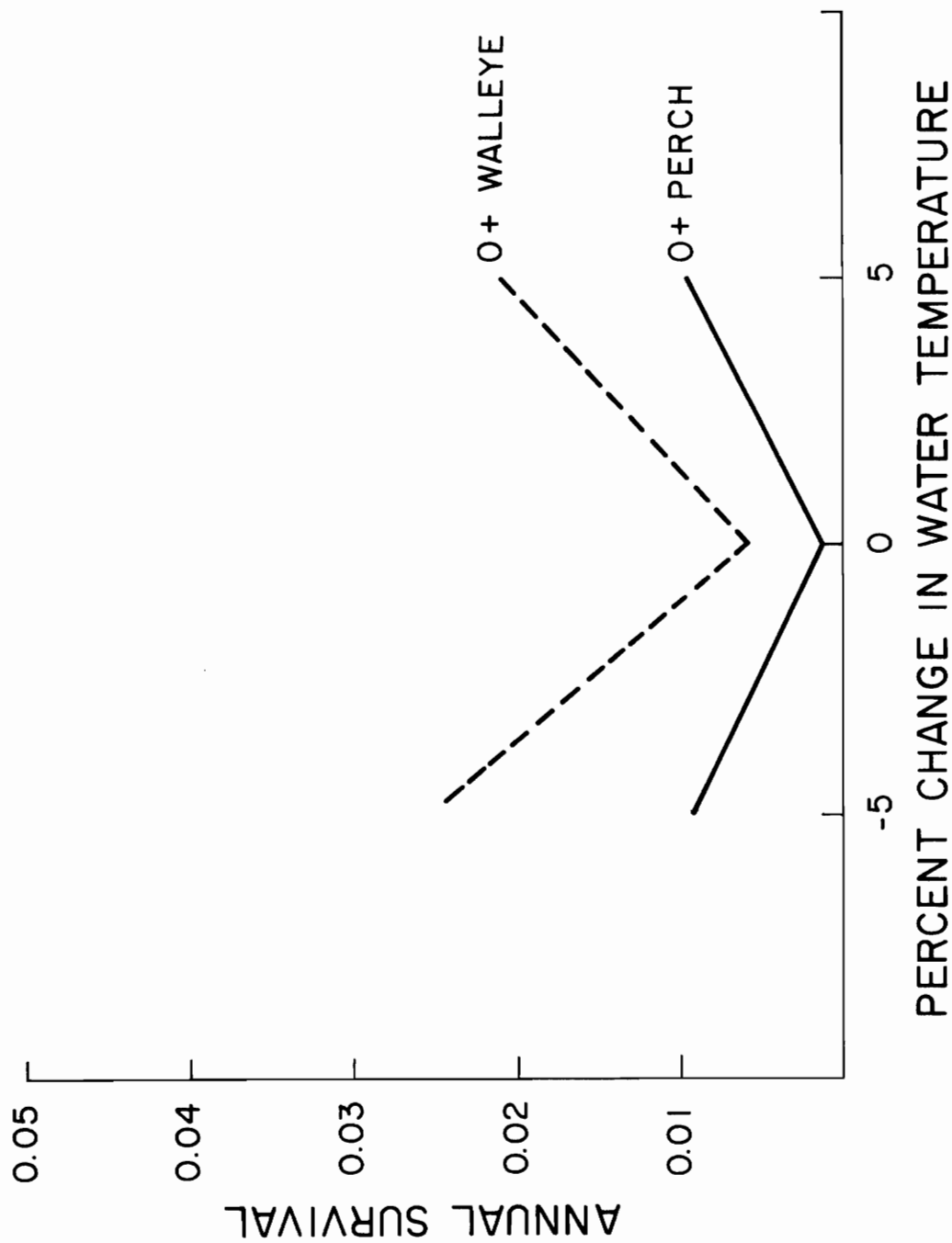


Fig. 10. Simulated annual survival rate of young perch and young walleye from May 20, 1972, to May 19, 1973, versus a percentage change in observed water temperatures.

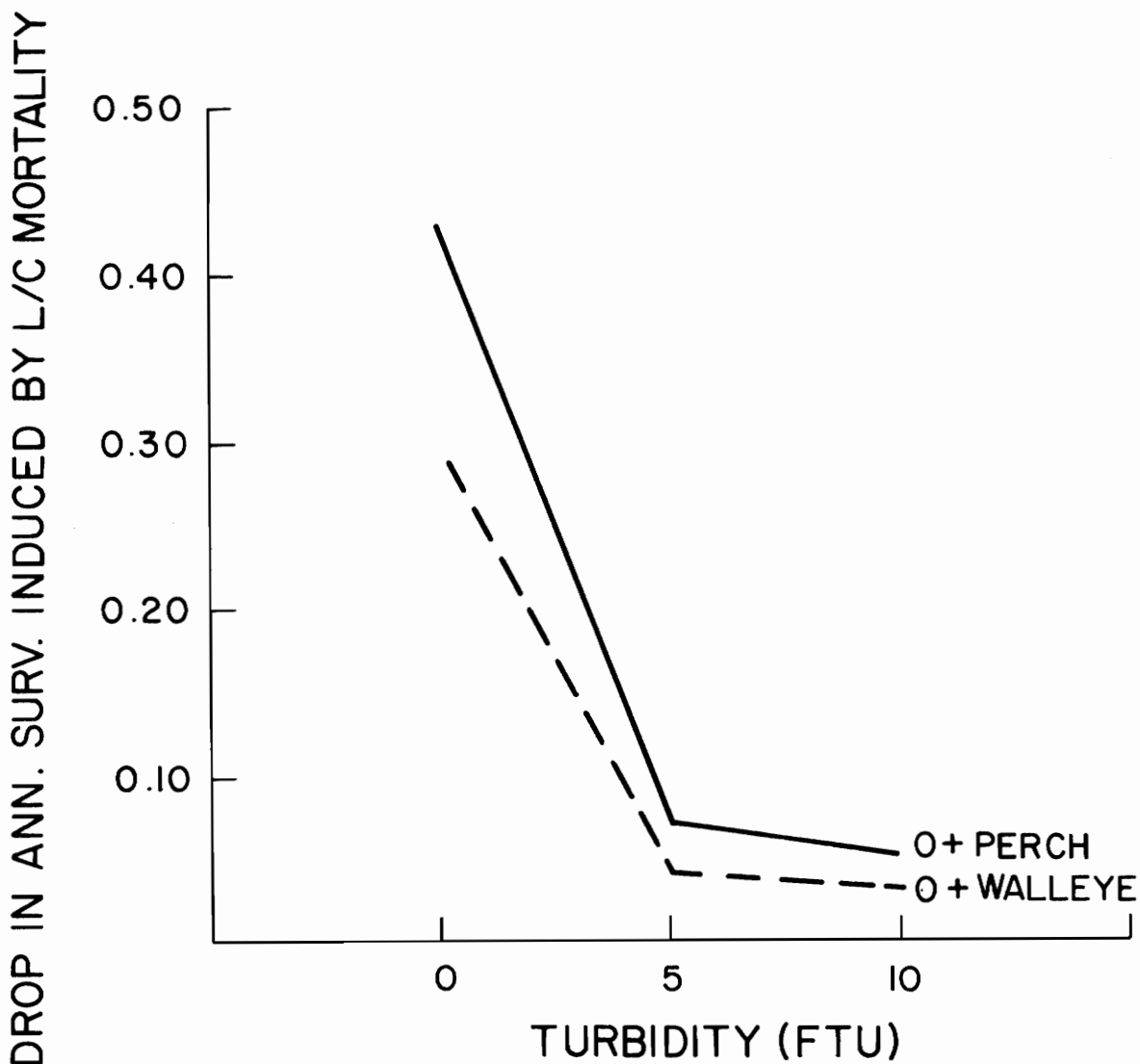


Fig. 11. Simulated changes in the reduction in annual survival rate for young perch and young walleye made by length-conditional mortality when turbidity was increased. Length-conditional mortality was an annual rate of mortality of 10 percent for fish 10 mm long.

turbidity was 10 FTU, survival rate of yellow perch fry increased only 57 percent from .1417 to .222. A study of the interaction between initial abundance of 0+ yellow perch and length-conditional mortality was also informative. At low initial abundance, survival rate of 0+ perch dropped 43 percent under extreme length-conditional mortality, but it dropped only 3 percent when initial abundance was highest (Fig. 12). Since the expected drop in survival due to the addition of length-conditional mortality was 3 percent, high initial abundance caused density-independent reductions in numbers.

Results from the analysis of variance for 0+ walleye were very similar to those for yellow perch (Table 8). All main effects were statistically significant ($P < .01$) except for initial abundance of 0+ walleye. This exception showed that mortality in this group was basically unrelated to their abundance and therefore density-independent. Turbidity was the most influential factor and increased the survival rate of walleye fry from .006 at 1 FTU to .175 at 10 FTU (Fig. 7). Initial abundance of young yellow perch acted as a buffer against mortality in young walleye; survival rate of walleye fry increased 930 percent over the range of initial abundance of yellow perch fry (Fig. 8). Effects of water temperatures on survival of walleye fry was

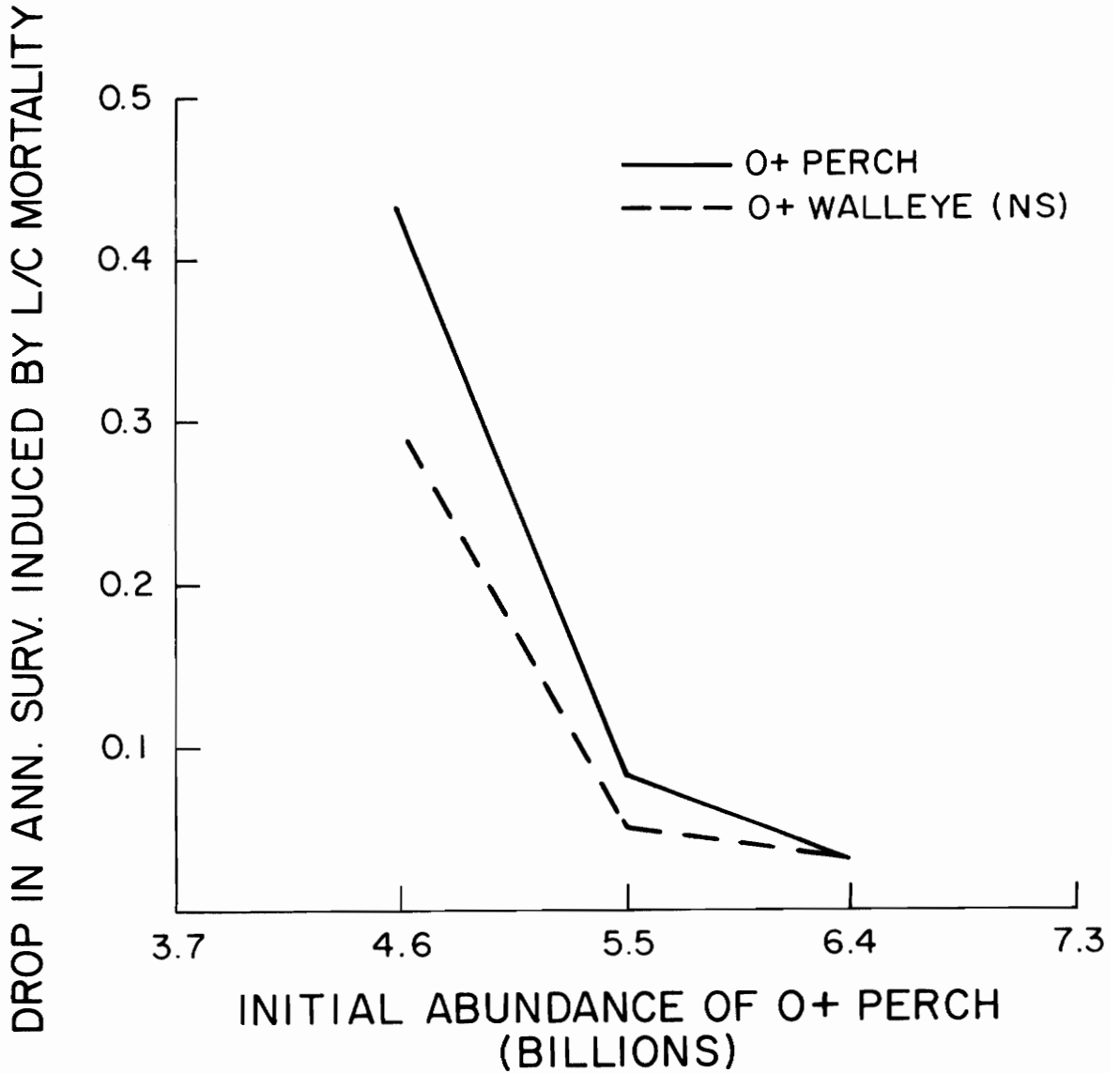


Fig. 12. Simulated changes in the reduction in annual survival rate for young perch and young walleye made by length-conditional mortality when initial abundance of young perch was increased. Length-conditional mortality was an annual rate of mortality of 10 percent for fish 10 mm long. NS denotes a statistically non-significant relationship ($P > .05$).

Table 8. Analysis of variance used to investigate effects of abundance of yellow perch fry (0+ PERCH), abundance of walleye fry (0+ WALLEYE), turbidity (TURB), water temperature (TEMP), and length-conditional mortality (L/C) on survival of walleye fry. Only significant (probability of larger F less than .05) main effects and interactions are listed.

Factors	Degress of freedom	Sums of squares
TURB	2	1.13431
0+ PERCH	2	.04336
TEMP	2	.01782
L/C	2	.00332
(0+ PERCH)*(TURB)	4	.01608
(0+ PERCH)*(TURB)*(TEMP)	8	.00907
(0+ PERCH)*(TEMP)	4	.00615
(TURB)*(L/C)	4	.00340
ERROR	112	.03865
CORRECTED TOTAL	243	1.31741

much the same as was seen for yellow perch fry. Survival rates increased as temperatures deviated from those observed in 1972 (Fig. 10).

For young walleye, several two- and three-factor interactions were statistically significant ($P < .01$). The mitigating effect of turbidity on the impact of length-conditional mortality was present for walleye fry as it was for perch fry. The 30 percent drop in the survival rate resulting from an increase in length-conditional mortality was reduced to about 3 percent when turbidity was increased from 1 to 10 FTU (Fig. 12). Effects of the interaction of abundance of perch fry and turbidity on survival of young walleye was also informative; as turbidity increased, the relationship between abundance of 0+ yellow perch and survival of young walleye began to disintegrate. At low turbidities, increased abundance of perch fry increased the survival rate 9.3 times, but at high turbidities, increased abundance enhanced the survival rate only by 30 percent from .175 to .227.

Mechanisms

Under all simulated conditions, the number of feeding periods in which satiation was achieved changed little for

all fish. All yellow perch except those seven years and older and all walleye except those five years and older attained satiation at the end of 100 percent of their feeding periods. Seven years and older yellow perch were unsated one feeding period and five years and older walleyes for only 18 of theirs. Most unsated conditions in walleyes occurred during mid May to mid June when young yellow perch and young walleye were limnetic. Changing length-conditional mortality, turbidity, or water temperature had no impact on the frequency with which predators were able to fill their stomachs.

Increasing length-conditional mortality did not alter composition of the diets of predators. Ingestion of 0+ yellow perch by walleyes seven years and older was simulated over the period of May 19 to July 21, 1972. Numbers of perch fry ingested by walleyes were the same regardless of the length-conditional mortality. By July 21, survival of 0+ yellow perch had been reduced 2 percent by length-conditional mortality. Growth in both instances was the same; young perch attained a length of 33 mm by July 21.

Increasing turbidity caused a reduction in losses of prey during the limnetic stage of fry. Typical of this situation was the ingestion of 0+ yellow perch by walleye seven years and older (Table 9). During their limnetic

Table 9. Simulated numbers of 0+ yellow perch eaten per individual walleye seven years or older per day under varying conditions during the period May 19 to July 21, 1972. "Control" denotes no induced variation in factors, "L/C" denotes only a change in length-conditional mortality, and "Turbidity" denotes only a change in turbidity. Turbidity was 10 FTU and length-conditional mortality was 10 percent annual mortality for fish 10 mm long.

Date	Number prey/predator		
	Control	L/C	Turbidity
May 19	865	865	262
26	326	326	265
June 2	265	265	265
9	155	155	155
16	127	127	122
23	25	25	22
30	23	23	23
July 7	21	21	21
14	20	20	24
21	19	19	25

stage, fewer 0+ yellow perch were eaten by walleyes when turbidity was at 10 FTU. After the limnetic stage, more fry were ingested than during the same period in the simulation with turbidity at 1 FTU. However, by this time survival of 0+ yellow perch was about four times greater in the more turbid situation. Simulated length of perch fry on July 21 was still 33 mm.

Water temperature indirectly influenced survival rates of young by affecting growth. By reducing water temperatures 5 percent, simulated growth of 0+ yellow perch was reduced 28 percent and of 0+ walleye 54 percent. By increasing temperature 5 percent, growth of 0+ yellow perch was increased by 25 percent and of 0+ walleye by 73 percent. Growth in all other life stages was affected, but all changes were within 10 percent.

DISCUSSION

Validation

Results of validation lended credibility to the model as a subject for experimentation in substitution for the fish community in Oneida Lake. Not only were simulated and observed values of dependent variables very similar, but so were their dynamics. Simulated fish grew and died as did their counterparts in Oneida Lake; their simulated dynamics were as sensitive to their abundance as were the dynamics of the fish they were intended to represent. Simulated predators ate in quantity and diet as did predators in Oneida Lake.

This fidelity to the fish community in Oneida Lake was more than sufficient to fulfill the goals of this research. The purpose behind the model experiments was to test hypotheses based on broad trends. Looking for the presence or absence of density-dependent dynamics under various regimes of certain abiotic and biotic factors was the goal, not exact prediction of numbers or growth of subjects.

Certain factors affected validation of the model by increasing deviations between observed and simulated data. Although deviations were not detrimental to attainment of

the goals and objectives of this research, a discussion of factors that caused them can show in some part why these deviations occurred.

Although one of the major factors that hindered validation was a lack of adequate data, this problem is no reflection on the excellent and intensive work conducted at Oneida Lake. Although large amounts of data were available, this information was not gathered for the purpose outlined here.

Missing information for some groups in the model made validation with available data more difficult, but not impossible. In a highly interactive community as in Oneida Lake, changes in a parameter will directly effect the dynamics of the life stage it describes and indirectly affect dynamics in other life stages. If no comparison could be made between observed and simulated values of dependent variables from life stages directly involved in parameter changes, comparisons were made for those life stages indirectly involved. By relying on this indirect comparison, validation was possible for those parameters describing life stages where observations from Oneida Lake were few. Effects of altering parameter values could be partially measured by looking at the indirect effects on dependent variables describing other life stages.

Deviations between observed and simulated abundance of yellow perch fry and walleye fry in mid May, 1973, were unimportant to validation. The 1973 year classes of both species were represented in the models only during the last few weeks of each simulation. Since model experiments were based on the 1972 year classes of walleye and and yellow perch, deviations between observed and simulated abundance of fry in the 1973 year classes had little impact on validation.

Deviations between observed and simulated growth by 0+ yellow perch were partly a consequence of the structure of the model. When fry "transferred" from limnetic to benthic habitats, parameter values describing these fish changed. Stomach size averaged 40 percent of body weight for limnetic fry, but was only 9 percent for benthic. Since amounts of food ingested daily in all simulations were determined by the size of stomachs, this reduction in stomach size severely limited simulated growth of benthic fry. However, as simulated fry did grow, they eventually surpassed observed growth by fry in Oneida Lake. A stomach size that was too small in June was too large in September. Some of this discrepancy was due to the linear nature of the parameter governing the relationship between body weight and maximum capacity of the stomach. In life stages occupied by

relatively faster-growing fish, stomach size would be better portrayed as a nonlinear function of body weight (Brett 1971). In life stages with relatively slower-growing individuals, the present procedure for calculating size of the stomach is adequate, as evidenced by the close fit seen in Fig. 5 for II+ walleye.

Differences in magnitudes of calculated and observed dynamics of yellow perch fry and walleye fry were probably due to the natures of the respective procedures used to calculate correlation coefficients. Those coefficients calculated from observations from Oneida Lake were collected over a number of years. Each year had different environmental and biotic conditions, all of which added variability to the relationships tested. Sampling error was included in estimates of abundance upon which these coefficients were based. In contrast, no environmental or biotic variability was present in the controlled simulation; only one factor was altered, abundance of yellow perch fry. Also, no sampling error was involved. Undoubtedly, some of this background variability should have been present. For example, Forney (1974) showed that yellow perch fry also served as a buffer against predation on white perch fry (Morone americana) and vice versa. By excluding white perch from simulations, relationships among taxa of fry as prey

were simplified. All of these factors caused coefficients based on simulations to be higher than those based on observations. However, the important fact in comparing these coefficients based on observed and simulated data is their agreement in sign.

Model Experiments

Effects of length-conditional mortality on survival of 0+ yellow perch and 0+ walleye were dramatic. Over the span of a year, the simulated fish community magnified losses from length-conditional mortality by an order of magnitude. However, the drop in survival of perch was not surprising; Forney (1971) showed that mortality of perch fry was density-dependent and depensatory. The cause was a stable predatory demand by walleyes that took a fairly constant number of prey which over time became an ever-increasing proportion of an ever-decreasing population.

Efficiency of predators and lack of competition among 0+ yellow perch were the reasons behind depensatory mortality. Except during mid May to mid June when fry of both species were limnetic, rations of predators were limited by size of their stomachs, not by their ability to capture prey. For most simulated days, all fish ended

feeding periods sated. Tarby (1975) observed only 20.6 percent of all yellow perch handled in the summer of 1972 with empty stomachs, and Forney (1974) found empty stomachs in 39.6 percent of all adult walleyes captured from 1968 to 1971. Although simulated frequencies of full stomachs were higher, "sampling" during simulations was conducted at the end of each feeding period, while sampling in Oneida Lake was either conducted during those periods when fish were not feeding and more stomachs would be empty or after fish had been confined in nets for an unknown period of time during which evacuation and fasting would have reduced stomach contents. As long as predators were efficient enough to fill their stomachs, a relatively constant weight of prey was ingested. Growth in predators and subsequently growth in size of their stomachs increased weight of prey ingested per predator, although natural and angling mortality of larger adults somewhat offset the resulting increase in total demand for 0+ yellow perch.

Lack of competition among 0+ yellow perch also affected this relationship. As long as competition was insignificant, any reduction in abundance of competitors did not effect their growth. In Oneida Lake, Tarby (1975) found little competition among yellow perch for food. Perch daily consumed only 4.2 percent of the standing crop of

their predominant prey, Daphnia sp. These cladocerans are known to have withstood daily losses of 25 percent to predators before their dynamics were significantly altered (Hall 1964). Without this competition, no decrease in abundance of perch fry caused an increase in their growth. Predators were able to remove more biomass of perch fry than fry could replace through growth. Until perch fry outgrew the size at which they were vulnerable to predation, predators removed ever-larger portions of an ever-dwindling population.

Magnification of simulated losses of 0+ walleye was not so much a direct result of length-conditional mortality and predation as it was a result of simulated losses of 0+ yellow perch. In Oneida Lake, annual rate of survival of 0+ walleye was independent of their own abundance, but was directly tied to the abundance of 0+ yellow perch (Forney 1974, 1976). Young yellow perch acted as a buffer for young walleyes against cannibalism. Results from the analysis of variance based on simulated survival of walleye fry were consistent with these findings. Losses of walleye fry to length-conditional mortality did not cause their reduction in survival, but losses in 0+ yellow perch did. As perch dwindled in numbers, more and more young walleyes were cannibalized.

Again this condition was the result of efficient predation and a lack of competition among perch fry. As long as predators were able to maintain full stomachs, any reduction in frequency of one item in their diet caused a complementary increase in another. As 0+ yellow perch became fewer, more 0+ walleye were ingested by predators. Like young yellow perch, young walleyes did not significantly compete among themselves for forage. Simulated growth of walleye and perch was not dependent on abundance, but water temperature. In Oneida Lake, growth of young walleyes was significantly correlated with air temperatures (Forney 1966). Again without this competition, mortality became compensatory.

The influence of initial abundance of 0+ yellow perch and turbidity on the impact of length-conditional mortality were of great importance. As numbers of young perch increased, magnification of loss from length-conditional mortality lost much of its impact. When initial abundance was great, predation by walleyes and losses from impingement and entrainment were not large enough to cause much compensation. Numbers of prey eaten by predators were so small compared to the total abundance that this removal of prey little affected the annual rate of mortality. By sheer numbers, simulated 0+ yellow perch had shifted their

dynamics from density-dependent to density-independent mortality.

Effects of turbidity on dynamics of fry under the stress of length-conditional mortality had much the same result as did initial abundance of young perch, but for a different reason. Since predators were unable to maintain full stomachs when fry were limnetic, a reduction in predatory efficiency directly affected ingestion by predators and hence survival of their prey at this time. As survival and abundance of fry increased due to the effect of turbidity, predators became less able to remove large numbers of prey, thereby causing the dynamics of 0+ yellow perch to shift from density-dependent to density-independent mortality. And since 0+ walleye were totally dependent on young perch as a buffer against cannibalism, they too experienced an overall increase in their survival rate.

Turbidity need not be the only factor that can reduce efficiency and impact density-dependent dynamics. Any factor that changes the relationships between predator and prey should have similar consequences. If the advantage is to the predator, dynamics should become more density-dependent, and if the advantage is to prey, dynamics should become more density-independent. Other factors that could influence dynamics in this manner could be chronic pollution

or presence of submergant vegetation.

Ability of circumstances to influence predatory efficiency and eventually the dynamics of their prey was somewhat limited. If efficiency of predators in Oneida Lake were nil, length-conditional mortality would account for a certain percentage of deaths. If by reducing numbers of fry, length-conditional mortality could stimulate individual growth, the period of danger to death from predation or by impingement and entrainment would be shortened, and compensatory mortality would hold losses down. But without this stimulated growth, the result of adding length-conditional mortality would be density-independent or compensatory mortality.

CONCLUSIONS

In this analysis, two phenomena are of paramount importance to assessing the impacts of impingement and entrainment on fish populations. Firstly, kinds of mortality exhibited in a fish population can differ under differing circumstances. And secondly, interspecific relationships can determine indirect effects of impingement and entrainment.

Variations in the kinds of mortality rates exhibited by young yellow perch and young walleye in Oneida Lake followed a predictable pattern. Firstly, compensatory mortality was based on density-dependent growth. No density-dependent growth was observed in this analysis, and no compensatory mortality was seen. By growing faster in response to a reduction in numbers, individuals can stabilize their annual rate of mortality by shortening their time of exposure to such length-conditional mortality as impingement and entrainment and predation. Secondly, depensatory mortality was dependent on density-independent growth in prey and on predation that removed significant numbers of prey. Depensatory mortality was exhibited when efficiency of predators maintained ingestion of prey at relatively constant and high levels. When increased growth of

individual prey did not result, these losses of prey to predation represented an ever-growing portion of an ever-dwindling population. And thirdly, density-independent mortality was based on density-independent growth and on predation that removed insignificant numbers of prey. High abundance of prey made predators as a group inefficient, and high turbidities reduced efficiency of individual predators; both factors caused predation to become a relatively insignificant source of mortality for prey.

The interspecific relationship between the annual rate of survival of young walleye and the abundance of young perch was crucial to assessing any impact of impingement and entrainment on the population dynamics of young walleye. As numbers of young perch declined, young walleye were increasingly exposed to cannibalism and experienced a subsequently reduced annual rate of survival. Even if only young perch had been impinged and entrained, mortality of young walleye would have increased because of this relationship.

The importance of these two phenomena to past and future analyses of the impact of impingement and entrainment, or any similar source of mortality, is great. Any analysis based on a single species will risk ignoring interspecific relationships that could completely reverse

the findings of the analysis if included. Any analysis predicated on unchanging population dynamics in a changing environment will be erroneous a significant percentage of the time.

These two phenomena must be incorporated into any future analysis of the impact of impingement and entrainment, or any similar source of mortality, if that analysis is to have any chance of success.

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APPENDIX A

Validation is a procedure in which a general model is made specific (Nolan 1972). A model is selected based on the relationship it will describe. Observations of certain aspects of the relationship are made and are used to estimate values of parameters in the model. Values of parameters are altered, and the resulting predictions made by the model are compared with appropriate observations. When the "fit" between observations and predictions is sufficient for the purpose of the modeler, the model has been validated.

An example of validation can be given using a simple situation. The model used to describe the relationship between body length and body weight in fish is usually an allometric equation:

$$W = aL^b$$

where W is weight, L is length, and a and b are parameters. Before this general equation can be made specific to a given population of fish, values for a and b must be estimated. Usually these estimates are made by "fitting" this equation

to a series of coupled measurements of body length and body weight from fish in the selected population. Most often this equation is transformed, and a least-squares procedure is used to "fit" the model. However, numerical procedures could be used to "fit" this equation in its present, curvilinear form. To do so, initial estimates of a and b must be available to start the procedure. An estimate of weight would be calculated for each value of length using the equation, and comparisons between observed and calculated weights for each length would be made. Values of parameters would be altered in a procedural manner until deviations between calculated and observed weights would be minimized.

Validation in a model as complex as the one concerning Oneida Lake proceeds as in the numerical fitting of the simpler model. Values of parameters are altered until observed and simulated variables are comparable. The degree of similarity necessary to stop the procedure is determined by the modeler.

Molan, R. L. 1972. Verification/validation of computer simulation models. Pages 1254-1265 in Proc. of the 1972 Summer Simulation Conf. Simulation Councils, LaJolla, California.

APPENDIX B

A. Introduction

For purposes of modeling, the aquatic community is divided into components. Fishes are separated from other organisms, divided into species, and species separated into "life stages." Organisms other than fish are also categorized into such groups. Although there is latitude in how the assignments of organisms to the various life stages can be made, in the following text life stages for fish correspond to various age-groups or parts of age-groups; all other, nonpiscine organisms are treated as "quasi-organisms." These latter groups are lumped into single categories; for instance, all zooplankton into one life stage and all benthic organisms into another. Treating nonpiscine components of aquatic ecosystems in this manner is not new to modeling. Eppley (1972) considered phytoplankton as a single entity in describing the influence of water temperature on the reproductive rate of cells. DiToro, O'Connor, and Thomann (1971) modeled the dynamics of phytoplankton in the San Joaquin-Sacramento estuary as a single group as did Fee (1973a, 1973b) for Lake Michigan. McIntire (1973) used this approach to simulate the dynamics

of periphyton in laboratory streams. Grenney (1975) treated the planktonic community of Auke Bay, Alaska, in this manner in modeling algal blooms.

Life stages for all organisms and their descriptive variables are arranged into a single matrix (X). Each column of this matrix corresponds to a single life stage, and each row to a single type of descriptive variable. Life stages corresponding to fish occupy the left-most columns in the matrix while those for nonpiscine organisms occupy the right-most. As individuals mature, cohorts of fish are allowed to travel from life stage to life stage across the matrix from left to right within those life stages (columns) allocated to their species; nonpiscine cohorts remain fixed in a single life stage.

Each life stage is described by seven, dependent (state) variables. Together these state variables constitute a column in the life stage matrix (X) that describes the cohorts within that life stage. Definitions for each of the seven elements are given in Table I. The first six elements reflect the current state of dependent variables. The last variable, maximum median weight, is the greatest weight attained by the members of mean length in that life stage during, or prior to, that time. Since growth in length is never lost while growth in weight often

Table I. List of dependent and independent variables and their definitions used in the model. When appropriate, units are in parentheses.

Name of variable (identifier)	Definition of variable
DX(I,M)	Daily amounts of change for the Mth state variable for the Ith life-stage (M=1,2,3,4,5,6,7) (1)=numbers (2)=current median weight (stomach contents included) (gm) (3)=mean length (m) (4)=stomach contents (gm) (5)=lower limit of size-distribution based on total length (m) (6)=upper limit of probability density function of length (m) (7)=maximum median weight (stomach contents excluded) (gm)
X(I,M)	Daily value of Mth state variable for the Ith life-stage (M=1,2,3,4,5,6,7) (1)=numbers (2)=current median weight (stomach contents included) (gm) (3)=mean length (m) (4)=stomach contents (gm) (5)=lower limit of size-distribution based on total length (m) (6)=upper limit of probability density function of length (m) (7)=maximum median weight (stomach contents excluded) (gm)

Table I. List of dependent and independent variables and their definitions in the model. When appropriate, units are in parentheses. (continued).

Name of variable (identifier)	Definition of variable
Z(M)	Daily value of Mth exogenous variable (M=1,2,3,4) (1)=water temperature (C) (2)=turbidity (JTU) (3)=wind velocity (m/sec) (4---->23)=instantaneous mortality rate due to fishing (/30 day month)

is, retention of this value allows use of length-weight relationships and stops growth in length until losses in weight are erased by renewed growth.

Often the term "typical" individual or "typical" fish is used in the text. This phrase refers to an individual with mean length, current and maximum median weights, and stomach contents as expressed in the life stage vector. Weights are described as "median", not "mean." As each cohort passes through different life stages, it is described by a mean length based on the midpoint of the uniformly distributed length of its members. Since weight is not linearly related to length, the weight corresponding to mean length in the "typical" individual is not itself a mean, but a median.

All dependent variables are altered through time. Corresponding to each vector of dependent variables is a vector of rates (\underline{DX}). For each element in the state vector there is a corresponding element in the vector of rates (Table I). These rates are the amounts that the corresponding dependent variables will change in a 24-hour day. The value for each rate variable is multiplied by the number of days in a time-step (\underline{DT}), and the product is added to the present state of the dependent variable to attain the value of the dependent variable one time-step in the future:

$$\underline{X}_{t+dt} = \underline{X}_t + DT \cdot \underline{DX} \quad A.(1)$$

This procedure is conducted for all life stages for each increment in time. All calculations of the elements of \underline{DX} are made such that Eq. A.(1) is linear with one exception. Elements in the first row of \underline{X} , the numbers of individuals within a life stage, are assumed to change in an exponential manner; increments are made as a constant percentage, not a constant number:

$$X_{(t+dt)1} = X_{(t)1} \cdot \text{Exp} \{ \text{Ln} \left(\frac{X_{(t)1} + DX_{(t)1}}{X_{(t)1}} \right) \cdot DT \} \quad A.(2)$$

Rates are calculated as a function of the biology of the animals and their relationship to their environment. In the model these functions utilize independent (exogenous) and dependent (state) variables (Table I), parameters for calculations (Table II), and switches to designate certain patterns of behavior by organisms (Table III). Certain temporary variables are stored internally during calculations and can be printed out (Table IV).

In the following sections, parameters and dependent variables are subscripted. When the predatory relationship

Table II. List of parameters and their definitions used in the model. When appropriate, units are in parentheses.

Name of variable (identifier)	Definition of variable
PACTIVE (I)	Linear constant in the calculation of the active metabolic rate for members of Ith life stage (mg Oxygen/gm/hr, later changed to gm/gm/sec)
PARC (I)	Subtended arc necessary for recognition of prey by predator of Ith life stage (radians, changed to tangent)
PBURST (I)	Burst speed of members of Ith life stage (body lengths/sec)
PCRUIS (I)	Cruise speed of members of Ith life stage (body lengths/sec)
PDEPTH (I)	Ratio of maximum body depth to total length in members of Ith life stage
PDIET (I)	Value of cost/benefit ratio of respiration to food intake of a single kind of prey beyond which fish from Ith life stage ignore that prey
PDIGST (I)	Assimilative efficiency as a fraction of the food evacuated the stomachs in Ith life stage
PDIMEN (M)	Dimension of the inhabited waters (M=1,2) (1)=bottom surface area (m ²) (2)=volume (m ³)
PESCAP (I)	Ratio of prey to predator burst speed at which 50% of prey escape ingestion by predators from Ith life stage

Table II. List of parameters and their definitions used in the model. When appropriate, units are in parentheses. (continued).

Name of variable (identifier)	Definition of variable
PEVACT(I)	Maximal evacuation rate for stomach contents of fish in Ith life stage (/sec)
PFAST(I)	Number of days members of Ith life stage must starve for crude mortality rate to be 50%/day
PFECND(I,2)	Coefficients for allometric relationship between weight of females from Ith life stage and their fecundity in numbers (M=1,2) (I,1)=linear component (I,2)=exponent
PFRY(I,M)	Lengths and weights of newly hatched fry of females from Ith life stage (M=1,2) (I,1)=length (m) (I,2)=weight (gm)
PHATCH(I)	Threshold of cumulative degree-days for hatching eggs from females in Ith life stage to hatch (C)
PGRAM(I)	Caloric value of a gram wet tissue from a member of Ith life stage (cal/gm)
PJTU(I)	Turbidity at which reaction distance of predators of Ith life stage is reduced 50% (JTU)

Table II. List of parameters and their definitions used in the model. When appropriate, units are in parentheses. (continued).

Name of variable (Identifiers)	Definition of variable
PLOG (I,M)	Coefficients of logistic growth for algae invertebrates in Ith life stage (M=1,2) (I,1)="r" when mean, daily water temperature is optimal (I,2)="k"
PLOVE (I)	Julian date of highest frequency of spawning for fish in Ith life stage (days, later changed to sequential date)
PLWREG (I)	Maximum value of exponent in length-weight relationship for fish from Ith life stage
PMOUTH (I,M)	Coefficients in relation between length of a fish from Ith life stage and diameter of its open mouth (M=1,2) (cm) (I,1)=intercept (I,2)=linear constant
PNUTRN (I,M)	Nutritional composition of members of the Ith life stage (M=1,2,3) (I,1)=fraction protein (I,2)=fraction carbohydrate (I,3)=fraction fat
POVA (I)	Weight of flaccid eggs of females from Ith life stage (gm)

Table II. List of parameters and their definitions used in the model. When appropriate, units are in parentheses. (continued).

Name of variable (identifier)	Definition of variable
PPHOTO (M)	Photoperiod (hr, later changed to sec) (1) = number of hours of daylight (sunrise to sunset) on summer solstice (2) = number of hours of daylight (sunrise to sunset) on either autumnal or vernal equinox (3) = number of hours during dawn and dusk each day
PPREF (I, J)	Preference of members of Ith life stage for members of Jth life stage as prey (range: 0---->1)
PRDMIN (I)	Minimum distance between schooling predators in Ith life stage (body lengths)
PSDA (I, M)	Fractions of ration consumed in SDA by members of the Ith life stage (M=1, 2, 3) (I, 1) = diet of pure protein (I, 2) = diet of pure carbohydrate (I, 3) = diet of pure fat
PSEX (I)	Fraction of number of fish from Ith life stage that are female
PSM (I, M)	Coefficients for calculation of standard metabolic rate for fish in Ith life stage (M=1, 2, 3) (I, 1) = linear constant (mg Oxygen/gm/hr, later changed to gm/gm/sec) (I, 2) = allometric constant (I, 3) = Q10 constant

Table II. List of parameters and their definitions used in the model. When appropriate, units are in parentheses. (continued).

Name of variable (identifier)	Definition of variable
PSSIZE(I)	Longitudinal dimension of a fish school in numbers of Ith life stage
PSTOM(I)	Linear relationship between median wet weight of member of Ith life stage and its stomach capacity
PSTRES(I)	Difference between isometric and allometric growth (exponents in length-weight relationships) at which 50% of members from Ith life stage die per 30 day month
PTHRM(I,M)	Coefficients for normalized, skewed relationship between water temperature and gastric evacuation rates in fish and increase rates for non-piscine organisms in Ith life stage (M=1,2,3) (I,1)=temperature at which rate is maximal (C) (I,2)=upper temperature at which rate is "0" (C) (I,3)=lower temperature at which rate is "0" (C, later changed to rate)
PWIND(I,M)	Coefficients for effect of wind on instantaneous mortality rate of eggs from females in Ith life stage (M=1,2) (I,1)=velocity below which no mortality occurs (m/sec) (I,2)=linear factor by which mortality is increased by wind velocity

Table III. List of switches and their definitions used in the model. When appropriate, units are in parantheses.

Name of variable (identifier)	Definition of variable
SETHBT (I)	Kind of feeding by members of Ith life stage (SETHBT=1) particulate predators (motile) (SETHBT=0) filter predators (SETHBT=-1) particulate predators (nonmotile)
SHABIT (I,M)	Habitat of members of Ith life stage (M=1,2,3,4) (I,1)=night (I,2)=dawn (I,3)=day (I,4)=dusk (SHABIT=2) demersal habitat (SHABIT=1) pelagic habitat
SLOVE (I,M)	Julian dates limiting spawning activity by fish in Ith life stage (M=1,2) (days) (I,1)=start of spawning season (later changed to sequential date) (I,2)=end of spawning season (later changed to sequential date) (SLOVE<0) life stage immature; no activity
SPROWL (I,M)	Kind of activity patterns exhibited by members of Ith life stage (M=1,2,3,4) (I,1)=night (I,2)=dawn (I,3)=day (I,4)=dusk (SPROWL=1) active and feeding (SPROWL=0) inactive and not feeding (SPROWL=-1) active and not feeding

Table III. List of switches and their definitions used in the model. When appropriate, units are in parantheses. (continued).

Name of variable (identifier)	Definition of variable
SSCHOL (I)	Gregariness of members of Ith life stage (SSCHOL=1) solitary predators (SSCHOL=0) schooling predators
SSELF (I)	Cannibalism among fish in Ith life stage (SSELF=0) no peer predation (SSELF=1) peer predation
STRANS (I)	Transfer of members of Ith into (I+1)th life stages (STRANS>0) Julian date at which transfer occurs (later changed to sequential date) (days) (STRANS<0) TL when transfer occurs (m) (STRANS=0) terminal life stage; no transfer
SWICH1	Decision variable for the specifications in the simulation (SWICH1=0) default specifications (SWICH1=1) user-supplied specifications
SWICH2	Decision variable for dump of temporary variables (SWICH2=0) no dump (SWICH2=1) dump
SWICH3	Decision variable for kind of time-step desired in simulation (SWICH4=0) constant time-step (SWICH4=1) variable time-step
SWICH4 (m)	Julian dates for Mth change in time-steps (days) (M=1,2,3,4,5)

Table IV. List of temporary variables and their definitions used in the model. When appropriate, units are in parentheses.

Name of variable (identifier)	Definition of variable
TAM(I)	Active metabolic rate for members of Ith life stage (gm/gm/sec)
TBURST(I)	Burst speed of fish in Ith life stage (m/sec)
TCRM(I,J,m)	Crude mortality rate of members of Jth life stage from predation by members of Ith life stage acting as a sole source of death during Mth period (/sec)
TCRUIS(I)	Cruise speed of fish in Ith life stage (m/sec)
TDIET1	Calculated cost/benefit ratio of capturing prey
TDIET2	Calculated cost/benefit ratio of a total diet based on a single prey item
TEATS(I,J,*)	Number of prey from Jth life stage eaten by a predator from Ith life stage during a segment of a day
TEATSB(I,J)	Prey biomass in Jth life stage ingested by a single predator in Ith life stage (gm)
TESCAP(I,J)	Fraction of attacks by predators of Ith life stage on prey of Jth life stage succeeding
TEVACT(I)	Current, thermally altered evacuation rate of fish in Ith life stage

Table IV. List of temporary variables and their definitions used in the model. When appropriate, units are in parentheses. (continued).

Name of variable (identifier)	Definition of variable
TEXTRA (I)	Ratio of current to maximal stomach capacity (TEXTRA>0) stomach partially empty (TEXTRA≤0) stomach sated
THATCH (I,M)	Accumulated degree-days since spawning for eggs from females in Ith life stage over M days
TRD (I,J)	Reaction distance between prey in Jth life stage and predators in Ith life stage (m)
TRM (I)	Energetic costs while cruising for members for Ith life stage (gm/gm/sec)
TSCHOL (I,J)	Fraction of reduction in searched area for a schooling predator in Ith life stage in search of members of Jth life stage
TSDA (I)	Fraction of ration available for growth after SDA and conversion due to caloric equivalence in fish in Ith life stage
TSM (I)	Standard metabolic rate of members of Ith life stage (gm/gm/sec)
TSTOM (I)	Maximum stomach capacity of members of Ith life stage (gm)
TWGAIN (I)	Current weight gain due to digestion (assimilation not included) (gm)
TXEGGS (I)	Number of eggs from females in the Ith life stage over M days

between the members of two life stages are involved in calculations, each of the corresponding variables and parameters will be subscripted. The subscript "i" designates the members of that life stage as predators; the subscript "j" labels organisms of that life stage as prey. Also, all dependent (state) variables will be subscripted to denote their appropriate row in \underline{X} (Table I). Often values for several parameters will be stored in an array under a single name to simplify calculations. When so grouped, identifiers are subscripted to designate various parameters in the calculations (Table II).

In the model certain calculations are repeated for different lengths of time. When phenomena are modeled for each "period," calculations are made for each segment of the 24 hour day: night, dawn, the daylight hours, and dusk. When phenomena are modeled for each "day," calculations are made once for each 24 hour day. Reasons for such a procedure can be found in section C.

The remaining text embraces biological logic behind the construction of those routines within the model that portray biological phenomena. How survival and mortality are calculated is described in section B.; Sections C., D., E., F., and G. address behavior, ingestion, respiration, digestion, and growth of fish, respectively; and the

dynamics of nonpiscine organisms and the maturation and reproduction of fish are discussed in the last sections H., I., and J., respectively.

B. Survival

B.1 Predatory Mortality

The model can address several kinds of predatory styles commonly found among fishes. For each life stage, a switch (SETHBT) designates the feeding of its members as either filter or particulate. Filter feeders strain their food from the water column by swimming at constant speed with mouths agape; particulate feeders attack each item of food individually. For each life stage, another switch (SSCHOL) designates the schooling proclivities of its members. A third switch (SHABIT) designates the relationship between the members of each life stage and the bottom as either limnetic or demersal; habitat preference can change from one period of the day to another (see section C.). Predatory behaviors in the model result from combining different kinds of feeding, gregariness, and habitation. These combinations are:

- 1) limnetic filter feeding in schools
- 2) limnetic, solitary filter feeding
- 3) limnetic, particulate feeding in schools
- 4) demersal particulate feeding in schools
- 5) limnetic, solitary parcticulate feeding
- 6) demersal, solitary particulate feeding

By manipulating values of SETHBT, SSCHOL, and SHABIT, other combinations are possible; however, the model handles only these six.

B.1.1 Solitary Filter Feeders

The number of prey ingested by solitary filter feeders is a function of the size of their mouth, speed, and abundance of its prey. When agape, the mouth is assumed to be round with diameter a linear function of body length (Northcote 1954, Wong and Ward 1972):

$$(\text{mouth diameter}) = \underset{1}{P\text{MOUTH}} + \underset{2}{P\text{MOUTH}} \cdot \underset{3}{X} \quad \text{B.1.1(1)}$$

The volume of water strained by a filter feeder in an interval of time is the product of the surface area of the open mouth and the distance traveled. Speed in meters/second is a linear function of body size:

$$(\text{cruise speed}) = \frac{\text{PCRUIS} \cdot X}{3} \quad \text{B.1.1(2)}$$

and the volume of strained water in m^3/sec is:

$$(\text{volume strained}) = \left(\frac{\{\text{Eq. B.1.1(1)}\}}{2} \right)^2 \{\text{Eq. B.1.1(2)}\} \cdot \text{PI} \quad \text{B.1.1(3)}$$

The number of prey encountered and ingested by the predator in a second is the product of the volume of strained water and the density of prey per meter cubed. All prey for the filter feeders are assumed to be mostly non-motile relative to the predator and randomly distributed in the limnetic environment. All organisms with burst speed greater than the cruise speed of the filter feeder are assumed to escape predation.

B.1.2 Solitary, Particulate Feeders

The volume of water processed by particulate feeders is not dependent on the size of their mouth, but on the limits of their visual perception. By definition particulate feeders actively attack their food. The initiation of an attack is a consequence of the location of an item of food relative to the limits of the sensory perception of the predator; if the location is outside these limits, no attack

occurs; if the location is inside, at least the opportunity for attack exists. Dimensions of the water volume from which the particulate feeder gets its food are therefore dependent on the limits of its eyesight.

The radius of the visual field of a particulate feeder is a function of its visual acuity (Nakamura 1958, Beukema 1968, Dill 1972, 1974), turbidity of water (Vinyard and O'Brien 1976), contrast in illumination between prey and background (Legrand 1967, Hester 1968, Ware 1973, Eggers 1977), ambulation of prey (Dill 1972, 1974), and size of prey (Brooks and Dodson 1965, Brooks 1968, Ware 1973) (visual recognition is assumed as the only stimulus for illiciting predatory attack). Fish are assumed to see equally distant in all directions. If predators are limnetic, their visual fields encompass spheres each with a predator at the center; if demersal, visual fields are hemispheres. As the limnetic predator moves, it searches a volume of water shaped like a cylinder; as the demersal predator moves, it searches a half cylinder. respectively. The radius of each cylinder is a linear function of the size of the prey (Nakamura 1958, Beukema 1968, Kerr 1971b) and an asymptotic function of the turbidity (Vinyard and O'Brien 1976):

$$(\text{visual radius}) = \frac{K \cdot Z}{j^3 \cdot 2} / \{ \text{Tan}(\text{PARC}) \cdot (Z + \text{PJTU}) \} \quad 2$$

B.1.2(1)

Not all of the listed factors have been incorporated in the model; only the effects of turbidity, visual acuity, and size of prey have been included. Other factors were excluded because either quantifiable information was lacking in the literature or their effects could be included with those of turbidity, visual acuity, and/or size of prey.

Speed (and the distance traveled) during predatory search is calculated as a relative velocity, the speed at which predator and prey approach one another. Calculations were taken from Gerristen and Strickler (1977) and Koopman (1956). Rate of encounter is calculated as a function of the cruising speeds of prey and predators {Eq. B.1.1(2)} and the visual field (radius) of predators {Eq. B.1.2(1)}:

$$(\text{encounter rate}) = \text{PI} \cdot \{ \text{Eq. B.1.2(1)} \}^2 \cdot$$

$$\frac{3 \cdot \{ \text{Eq. B.1.1(2)} \}^2 + \{ \text{Eq. B.1.1(2)} \}^2}{3 \cdot \{ \text{Eq. B.1.1(2)} \}} \quad \text{B.1.2(2)}$$

When the predator is demersal, the rate of encounter with limnetic prey is halved, thereby addressing the nature of the volume of water searched by a demersal predator.

When both predator and prey are demersal, the predator sweeps a rectangular area in search of prey. Since the width of this area is twice the visual radius, calculations for the encounter rate are taken directly from Koopman (1956):

$$(\text{encounter rate}) = 4 \cdot \left(\sum_i \{ \text{Eq. B.1.1(2)} \} + \sum_j \{ \text{Eq. B.1.1(2)} \} \right) \cdot$$

$$\{ \text{Eq. B.1.2(1)} \} E(A) \quad \text{B.1.2(3)}$$

A is the product of the cruise speeds of predator and prey divided by the square of their sums. The solution to E(A), the elliptical integral of the second kind, is a series expansion; in the model this series is calculated to five terms.

B.1.3 Escape and Preference

In the model particulate feeders, unlike their filtering peers, are allowed to discriminate in selecting items of food. A null value in PPREF designates that predators from the Ith life stage will either totally ignore prey from the Jth life stage as they are encountered or will not encounter them at all (ie., limnetic predators and demersal prey). A value of unity designates that these

predators will attack all such prey as encountered. Between these values, PPREP designates a degree of selection based on some behavioral aversion against ingesting prey or some behavioral mechanism that increases success against predatory attacks. As an example, larval and fingerling walleye (Stizostedion vitreum vitreum) often respond to attack by using erratic patterns of escape especially effective against older members of their species (Cuff 1973, 1977).

In the model prey are allowed to successfully evade predatory attack. Chance of such success depends on the relationship between burst speeds of predator and prey. Probability of capture asymptotically increases as the difference increases:

$$(\text{burst speed}) = \text{PBURST} \cdot X_3 \quad \text{B.1.3(1)}$$

(capture probability) =

$$\frac{\text{PESCAP}_i}{\left[\frac{\text{Eq. B.1.3(1)}_j}{\text{Eq. B.1.3(1)}_i} + \text{PESCAP}_i \right]} \quad \text{B.1.3(2)}$$

PESCAP is the ratio of prey to predator burst speeds at which 50% of the attacks are successful.

The combination of preference and escape are used to

reduce the rate of encounter to the rate of ingestion. The latter rate is the product of the rate of encounter (for example, {Eq. B.1.2(3)}), PPREF, and Eq. B.1.3(2):

$$\begin{aligned}
 (\text{ingestion rate}) &= \{ \text{Eq. B.1.3(2)} \} \cdot \{ \text{Eq. B.1.2(3)} \} \\
 &\cdot \text{PPREF} \qquad \qquad \qquad \text{B.1.3(3)}
 \end{aligned}$$

B.1.4 Survival from Predation

The crude rate of mortality for prey from the jth life stage due to predation by fish in the ith is calculated from the rate of ingestion. Benthic predation is modeled per square meter and planktonic predation per cubic meter in initial calculations. The rate of ingestion so far calculated is the number of prey ingested by a predator over a square or in a cubic meter per second when the density of predators and density of prey are both one individual per square or cubic meter. These units are used because cruising speeds are specified in m/sec. The number of prey ingested per square or cubic meter per second is the product of the rate of ingestion, density of prey, and density of predators per unit of area or volume:

$$\begin{aligned}
 (\text{mortality})_{ij} &= X_i \cdot X_j \cdot \{ \text{Eq. B.1.3(3)} \} \\
 &\frac{\text{PDIMEN}_i \cdot \text{PDIMEN}_j}{i \quad j} \qquad \qquad \qquad \text{B.1.4(1)}
 \end{aligned}$$

Obviously this value varies with numbers of predators and prey. However, over a span of a second, these numbers are assumed to be constant. If Eq. B.1.4(1) provides the number of deaths due to predation, then the quotient of Eq. B.1.4(1) divided by the density of prey per unit of area or volume at the beginning of the period is the crude rate of mortality for the entire lake:

$$\text{(crude mortality rate)}_{ij} = \{\text{Eq. B.1.4(1)}\} \cdot \text{PDIMEN} / X_j$$

B.1.4(2)

The crude rate of survival is calculated from the crude rate of mortality. Since these two rates are complementary, the former rate is the difference of the latter from unity:

$$\text{(crude survival rate)}_{ij} = 1 - \{\text{Eq. B.1.4(2)}\}$$

B.1.4(3)

B.1.5 Schooling

Whatever causes some fishes to school, the subsequent proximity of individuals within a school causes competition for food (Brock and Riffenburgh 1960, O'Connell 1972). As the school moves forward, those prey ingested by the

vanguard will not be available for attack by those predators in the rear. Also, a member is laterally competitive with his immediately adjacent peers; when visual fields overlap, the presence of a single prey can illicit several attacks, only one of which will be successful.

In the model the calculation of the effects of lateral competition on the survival of prey closely follows the work of Eggers (1976). The school is conceptually divided into subunits of nine individuals each; the subunits overlap so that each individual is a member of nine different, but contiguous subunits. The relationship among these fish is analogous to the relationship among the corners and center of a cube. This icosahedral configuration is the most compact, spatial structure found in fish schools (Cullen, Shaw, and Baldwin 1965, Van Olst and Hunter 1970, Pitcher 1973). The degree of overlap among visual fields is a function of the distance between members and the visual radius. The degree of encroachment upon the visual field of the central member of each subunit by the fields of its lateral peers is calculated as a weighted average of surface areas. By projecting the cube onto a plane, the structure becomes two-dimensional (Fig. I). As the distance between lateral and central members of the flattened subunits shrink, their visual fields overlap to an ever greater

degree. Certain segments of their fields are now shared by three, five, seven, or nine individuals. If a particular segment of a visual field is shared equally by "n" individuals, the probability that a certain predator successfully attacks a prey that is assumed to be enters the segment is "1/n." As a consequence, the surface area of each segment is divided by the number of individuals sharing it and the subsequent quotients are summed. The factor by which the number of prey ingested by a single, solitary predator is reduced to that of a single, schooled predator, is this sum divided by the surface area of an unencroached, projected visual field. Since all fish in a school are the central members of a subunit, the product of this factor and the crude rate of mortality is the crude rate of mortality adjusted lateral competition in for schools.

There are some obvious assumptions. Schools must be large, thereby limiting the fraction of individuals on the periphery of the school, and spatial relationships must be, and remain, icosahedral. The visual field of the central member of each subunit must not overlap with that of the central member of any other subunit.

The distance between the central member of each subunit and its peers is, within limits, a function of the availability of food (Keenleyside 1955, Hunter 1966). In the

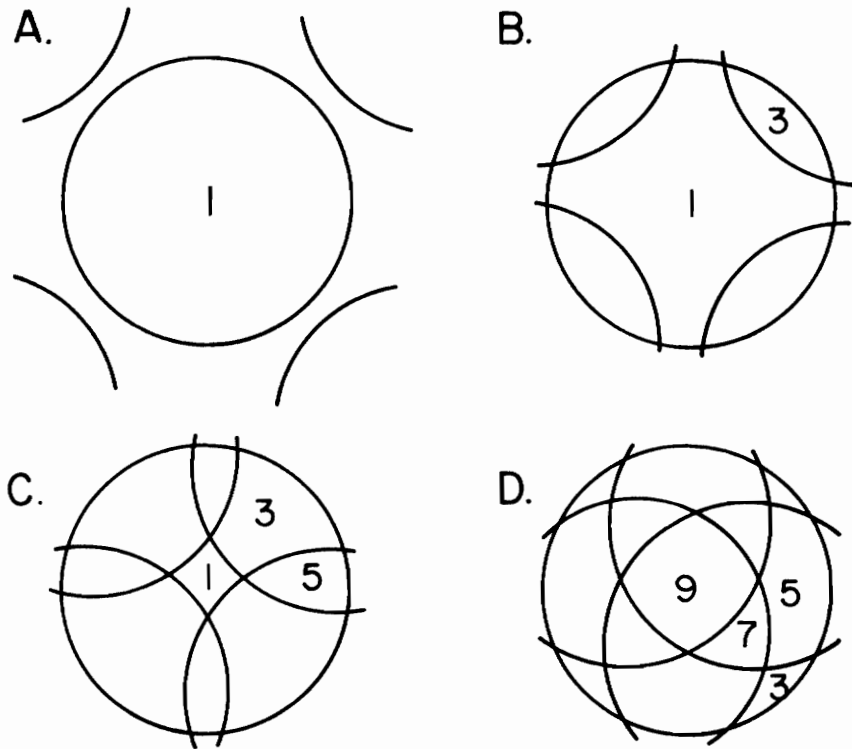


Fig. I. Examples of the degrees of encroachment among the visual fields of members in a fish school with an icosahedral (cubed) configuration. Visual fields have been reduced from three to two dimensions for clarity thereby doubling the number of encroaching onto each of the designated areas. The number of individuals encroaching on any particular area or on any similar area are the numbers in each diagram. (A. no encroachment; B. encroachment between central and corner members; C. encroachment among central and corner members and between corner members lateral and perpendicular to the line of travel for the school; D. encroachment among central and all corner members)

model this distance is calculated as a function of a temporary variable TRATIO, the current value of the cost/benefit ratio of energetics to ingestion. The value of TRATIO is the ratio of the energetic costs (gms of wet weight) of attacking prey to the energetic benefits (gms of wet weight) of the food thusly procured. The distance between central and lateral members is assumed to be a linear function of TRATIO. When the activity of swimming is impaired by the closeness of members in a school, the minimum distance between members is reached (Breder 1959, 1965):

$$(\text{minimum distance}) = \text{PRDMIN} \cdot X \quad \text{B.1.5(1)}$$

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Since the integrity of most schools is maintained by sight (Atz 1953, Shaw 1961, Blaxter and Holliday 1963, John 1964, Thines and Vandenbussche 1966, Hunter 1968, Whitney 1969), the maximum distance is the visual radius {Eq. B.1.2(1)} for fish of their own size, and when TRATIO is between (0,1), the linear relationship is used:

$$(\text{distance}) = (\{\text{Eq. B.1.2(1)}\} - \{\text{Eq. B.1.5(1)}\}) \cdot \text{TRATIO} + \{\text{Eq. B.1.5(1)}\} \quad \text{B.1.5(2)}$$

TRATIO is never greater than unity (see section B.1.7).

Longitudinal competition among members of a school (competition with all those forward of a particular member) is calculated as an average value. The crude rate of mortality, adjusted for lateral competition, is used to calculate a new crude rate of survival. The new crude rate is the rate of survival of prey under predation by a single predator among a group of predators. This singular rate is calculated as the antilog of the quotient of the instantaneous rate of mortality (the natural log of the crude rate of survival) divided by the number of predators in the group:

$$\text{(single crude survival rate)} = \exp(\text{Ln}\{\text{Eq. B.1.4(3)}\} / X_1)$$

B.1.5(3)

The singular crude rate of mortality is the complement of the single crude rate of survival:

$$\text{(single crude mortality rate)} = 1 - \{\text{Eq. B.1.5(3)}\}$$

B.1.5(4)

The probability of a prey being eaten by the forward-most predator of a school is Eq. B.1.5(4), by the next predator the product of Eq. B.1.5(3) and Eq. B.1.5(4), by the next

predator the product of Eq. B.1.5(4) and the square of Eq. B.1.5(3), etc. The probability of survival for a prey beyond the nth position in a longitudinal tier of predators is the complement of the product of Eq. B.1.5(4) and Eq. B.1.5(3) raised to the (n-1)th power:

$$(\text{survival probability}) = 1 - \{\text{Eq. B.1.5(4)}\}$$

$$\bullet \{\text{Eq. B.1.5(3)}\}^{n-1} \quad \text{B.1.5(5)}$$

The average, crude rate of survival is the quotient of the integral of {Eq. B.1.5(5)} from one to the number of fish in a horizontal row of the school (PSSIZE) divided by that number:

$$(\text{average crude survival rate}) =$$

$$(\text{PSSIZE}-1)^{-1} \int_1^{\text{PSSIZE}} \{\text{Eq. B.1.5(5)}\} dn \quad \text{B.1.5(6)}$$

$$1 - \frac{\{\text{Eq. B.1.5(4)}\} \bullet (\{\text{Eq. B.1.5(3)}\}^{\text{PSSIZE}} - \{\text{Eq. B.1.5(3)}\})}{\{\text{Eq. B.1.5(3)}\} \bullet (\text{PSSIZE}-1) \bullet \text{Ln}\{\text{Eq. B.1.5(3)}\}}$$

$$\text{B.1.5(7)}$$

Eq. B.1.5(7) is the average crude rate of survival for

individual, schooling predators. This rate is expanded to represent the entire population; the crude rate of survival, adjusted for both lateral and longitudinal competition, is the antilog of the product of the new instantaneous rate of mortality (the natural log of {Eq. B.1.5(7)}) and the number of predators in the population:

$$(\text{crude survival rate}) = \exp(\text{Ln}\{\text{Eq. B.1.5(7)}\} \cdot X)$$

B.1.5(8)

The crude rate of mortality, adjusted for competition in schooling fish, is the complement of Eq. B.1.5(8):

$$(\text{crude mortality rate}) = 1 - \{\text{Eq. B.1.5(8)}\}$$

B.1.5(9)

Again certain assumptions are included in the calculations. Size of schools must remain constant and uniform throughout the life stage. Also, predatory efficiency must be similar for all members within a school.

B.1.6 Prey Selection

In the model each life stage of predators is assigned a set of life stages upon whose occupants they will prey. The

calculations for the rates of encounter, ingestion, and metabolism are conducted for this set in ascending order of the lengths of the prey in each life stage. If PPREF, density of prey, or density of predators is zero, the associated calculations for that life stage are omitted. Calculations will continue until the prey are too large for ingestion by the predator; the execution then proceeds to another life stage of predators and the process is repeated.

Members of each prey life stage are tested against the size of the mouth of the predator to determine their ingestibility. Since fish generally ingest prey head first (Deedler 1951, Hoogland, Morris, and Tinbergen 1956, Nursall 1973), the depth of body of the prey compared to the diameter of the open mouth of the predator is the criterion by which this test is made. Maximum size of prey ingested by a predator is the quotient of the diameter of its mouth {Eq. B.1.1(1)} divided by the ratio of the maximum depth to length of prey (PDEPTH):

$$(\text{maximum length}) = \frac{\{\text{Eq. B.1.1(1)}\}_i}{PDEPTH_j} \quad \text{B.1.6(1)}$$

By comparing Eq. B.1.6(1) against the limits of length distributions for each life stage of prey, calculations for that cohort are either conducted, omitted, or modified. If

Eq. B.1.6(1) is greater than the upper limit on the distribution, the calculations for the various rates are made. If Eq. B.1.6(1) is less than the lower limit, all calculations of the rates for predation by the predators on that life stage are forgone, and the execution of the model proceeds to another life stage of prey.

If Eq. B.1.6(1) is between these two limits, the prey life stage is split for the calculation of rates. The lower limit of the distribution remains the same, but the new upper limit is Eq. B.1.6(1); the new mean length is the average of these new limits and the new median weight is calculated with a length-weight regression. After all subsequent calculations are made with these new values, the crude rate of mortality is adjusted to encompass the entire life stage of prey. In the model predators are allowed to prey upon their peers. When this occurs, the life stage is split at the value of Eq. B.1.6(1); new limits and means are calculated in the above manner for both the prey and predators. Again the crude rate of mortality is adjusted.

Some bias will occur when peers prey upon one another. As the smaller members of a life stage are eaten by the larger, estimates of the crude rate of mortality between this life stage as predators and other life stages are no longer constant (see section B.1.4). This bias should

remain inconsequential as long as time-steps in the model remain short.

Calculations of rates of ingestion, metabolism, etc. are based on these new sets of values. When the life stage of prey is split, the rate of ingestion {Eq. B.1.3(3)} is reduced by the fraction of the life stage immune to predation. The crude rate of mortality is calculated as the product of the rate of ingestion and the number of predators. This product is changed through Eq. B.1.4(1 thru 3, inclusively) to the proper units. When members of the life stage prey upon their peers, the same procedure is followed except that the number of predators is reduced as well.

B.1.7 Optimal Diet Breadth

One of the many theories of prey selection is that predators will select only those prey that constitute an economical diet (MacArthur and Pianka 1966, Emlen 1966, Schoener 1971, Werner and Hall 1974). The predator will select only those items that will provide it the maximum amount of energy as food for the energy invested in its capture. The predator will encounter, attack, and ingest a

certain number of prey from a particular life stage. Attacking consumes amounts of metabolic energy; ingesting provides the raw materials to replace this energy and provides a surplus for growth. These metabolic costs and gains are respectively the numerator and the denominator of a cost/benefit ratio. The cost/benefit ratio is calculated for each life stage of prey with respects to a given life stage of predators. The numerator and the denocminator of this ratio are based on the respiration and ingestion of the individual, not the life stage. The numerator is the metabolic cost of catching one prey. Each attack is supposably conducted at burst speed and launched from a distance from the prey equivalent to the visual radius of the attacker. Given this known distance and speed, the predator must invest a certain amount of time, calculated as the ratio of visual radius {Eq. B.1.2(1)} to burst speed {Eq. B.1.3(1)}:

$$(\text{time/attack}) = \{\text{Eq. B.1.2(1)}\} / \{\text{Eq. B.1.3(1)}\}$$

B.1.7(1)

If a predator is totally successful in catching prey, Eq. B.1.7(1) is also the time spent to capture a single prey; if a predator is not so effective, Eq. B.1.7(1) is divided by the rate of success as affected by evasion by prey {Eq.

B.1.3(2)} and lateral competition within schools:

$$(\text{time/successful attack}) = \{\text{Eq. B.1.7(1)}\} / \{\text{Eq. B.1.3(2)}\}$$

B.1.7(2)

Since respiration is assumed to be maximal at burst speeds, the numerator of the cost/benefit ratio is calculated as the product of the cost of burst speed per second {Eq. E.2(1)} and the time necessary to secure a prey:

$$(\text{numerator}) = \text{Eq. B.1.7(2)} \cdot \{\text{Eq. E.2(1)}\}$$

B.1.7(3)

The denominator of the ratio is the product of the weight of a prey, the caloric equivalence between prey and predator {Eq. F.3(1)}, the weight retained after Specific Dynamic Action {Eq. F.1(4)}, and the fraction assimilated (PDIGST):

$$(\text{denominator}) = \text{PDIGST} \cdot X \cdot \{\text{Eq. F.3(1)}\} \cdot \{\text{Eq. F.1(4)}\}$$

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B.1.7(4)

Longitudinal competition within schools is not included in calculating costs of attack. This kind of competition does not result in thwarted attacks by out-competed predators.

In the calculation of optimal breadth of diet, the

cost/benefit ratio is the determining factor. For a particular combination of life stages, one as predator and the other as prey, the cost of capture for predators could be greater than the benefits gained through ingestion. If so, the cost/benefit ratio is equal to or greater than unity. The predator is assumed to ignore the prey from that life stage, and the crude rate of mortality {Eq. B.1.5(7)} is set to zero.

A problem exists with the calculation of optimal breadth of diet for the schooling predator. When the distance between lateral members in a school is calculated, TRATIO is used (section B.1.5); at that time, only the current running average is available. For a life stage of predators, the value of TRATIO for each cohort of prey is a running average over all prey by ascending order of the lengths of prey. Value of TRATIO for the life stage with the smallest prey is the initial entry into the current average, the value for the life stage with the next smallest prey is added into the current average, and so on. The greater the number of life stages included in the calculation of the current running average, the closer the approximation to the true value of distance in the model. The problem is extreme in the calculations for the life stage of potential prey with the smallest members. When a value for TRATIO is

needed, none exists. Because the dependence of optimal breadth of diet and distance among fish in schools is mutually obligative, this aspect of the problem requires an initial value for TRATIO not based on the rate of ingestion of the predator that day. For the first day, TRATIO is assigned a random number between (0,1). This number is used to calculate the distance among the schooled predators; it is not used in the running average of TRATIO and the calculation of optimal breadth of diet. Beyond the first day, values of TRATIO from the previous day are used.

Nutritionally inadequate prey are also ignored by predators in the model. If a total diet of a particular kind of prey does not provide enough nutrition to support maintenance of the predator during its daily activities, this kind of prey is ignored. The potential amount of food evacuating the stomach to the gut in a day is calculated {Eq. D.1(2)}; this value is reduced by those factors mentioned earlier {Eq. B.1.7(4)} to provide a denominator:

$$(\text{denominator}) = \{\text{Eq. D.1(2)}\} \cdot \{\text{Eq. P.3(1)}\} \cdot \{\text{Eq. F.1(4)}\}$$

•PDIGST

B.1.7(5)

The numerator is the cost of capturing all prey passing into the gut {Eq. B.1.7(3)} during a feeding period plus the cost

of respiratory maintenance through the balance of the day. This latter cost is calculated by varying the pattern of diel activity (see section C.). Times spent cruising and resting are calculated (T_{TIME}), and are multiplied by their respective energetic costs per second [Eq. E.3(6) and Eq. E.1(1)]. All such costs are summed to form the numerator:

$$(\text{numerator}) = T_{\text{TIME}2} \cdot \{\text{Eq. E.3(6)}\} + T_{\text{TIME}1} \cdot \{\text{Eq. E.1(1)}\}$$

B.1.7(6)

The value of the ratio of the numerator to the denominator is compared to PDIET. If the ratio is greater, that kind of prey is removed from the diet of the predator; if the ratio is not, those prey are retained in the diet.

B.1.8 Maximal Predatory Rate

Each predator has a maximal rate of ingestion above which it can not physically catch and eat more prey. If each capture requires a given amount of time, the maximal rate of capture per period is determined by the length of the period.

For each life stage of predators in the model, the maximal rate of ingestion is compared to that determined through the calculated, crude rate of mortality. The number of captures per predator per second from a particular life stage of prey is calculated as the product of the number of prey, the reciprocal of the number of predators, and the crude rate of mortality {Eq. B.1.5(9)}:

$$(\# \text{ captured/second}) = X_{j1} \cdot \{ \text{Eq. B.1.5(9)} \} / X_{ij \ i1} \quad \text{B.1.8(1)}$$

The maximal rate of capture per second is the reciprocal of the number of seconds needed to capture a single prey {Eq. B.1.7(2)}:

$$(\text{maximal rate/second}) = 1 / \{ \text{Eq. B.1.7(2)} \} \quad \text{B.1.8(2)}$$

If Eq. B.1.8(2) is larger than Eq. B.1.8(1), no further calculations are made. However, if the maximal rate is smaller, a new crude rate of mortality is calculated as the product of the maximal rate, the number of predators, and the reciprocal of the number of prey:

$$(\text{crude mortality rate}) = X_{i1} \cdot \{ \text{Eq. B.1.8(2)} \} / X_{ij \ j1} \quad \text{B.1.8(3)}$$

B.2 Non-predatory Mortality

B.2.1 Starvation

One of the major, potential causes of death in newly hatched fry is starvation (Cushing 1973). If appropriate foods are not available during the "critical period" (Braun 1971) immediately after hatching, fry will starve within a few days. Marr (1956) reviewed several studies on the role of starvation in the dynamics of several pelagic, marine species and concluded that the role was small. Kramer (1969) believed that food was too abundant in most freshwaters for starvation to severely affect year-class strengths. If starvation is not often a major cause of mortality, its potential to be such is still present. Toetz (1966) found through lab studies that a "critical period" exists in the development of bluegill sunfish (Leponis macrochirus). Braun (1967) discovered that if the eggs of the whitefish Coregonus wartmanni hatched too early, before the vernal growth of zooplankton, heavy mortalities due to starvation could occur just after yolk absorption.

In the model severity of starvation is a function of the number of days that fish have failed to retain food in the stomach with no growth. When starvation is treated as

the sole source of death, the fraction of the life stage dying due to this cause (crude rate of mortality) is assumed to asymptotically approach unity as starvation continues. The resultant crude rate of survival is calculated as the ratio of the number of days of starvation needed to kill 50% of the life stage per day (PFAST) to the sum of this value and the number of days the fish have starved (TFAST):

$$\text{(crude survival rate)} = \frac{\text{PFAST}}{\text{PFAST} + \text{TFAST}} \quad \text{B.2.1(1)}$$

This crude rate is changed into a relative rate by finding its natural log and dividing it by the number of seconds in a day:

$$\text{(relative mortality rate)} = \text{Ln}\{\text{Eq. B.2.1(1)}\} / 86400. \quad \text{B.2.1(2)}$$

If at any time fish grow during a day, TFAST is set to zero. Otherwise, TFAST is incremented for each consecutive day of starvation.

B.2.2 Debilitation

Often poor health in fish acts as a trigger allowing other agents to cause death. Chronic infections can become lethal when health wanes from starvation or poor nutrition. Large numbers of adults can perish after spawning due to the large amounts of energy expended in reproduction. Thermal and/or chemical stress is more pernicious to fish in poor health.

In the model the effect of poor health on mortality is a function of the degree of condition. The relationship between weight and length is assumed to offer a good index of health (Ricker 1975). As weight is lost, this relationship becomes something less than optimal. As this discrepancy increases, so does the chance of death due to poor health. Loss in health (condition) is calculated with the standard length-weight relationship (Beverton and Holt 1957, Ricker 1975). The linear parameter in the relationship is calculated as the ratio of the maximum median weight and the mean length raised to a power indicative of good condition (PLWREG):

(linear parameter) = X

$$\frac{-7}{(X \cdot 1000)^3} \text{PLWREG}$$

B.2.2(1)

The exponent in the current length-weight relationship is calculated as the ratio of the log of current median weight divided by the linear parameter {Eq. B.2.2(1)} to the log of the mean length:

$$\text{(current exponent)} = \frac{\text{Ln}(X / \{\text{Eq. B.2.2(1)}\})}{\text{Ln}(X)} \quad \text{B.2.2(2)}$$

$$\text{(difference)} = \text{PLWREG} - \{\text{Eq. B.2.2(2)}\} \quad \text{B.2.2(3)}$$

As the above difference increases, chance of survival decreases asymptotically. The crude rate of survival from debilitation acting "alone" is calculated as the ratio of the difference at which 50% of the life stage will die during a 30 day month (PSTRES) to the sum of this value and the current difference in exponents {Eq. B.2.2(3)}:

$$\text{(crude survival rate)} = \frac{\text{PLWREG} - \text{PSTRES}}{\text{PLWREG} - \text{PSTRES} + \{\text{Eq. B.2.2(3)}\}} \quad \text{B.2.2(4)}$$

The crude rate of survival is changed into the relative rate of mortality per second by finding its natural log and dividing it by the number of seconds in a month:

(relative mortality rate) = $\ln\{\text{Eq. B.2.2(4)}\} / 2592000.$

B.2.2(5)

After the relative rate of mortality due to debilitation has been calculated, it is added to the relative rate from the previous section.

B.2.3 Angling Mortality

Death due to angling is allowed in the model. During each time-step, values for the relative rates of mortality due to angling for each life stage of fish are input as exogenous variables. These rates are divided by the number of seconds in a time-step to adjust for scale and the quotient is added to the relative rates from the two previous sections. For each life stage, this final sum is used as the total, relative rate of mortality per second due to causes other than predation.

C. Diel Activity

Because fish vary their activities throughout the day (Hasler and Villemonte 1953, Emery 1973, Ryder 1977, Werner et al. 1977), each 24 hour day is divided into several

periods. Night is the first period addressed by the model, dawn is the next, day follows, and dusk is the last period. Lengths of all periods are measured in seconds.

Lengths of these periods are either inputs to the model or calculated with a trigonometric equation. Lengths of dawn and dusk are equivalent and are inputs. Length of day is the result of a sine wave based on the sequential (Julian) date (JD):

$$(\text{day length}) = \underset{1}{\text{PPHOTO}} + \underset{2}{\text{PPHOTO}} \cdot \text{Sine}\{2\text{PI} \cdot (\text{JD} - 80) / 365\}$$

C. (1)

Length of night is calculated as the number of seconds in 24 hours minus those calculated for day and those input for dawn and dusk.

Behavior of members of each life stage can be changed from period to period. Arrays SPROWL and TPROWL contain information that designates behavior for fish in a given life stage during a given period. Possible behaviors are feeding while mobile, not feeding but mobile, and not feeding while sedentary. If fish within a life stage are supposedly feeding during a period, but no prey are available, TPROWL is changed such that these fish will not

feed and will remain sedentary.

In the model the activity of fish determines their relative immunity or exposure to predation. For protection against predatory mortality while feeding, many fish adopt behavioral mechanisms, such as schooling (see Williams 1964, Hamilton 1971, Emery 1973, Vine 1971, 1973, Seghers 1974), quiescence (Hasler and Villemonste 1953, Emery 1973), and hiding in and about natural obstructions (Werner et al. 1977). Often prey are vulnerable only when they expose themselves. Johannes and Larkin (1961) found that rainbow trout, Salmo gairdneri, foraged only on amphipods that appeared at the edge of beds of submerged vegetation. Nursall (1973) discovered that predation on schooling shiners and young perch, Perca flavescens, was most effective when their schools were either building at dawn or dispersing at dusk. Ware (1972) cited three other studies that tended to support the hypothesis that predation is dependent on exposure of prey. Hasler and Villemonste (1953) suggested that the quiescence of yellow perch (Perca flavescens) at night aided their evasion of nocturnal predation. When fish are feeding or are sedentary, the model assumes that they are immune to predation; only when fish are mobile and not feeding are they exposed to attack.

There is one exception to this rule. While feeding,

fish are considered susceptible to attack by members within their own life stage. Only under these conditions will the number of fish be reduced while feeding (section B.1.6).

Habitat preference by members of the Ith life stage can also vary throughout a 24 hour period. Organisms can be limnetic while feeding or demersal while quiescent; any other combination of limnetic or demersal preferences for any of the four periods is possible (SHABIT).

D. Ingestion

D.1 Evacuation of the Stomach

In the model digestive evacuation is important as an index of satiation and as the source of all growth. Since hunger and satiation have a strong influence on the rate of feeding (Ishiwata 1968a, 1968b, Brett 1971, Ware 1972), the rate of evacuation in the stomach indirectly affects the rate of feeding. Since most digestion in fish occurs beyond the stomach in the gut (Phillips 1969), the amount evacuated represents growth in weight of the individual.

The amount of material evacuated from the stomach is dependent upon the amount present, the size of the stomach, and the temperature (Brett and Higgs 1970). Each second a

fraction of the volume represented by the maximum capacity of the stomach can be evacuated if enough food is present. Maximum capacity of the stomach in grams is calculated as a linear function of weight (Brett 1971):

$$(\text{stomach capacity}) = \text{PSTOM} \cdot X \quad \text{D.1(1)}$$

The fraction of capacity evacuated per second is a skewed function of water temperature (Fig. II). As water temperature increases from a minimum, gastric evacuation approaches some maximal value from "0;" as water temperature rises beyond that temperature at which maximality is reached, gastric evacuation declines towards "0." The relationship requires values for four different parameters: the maximal value of the rate, the optimal temperature at which the rate is maximal, the water temperature below the optimum at which the rate drops to "0," and the water temperature above the optimum at which the rate drops to "0." In the model the minimum temperature is altered into a rate of decline before all values are used in the normalized equation of Lassiter and Kearns (1973):

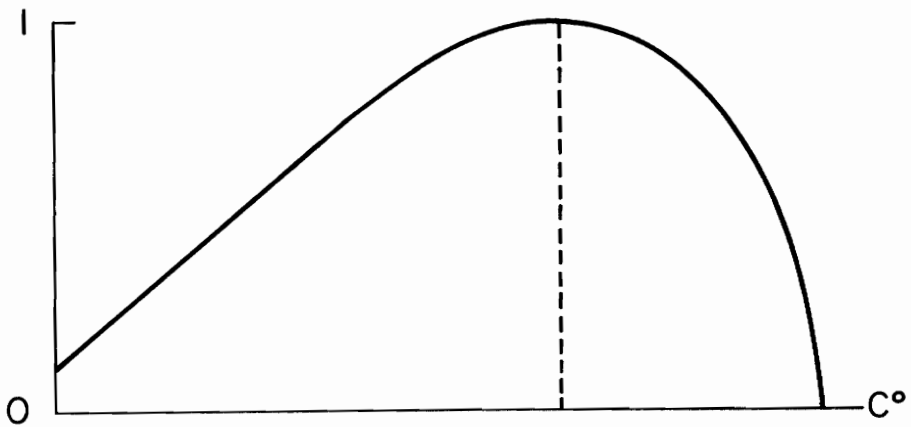


Fig. II. Normalized equation used in calculating rates of gastric evacuation for fish and rates of increase for nonpiscine organisms. Rates are calculated a functions of water temperature.

$$A = \frac{P_{THRM} - Z}{P_{THRM} - P_{THRM}} \frac{2-1}{2 \quad 1}$$

$$(\text{tempered rate}) = \exp\{P_{THRM} \cdot (Z - P_{THRM})\}$$

$$\bullet A \frac{P_{THRM} \cdot (P_{THRM} - P_{THRM})}{3 \quad 2 \quad 1} \bullet PEVACT \quad D.1(2)$$

The amount evacuated a stomach during period is the product of the number of seconds in the period (TSECND) and the rate of evacuation per second:

$$(\text{amount evacuated}) = PEVACT \cdot Z \cdot \{Eq. D.1(1)\} \cdot TSECND$$

D.1(3)

If the fish has an empty stomach at the start of any period and does not feed, no contents are evacuated.

The amount of stomach contents remaining at the end of any period is a function of the rates of evacuation and ingestion and the stomach capacity of the fish. The amount of food needed to fill the stomach at the end of the period is the volume of the stomach empty at the start of, and the amount evacuated at the end of, the period:

$$(\text{stomach emptiness}) = \{ \text{Eq. D.1(1)} \} - X + \{ \text{Eq. D.1(3)} \}$$

4

D.1(4)

The stomach can not evacuate more food than is present at the beginning of, plus the amount ingested during, a time period. When Eq. D.1(4) is negative, the stomach is considered empty for the start of the next period (Eq. D.1(4) is set to zero), and the amount evacuated is the sum of the contents of the stomach at the beginning, and the amount of food ingested during the period.

D.2 Feeding

D.2.1 Unsated Feeding

The amount of material ingested by members of any life stage is a function of their activity and their rates of ingestion. During any period when fish are not feeding, their rates of ingestion are zero. When feeding, the magnitudes of their rates of ingestion are affected by their predation and deaths of prey from other causes.

The number of fish from the Jth life stage ingested by the members of the Ith life stage is a function of

competitive predation. From section B.1.4, the elements of TCRM are crude rates of mortality per second for each "IJ" combination of life stages; each "IJ" combination represents the predatory relationships between members of two life stages only. Crude rates of survival are calculated for each combination as the complements of the crude rates of mortality {Eq. B.1.4(3)}. The natural logarithm of this survival rate is the relative rate of mortality (Ricker 1975):

$$\text{(relative mortality rate)}_{ij} = \ln\{\text{Eq. B.1.4(3)}\}_{ij} \quad \text{D.2.1(1)}$$

For each life stage of prey, the relative rates of mortality due to noncompetitive predation are summed over all life stages of predators and added to the relative rate of mortality for causes of death other than predation (TRRMN):

$$\text{(relative mortality rate)}_j = \sum_{i=1}^{NCH} \{\text{Eq. D.2.1(1)}\}_i + \text{TRRMN}_j \quad \text{D.2.1(2)}$$

The number of fish in any life stage that survive over a

period is the base of natural logarithms raised to the product of their relative rate of mortality {Eq. D.2.1(2)} and the length of the period in seconds (TSECND):

$$(\text{number left}) = X_1 \cdot \exp(\{\text{Eq. D.2.1(2)}\} \cdot \text{TSECND}) \quad \text{D.2.1(3)}$$

The total number of deaths in a life stage during any period is the number of fish present at the beginning of the period minus the number surviving at the end:

$$(\text{number dead}) = X_1 - \{\text{Eq. D.2.1(3)}\} \quad \text{D.2.1(4)}$$

The ratio of the two relative rates, Eq. D.2.1(1) and Eq. D.2.1(2), is the fraction of the deaths in the Jth life stage of prey attributable to predators from the Ith life stage:

$$(\text{fraction of deaths}) = \frac{\{\text{Eq. D.2.1(1)}\}_i}{\{\text{Eq. D.2.1(2)}\}_j} \quad \text{D.2.1(5)}$$

The number of dead from the Jth life stage of prey killed by

the Ith life stage of predators is the product of this fraction and the total number of dead:

$$(\text{number dead})_{ij} = \{\text{Eq. D.2.1(4)}\}_j \bullet \{\text{Eq. D.2.1(5)}\}_i \quad \text{D.2.1(6)}$$

The number of fish ingested by the predators in any Ith life stage is the sum of all Eq. D.2.1(6) over J:

$$(\text{numbers eaten})_i = \sum_{j=1}^{NCH} \{\text{Eq. D.2.1(6)}\}_{ij} \quad \text{D.2.1(7)}$$

The weight of the food ingested by the predators from the Ith life stage is the sum of the products of Eq. D.2.1(6) and the weight of the individual over all "J" with "I" constant:

$$(\text{weight eaten})_{ij} = \{\text{Eq. D.2.1(6)}\}_{ij} \bullet X_{ij} \quad \text{D.2.1(8)}$$

$$(\text{weight eaten})_i = \sum_{j=1}^{NCH} \{\text{Eq. D.2.1(8)}\}_{ij} \quad \text{D.2.1(9)}$$

The weight of food eaten by a single predator in the Ith life stage is the weight ingested by all members divided by the number of members in the life stage:

$$\text{(relative weight eaten)} = \{\text{Eq. D.2.1(9)}\} / X_1 \quad \text{D.2.1(10)}$$

Numbers in each life stage are temporarily adjusted for mortality after each period to ensure a valid value for abundance in the next.

When members of a life stage prey upon their peers or upon only a segment of another life stage, Eq. D.2.1(8 and 9) are calculated using prey weights adjusted for size-selective predation (section D.3).

D.2.2 Sated Feeding

When the amount of food ingested by a predator during a period is greater than the available volume of empty stomach, it is reduced. Since the rate of ingestion and hence predatory attack is inversely related to hunger (Ishiwata 1968a, 1968b, Brett 1971, Ware 1972), the model assumes that the predator will reduce its rate of ingestion to ensure its satiation at the end of the period. If Eq.

D.2.1(10) is greater than Eq. D.1(4), the former is assigned the value of the latter. The numbers of prey in each life stage killed by the predators in an Ith life stage are then reduced by the ratio of the volume in the stomach available {Eq. D.1(4)} to the volume ingested when predators remain unsated during the period {Eq. D.2.1(10)}:

$$\text{(number dead)}_{ij} = \frac{\{\text{Eq. D.1(4)}\}_i \cdot \{\text{Eq. D.2.1(6)}\}_{ij}}{\{\text{Eq. D.2.1(10)}\}_i}$$

D.2.2(1)

Weight of food ingested by these sated predators is the volume of stomach available {Eq. D.1(4)}. Numbers, weights, and relative weights of food items eaten by predators of the Ith life stage {Eq. D.2.1(7 thru 10, inclusively)} are recalculated based on the number of prey eaten by a sated predator.

When the number of prey killed is reduced in this manner, the new survivors are exposed to death from other causes. During the period, this exposure will increase the rations to all previously unsated predators. In the model, this increase is calculated by handling sated predators first. Initially, all life stages are ranked by their degree

of satiation relative to the size of their members' stomachs (TEXTRA). All values associated with sated predators are adjusted {Eq. D.2.2(1) and Eq. D.2.1(7 thru 10, inclusively)}; the numbers of prey eaten by sated predators are removed from their life stages; and for each life stage of prey, relative rates of mortality due to uncompetitive predation from sated predators {Eq. D.2.1(1)} are removed from their total relative rate of mortality {Eq. D.2.1(2)}:

$$\begin{aligned} & \text{(adjusted relative mortality rate)} = \\ & \left\{ \begin{array}{l} \text{Eq. D.2.1(2)} \\ j \end{array} \right\} - \left\{ \begin{array}{l} \text{Eq. D.2.1(1)} \\ ij \end{array} \right\} \quad \text{D.2.2(2)} \end{aligned}$$

The number of prey escaping death because of satiation of their predators is summed. When calculations for all sated predators have been so completed, all calculations for unsated predators are made. New values for Eq. D.2.1(3 thru 10, inclusively) are calculated, only this time with numbers and mortality rates adjusted for the influence of sated predators. Mortality is calculated for those prey escaping death through satiation of other predators, and these new additions to the diet of unsated predators are added to their previous ration. If any previously unsated predators have become sated, new adjustments are made, and the process

is repeated; if all predators are still unsated, their mortalities and rations are based on these new calculations.

D.3 Size-selective Predation

Size-selective predation will fracture the competitive nature of predators. When predators discriminate by size within a single life stage of prey, some prey are exposed to predation while some will not. A number of groups of predators may compete for the smaller prey within a life stage, but if one or more of these predatory groups are size-selective, their members will not compete with those of other groups for larger prey. This phenomenon divides the life stage of prey (Fig. III). In the model groups of prey are split or divided when preyed upon by size-discriminating predators. If a group of prey have "n" groups of predators and "m" of these prey size-selectively, the prey are temporarily split into "n+1" divisions. Calculations from sections D.2.1 and D.2.2 are made on each subdivision. All those prey eaten by size-selective predators are counted for later calculations concerning length distributions (see section G.1).

In the model numbers of fish and invertebrates are

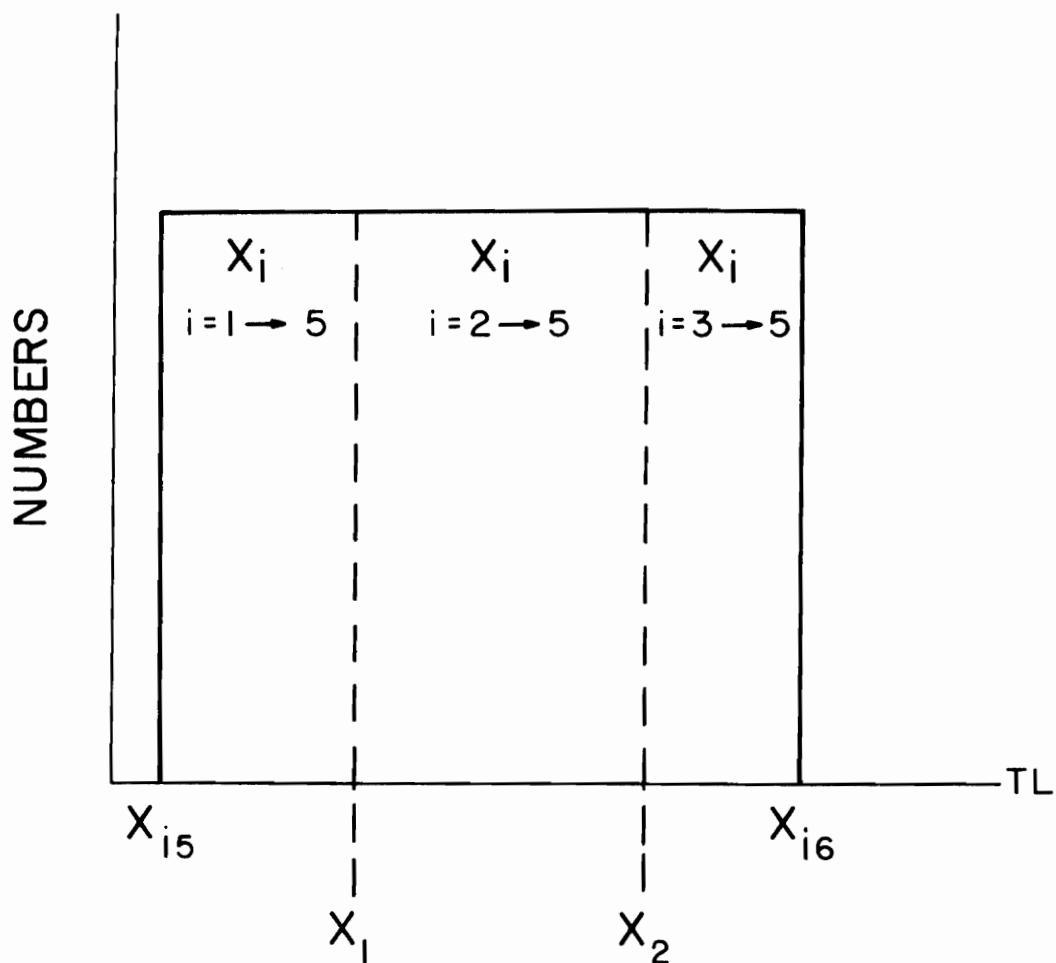


Fig. III. A schematic of a split life stage of prey divided by size-selective predation. Predators represented by subscripts "1" and "2" prey size-selectively. In the first compartment of the length distribution of prey, all five groups of predators compete; in the second, all but group "1" compete; and in the third, only groups subscripted "3" through "5" compete for prey.

decremented as fractions of life stages. Numbers killed through predation are added to those lost through other causes. These mortalities are calculated as a fraction of numbers surviving (TKSPLT). Calculations based on splitting life stages are simplified by treating mortalities in this manner.

E. Respiration

Respiration is the loss of energy due to maintenance and activity of the fish. By definition respiration is measured in units of energy. In the model respiration is measured as losses in wet weight. Conversions from units of calories or milligrams of oxygen to units of wet weight are conducted during the input of the appropriate parameters (PACTVE, PSM). In converting calories to wet weight, PGRAM is used; in converting milligrams oxygen to wet weight, the constant 3.42 cal/mg oxygen is used (RQ=.85) (Warren and Davis 1967).

E.1 Standard Metabolism

Standard metabolism continues regardless of the activity of the fish and is therefore a part of both active

and routine metabolisms (Kramer 1969; Weatherley 1976). When fish are feeding, or are not feeding but mobile, the standard metabolic rate is included in the calculations of active and routine rates. When fish are sedentary, they are respiring at the standard rate only. The standard rate is an allometric function of water temperature and size of the individual (Kramer 1969):

$$(\text{standard metabolism}) = \text{PSM}_1 \cdot X_2 \cdot \frac{\text{PSM}_3}{10} \quad \text{E.1(1)}$$

During any period when the fish is sedentary, the loss in weight due to metabolism is the product of the standard rate and the length of the period:

$$(\text{metabolic costs}) = \{\text{Eq. E.1(1)}\} \cdot \text{TSECND} \quad \text{E.1(2)}$$

E.2 Active Metabolism

Active metabolism is the most intense respiration possible (Fry 1957). No uptake of oxygen beyond this level is possible; any further exertion by the fish is the result of anaerobic respiration.

The active metabolic rate for the individual is calculated much as was for the standard rate. The active metabolic rate is calculated as a linear function of the standard rate (Kramer 1969):

$$(\text{active metabolism}) = \text{PACTIVE} \cdot \{\text{Eq. E.1(1)}\} \quad \text{E.2(1)}$$

E.3 Routine Metabolism

Routine metabolism is the bioenergetic cost of basal maintenance plus those of spontaneous activity (Kramer 1969). Basal maintenance is standard metabolism, and spontaneous activity is the most intense activity possible, no activity at all, or anything inbetween.

Since the routine metabolic rate is so dependent on spontaneous activity, the nature of its calculation varies dramatically among the different periods in a day. When fish are sedentary, their routine rate is equal to their standard rate {Eq. E.1(1)}; when fish are feeding, their routine rate is greater. Searching and attacking require the expenditure of energy beyond that required for quiescence. This expenditure is calculated much as was done for the optimal breadth of diet (section B.1.7). Each attack consumes a certain amount of time and a certain

amount of energy. When the predator is not attacking, it is cruising in search of prey. The number of attacks on prey of any life stage during any period is the product of the number of prey caught to prey encountered:

$$(\# \text{ attacks})_{ij} = \{ \text{Eq. D.2.1(6)} \}_{ij} / \{ \text{Eq. B.1.3(2)} \}_{ij} \quad \text{E.3(1)}$$

If the predator is a schooling predator, the number of attacks must be increased within the school:

$$(\# \text{ attacks})_{ij} = \{ \text{Eq. E.3(1)} \}_{ij} / T_{SCHOL} \quad \text{E.3(2)}$$

Distance traveled by an individual predator in attacking is the sum over all life stages of prey of the product of the number of attacks, the reactive distance, and the reciprocal of the density of predators:

$$(\text{distance}) = \left(\sum_{j=1}^{NCH} \{ \text{Eq. E.3(1)} \}_j \cdot \{ \text{Eq. B.1.2(1)} \}_{ij} \right) / X_{i1} \quad \text{E.3(3)}$$

The time during a period consumed by a predator in attacking

is the product of the distance it travels while attacking and the reciprocal of its burst speed:

$$(\text{time attacking}) = \{\text{Eq. E.3(3)}\} / \{\text{Eq. B.1.3(1)}\} \quad \text{E.3(4)}$$

When this distance is travelled, the predator is assumed to be respiring at the active metabolic rate. Therefore, cost of attacking prey is the product of the active rate {Eq. E.2(1)} and the number of seconds spent at burst speed:

$$(\text{attack cost}) = \{\text{Eq. E.3(4)}\} \cdot \{\text{Eq. E.2(1)}\} \quad \text{E.3(5)}$$

When not attacking, a predator is assumed to be searching at cruising speed. In the model the metabolic costs of swimming are assumed to be linearly related to speed. With standard and active metabolic rates as lower and upper limits {Eq. E.1(1) and Eq. E.2(1), respectively}, the routine rate at cruising speed is somewhere inbetween:

$$\begin{aligned} (\text{routine metabolism}) = & \\ & \frac{\{\text{Eq. E.2(1)} - \text{Eq. E.1(1)}\} \cdot \{\text{Eq. B.1.1(2)}\}}{\{\text{Eq. B.1.3(1)}\}} \\ & + \{\text{Eq. E.1(1)}\} \quad \text{E.3(6)} \end{aligned}$$

The time spent searching by a predator is the complement of the time spent attacking. The metabolic cost of searching during a period is the difference between the number of seconds in a period and the number of seconds spent attacking, multiplied by the routine rate at cruising speed:

$$\text{(search costs)} = \{\text{TSECND} - \text{Eq. E.3(4)}\} \cdot \{\text{Eq. E.3(6)}\}$$

E.3(7)

Total metabolic expenditure for feeding during a period is the sum of the cost due to attacking and searching:

$$\text{(metabolic costs)} = \{\text{Eq. E.3(5)}\} + \{\text{Eq. E.3(7)}\} \quad \text{E.3(8)}$$

When fish are not feeding, but are still moving, they are neither searching nor attacking, but are being sought and attacked. Each successful escape requires energy. The number of successful attacks and the total number of attacks upon the members of the Jth life stage by predators in the Ith life stage are known [Eq. D.2.1(6) and Eq. E.3(2), respectively]. The difference between the number of attacks thwarted and the number successful in the Jth life stage is the number of escapes:

$$(\# \text{ escapes})_{ij} = \{\text{Eq. E.3(1)}\}_{ij} - \{\text{Eq. D.2.1(6)}\}_{ij} \quad \text{E.3(9)}$$

This number of escapes is for the entire life stage.

Generally, predators cull the weaker, less fit prey from a life stage. In the model a prey that successfully evades predatory attack is assumed to continue doing so. All escapes made during the period are made by the surviving prey; no prey once having escaped will fail to do so again during the remainder of the period. Number of escapes made by a single prey is the number of escapes divided by the number of prey surviving:

$$(\# \text{ relative escapes}) = \{\text{Eq. E.3(9)}\} / \{\text{Eq. D.2.1(3)}\} \quad \text{E.3(10)}$$

The number of escapes per individual is multiplied by the reaction distance of the attacking predator to calculate the distance traveled by a prey from the Jth life stage in escaping from the predators in the Ith life stage:

$$(\text{distance})_{ij} = \{\text{Eq. E.3(10)}\} \cdot \{\text{Eq. B.1.2(1)}\}_{ij} \quad \text{E.3(11)}$$

Eq. E.3(11) is summed over all possible "I" life stages to obtain the total distance traveled in escaping. Since the model assumes that prey escape at burst speed, previously documented equations can be used in further calculations. If the text containing Eq. E.3(4 thru 7, inclusively) is altered to account for escape instead of attack, these equations can be, and are, used to calculate the routine metabolism of prey when they are moving, but not feeding.

When predators prey upon their peers, routine metabolism is calculated as the sum of both the aforementioned procedures. The number of attacks and the number of escapes are both calculated and summed. By using the above formulations, the amount of time and energy used in attacking and escaping are used to separate the period into segments and to calculate the routine metabolic rate.

F. Digestion

F.1 Specific Dynamic Action

Specific Dynamic Action, hereafter called SDA, is an entropic tax paid during food conversion (Ware 1975). SDA is initiated by the fish just after ingestion and continues till the alimentary canal has been vacated. SDA has been

thought the result of deamination of proteins (Warren and Davis 1967, Beamish 1974) or exchanges of energy among amino acids in plasma and structural proteins (Morgan 1974). Kerr (1971a), Beamish (1974), and Weatherley (1976) described the magnitude of SDA as directly proportional to the energy of the ration.

The nutritional composition of prey has a pronounced influence on the magnitude of SDA in predators. The higher the ratio of protein to carbohydrate to lipid in the ration, the higher the magnitude of SDA. Beamish (1974) discovered that a ration composed solely of protein induced an energy loss from SDA of 30%, a ration of carbohydrate 5%, and a ration of lipid 13% their caloric values when fed to largemouth bass (Micropterus salmoides). In the model the fraction of a mixed ration consumed by SDA is determined by the relative amounts of proteins, carbohydrates, and lipids in the diet, each weighted by fractions similar to those above. For the initial calculations of the amount of energy consumed in SDA, each life stage is treated separately. The fraction of the prey that is protein (PNUTRN) is multiplied by the fraction of a ration of pure protein consumed in SDA by the predator (PSDA); equivalent computations are made for carbohydrates and lipids. The three products are then summed for all combinations of life

stages:

$$\text{(fraction burned)}_{ij} = \sum_{i=1}^3 \text{PNUTRN}_{j} \cdot \text{PSDA}_{i} \quad \text{F.1(1)}$$

The value of Eq. F.1(1) is the fraction of food lost per gram of prey to the predator from the Ith life stage through SDA.

Before further calculations can be made, several changes in the nature of SDA must be considered. The ration upon which SDA acts is not the ingested, but the digested food. The amount of SDA during a period is dependent upon the amount of food that enters the gut, not the stomach. In the model calculations of the magnitude of SDA are based upon the amount of food evacuated from the stomach. Since relative densities of prey in the diet of predators are assumed to be unchanging for short periods of time, these relative densities are used in further computations as approximations of the nutritional composition of evacuated food. If within a period food is evacuated from the stomach but none is ingested, no ration is available upon which to base the calculations of SDA. In this instance, the fraction of the evacuated materials from the period before is used. On the first day when no such fraction is

available, a random number between zero and the fraction burned in SDA for a ration of pure protein is used.

The fraction of ration burned in SDA is computed as the sum of the SDA accrued by ingesting prey from each life stage. The contribution to SDA by each life stage of prey represented in the ration is the product of the weight of these prey [Eq. D.2.1(10)] and the fraction of diet represented by these prey burned in SDA [Eq. F.1(1)]:

$$(SDA/prey\ life\ stage) = \{Eq.\ D.2.1(10)\} \cdot \{Eq.\ F.1(1)\} \tag{F.1(2)}$$

These values of life stage-specific SDA are summed over life stages, and the sum is then divided by the total weight of the ration to obtain the fraction per gram of ration lost to SDA:

$$(SDA\ fraction) = \left(\frac{\sum_{j=1}^{NCH} \{Eq.\ F.1(2)\}_j}{Eq.\ D.2.1(10)} \right) \tag{F.1(3)}$$

The fraction of the ration that survives SDA is the complement of the above equation:

$$(\text{fraction ration surviving SDA}) = 1 - \{\text{Eq. F.1(3)}\} \quad \text{F.1(4)}$$

In all of the above equations, corrections are made for satiation and deprivation before calculations are initiated.

F.2 Assimilation Efficiency

Not all of the food that survives SDA becomes fish flesh. A certain quantity, its magnitude determined by the assimilative efficiency of the predator, is egested as fecal material.

There is some question about what factors affect assimilative efficiency. Kinne (1960) reported that temperature and salinity affected efficiency in euryplastic fish. Molnar and Tolg (1962) found the rate of digestion in largemouth bass to be temperature dependent. Seaburg and Moyle (1964) observed a similar relationship between assimilative efficiency and water temperature in several warm-water species. However, Kelso (1972) found that only size of walleye and its type of prey affected assimilative efficiency for that species.

In the model assimilative efficiency is assumed to be constant. No effects of temperature, salinity, or other factors are modeled. Any effects due to size of the

predator can be addressed by specifying different constants for different life stages.

F.3 Weight Gain

Before the amount of food evacuating the stomach can be transformed into somatic tissue, a further complication must be resolved. Quality in digested food as measured in calories per gram is not always the same as the flesh it will become. Often there is not a one-to-one relationship between the energy content of a gram of predator to a gram of prey. As a correction for this discrepancy, the ratios of the energy contents (PGRAM) of a gram of prey to a gram of predator are calculated for all possible combinations of life stages:

$$\text{(energy ratio)}_{ij} = \frac{\text{PGRAM}_j}{\text{PGRAM}_i} \quad \text{F.3(1)}$$

Application of this energy ratio to the digested foods present some of the same problems as did the calculation of SDA in the previous section. Again, the energy ratio is calculated for each component of the ration, not the digested food. As in the earlier situations, the

composition of the ration is assumed to be closely approximated by that of the digested food. Each component of the ration is multiplied by the appropriate energy ratio for the life stages involved:

$$(\text{weight eaten})_{ij} = \{\text{Eq. D.2.1(8)}\} \cdot \{\text{Eq. F.3(1)}\} \quad \text{F.3(2)}$$

Weight of prey from the Jth life stage eaten by a single predator from the Ith life stage is the dividend of the total weight eaten and the density of predators:

$$(\text{relative weight eaten})_{ij} = \{\text{Eq. F.3(2)}\} / X_{i1} \quad \text{F.3(3)}$$

The factor by which digeseted food is changed from grams of prey to grams of predator is calculated as the sum of all the relative weights eaten from each life stage of prey and their appropriate energy ratios divided by the total weight of the ration:

$$(\text{energy factor})_i = \frac{\sum_{j=1}^{NCH} \{\text{Eq. F.3(3)}\}_j}{\{\text{Eq. D.2.1(10)}\}} \quad \text{F.3(4)}$$

As with the calculations in SDA, if no food was eaten during the day, the value of Eq. F.3(4) from previous periods is used. On the first day, no value for this equation is available; a value of unity is assumed.

Actual gain in weight from digestion during the day is the product of the fraction of food surviving SDA, the efficiency of assimilation, and the factor for energy equivalence:

$$(\text{weight gain}) = \text{PDIGST} \cdot \{\text{Eq. F.1(4)}\} \cdot \{\text{Eq. F.3(4)}\}$$

F.3(5)

G. Rate of Change in Weight

G.1 Statistical Gains in Weight

Weights of members of a life stage can be increased "statistically" by predation on segments of a life stage. If only smallest members are eaten, the length distribution of a life stage is narrowed, and its median weight and mean length increase. Examples of increasing mean lengths of fish during periods of no growth are common in the literature (e.g., Forney 1966, Chevalier 1973).

In the model the sizes of fish within a life stage are

considered to be uniformly distributed. Although numerous kinds of length distributions are exhibited by different populations, the uniform distribution can be used as an approximation. Precedent for treating age-groups within a species in such a manner can be found in the literature (Eraslan et al. 1976). The length distribution of each life stage is bounded by lower and upper limits representing the TL of the smallest and the largest members in the life stage, respectively. The densities at both limits and at all intermediate points are equivalent. Mean length is midway between the limits, and the area of the distribution represents the total density of the life stage.

In the model predation upon a segment of a life stage alters the lower limit of its length distribution. How a life stage of prey is so distinguished by a life stage of predators was described in section B.1.6. For each life stage, the fraction of the membership eaten by length-discriminating predators during the day is calculated, representing a segment of area in the length distribution of prey. Since individuals eaten in this manner are by definition the smaller in the life stage, the segment is subtracted from the lower portion of the distribution (Fig. IV). Since the uniform distribution is rectangular and its height is known for all sizes, the increase in the lower

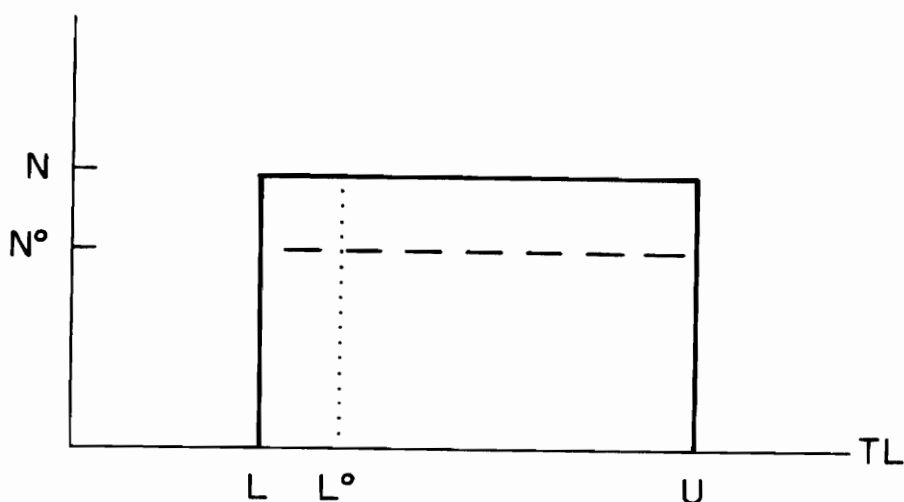


Fig. IV. Manner in which length distributions of prey are influenced by size-selective and nonsize-selective predation. (U) is the upper limit by length, (L) is the lower limit, (L°) is the lower limit after predation on only the smallest members of the life stage, removing a number represented by the area to the left of the dotted line, (N) is the number of individuals at any length, and (N°) is the number at any length after predation on all members, removing a number represented by the area above the dotted line.

limit in the distribution can be calculated. The upper limit of the distribution is left unaltered. Change in the mean length is half that in the lower limit. Increase in the maximum median weight is the difference between the old maximum and the new, the latter calculated as the result of a length-weight regression on the new mean length. Increase in the current median weight is the same as that in the maximum. Weight of stomach contents is increased accordingly through maintaining the fraction filled in a larger stomach {Eq. D.1(1)}.

If no predation occurs in the aforementioned manner for a prey life stage, no "statistical" adjustment of size is made.

G.2 Physiological Gains in Weight

Mean weight of fish in a life stage can "physiologically" change in a number of ways. Ingestion adds bulk to the stomach while egestion subtracts. Assimilation converts food into somatic and reproductive tissue.

Maximum and current median weights, mean lengths, and the limits of length distributions can be increased by growth in the individual. Change in the current median

weight is the sum of the mass lost due to respiration and egestion and the mass gained through ingestion and assimilation (for clarity Eq. E.1(2) represents the respiration that occurs daily):

$$\begin{aligned} (\text{weight change}) = & \{\text{Eq. D.2.1(10)}\} - \{\text{Eq. E.1(2)}\} \\ & - \{\text{Eq. D.1(3)}\} + \{\text{Eq. F.3(5)}\} \qquad \qquad \qquad \text{G.2(1)} \end{aligned}$$

If at the end of a time-step change in growth has pushed current median weight over its maximal value, the length distribution is altered. Since growth is estimated for fish of mean length only, proportional growth must be calculated for those fish at the extremes of the length distribution. As the extrema of this distribution change, so do the current and maximal median weights.

Lengths at extremes of the length distribution are altered by using standard length-weight relationships. If the current median weight is below the maximal (plus stomach contents), a new value for the exponent is calculated [see Eq. B.2.2(2)]. With the value of the exponent known, weights corresponding to the extreme lengths in the distribution are calculated:

$$\text{(minimum weight)} = \{\text{Eq. B.2.2(1)}\} \cdot X \frac{\{\text{Eq. B.2.2(2)}\}}{5} \quad \text{G.2(2)}$$

$$\text{(maximum weight)} = \{\text{Eq. B.2.2(1)}\} \cdot X \frac{\{\text{Eq. B.2.2(2)}\}}{6} \quad \text{G.2(3)}$$

Since growth was calculated for fish with current median weight only, growth in fish of extreme size is calculated as a proportion of their weight. Increases at the extrema are the products of the fraction of increases for those fish of median weight over a time-step and the weights of fish at the extremes:

$$\text{(low growth)} = \{\text{Eq. G.2(2)}\} \cdot \{\text{Eq. G.2(1)}\} \cdot \text{DT} / X \frac{2}{2} \quad \text{G.2(4)}$$

$$\text{(high growth)} = \{\text{Eq. G.2(3)}\} \cdot \{\text{Eq. G.2(1)}\} \cdot \text{DT} / X \frac{2}{2} \quad \text{G.2(5)}$$

Growth in fish at the extremes are added to their weights, and these sums are used in calculating the new lengths by reversing the length-weight relationship. Treating growth in this manner allows the length distribution to expand as the fish within the life stage grow larger. New mean length is calculated as the average of the new lengths of the fish at the extremes; New current and maximal median weight are

calculated as a function of new mean length with the specified length-weight relationship.

If growth has not pushed current median weight in a life stage above its maximum value, mean length and the limits of the length distribution are not altered. Only current median weight is changed.

H. Life Stages Representing Nonpiscine Organisms

Populations of fish are interacting components of ecosystems and can occupy several trophic levels. Many fish are phytophagous, eating microscopic plants. Others, though carnivorous, do not eat other fish, but consume zooplankton or benthos. Throughout the life history of many species, their eating habits mature from herbivory to carnivory to piscivory. Elements of the diets of fishes that pertain to organisms other than fish can be nutritionally important.

In the model the dynamics of nonpiscine organisms (invertebrates, algae, etc., hereafter referred to as "invertebrates"), are handled in an empirical fashion. As many life stages of invertebrates as desired can be included in the model. The habitats utilized (SHABIT), the periods of activity (SPROWL), the weight, the diameters, and the caloric (PGRAM) and the nutritional (PNUTRN) values for the

members of each life stage are constants provided by the user. The members of these life stages are preyed upon by fish as if they were from any other life stage, save that they have no length distribution. All invertebrates within a life stage are assumed to be of one size. The numbers of each life stage are decremented through predation by fishes and by death from extremes of water temperature. No calculations concerning the bioenergetics of these organisms are made. A logistic equation is used to estimate the increase in numbers resulting from reproduction. The intrinsic rate of increase "r" is influenced by temperature. As water temperature increases from a minimum, "r" approaches some maximal value from "0;" as water temperature rises beyond that temperature at which maximality is reached, "r" declines towards zero. Outside of these extrema, "r" becomes negative, and a reduction in numbers results. The relationship requires values for four different parameters; the maximal value of "r," the optimal temperature at which "r" is maximal, the water temperature below the optimum at which "r" drops to zero, and the water temperature above the optimum at which "r" drops to zero. Eq. D.1(2) is used to temper "r" to water temperature, only PLOG(I,1) is used instead of PEVACT(I). The rate of increase in numbers of invertebrates during a day is the

In the model cohorts are allowed to transfer from one life stage to another. All cohorts are "contained" within a vector of life stages in ascending order by age (see Volume I). For example, a species with "n" life stages is assigned to the first "n" elements of the vector, another species with "m" life stages is assigned to the next "m" elements, and so on. Often positions (life stages) in the vector will be "vacant", as there are no cohorts present to fill them at that time. For instance, the change from limnetic to demersal life by percid fry in their first season of growth is a transfer operation; for that period of their life, two positions in the vector must be present, one occupied before the descent to the bottom and one after. Species within the vector are separated by the switch STRANS. All transfer occurs from lower elements within the vector ("I" positions) to higher elements ("I+1" positions). The only exception is the oldest life stage within each species; no transfer is allowed out of this position.

Transfer can be triggered by either date or growth. In the former case, all members of the cohort in the "I" position of the life stage vector are transferred into the "I+1" position on a given date. If the "I+1" position is vacant, all state variables of the life stage from below are transferred as they are. If the "I+1" position is occupied,

state variables for the cohort resulting from the transfer are composites of those in the two positions. Of the four limits of the length distributions from cohorts in the two positions, the lowest and the highest become the new limits for the new composite cohort in the "I+1" position.

Abundance in the composite cohort is the sum of numbers of cohorts from both the "I" and the "I+1" positions. Mean length, maximum median length, and weight of stomach contents are calculated as described earlier (section G.1), except the last calculations are weighted by the number within the transferring cohort and averaged. If growth is the same for both cohorts before transfer, current median weight is calculated with a length-weight relationship based on the common exponent. However, if growth is dissimilar, a new value of the exponent is calculated. First, height of each length distribution is calculated:

$$(\text{height}) = X_1 / (X_6 - X_5) \quad \text{I. (1)}$$

Second, biomass of each cohort is calculated:

$$(\text{biomass}) = \text{TLWREG}_1 \cdot \text{Eq. I. (1)} \cdot (X_6^{\text{TLWREG}_2} - X_5^{\text{TLWREG}_2}) \quad \text{I. (2)}$$

Third, biomasses are summed:

$$(\text{biomass}) = \{\text{Eq. I. (2)}\}_i + \{\text{Eq. I. (2)}\}_{i+1} \quad \text{I. (3)}$$

The new length distribution of the composite cohort now in the "I+1" position is used to calculate a new value for the exponent. Eq. I.(2) is set up with the values for biomass and height of the distribution for the new cohort. Since exponents in this equation cannot be combined into a single variable for solution, their value is approximated numerically. This approximation is used in the length-weight relationship to calculate the current median weight.

When transfer is triggered by growth, some procedures are different from those previously discussed. As members of a cohort in the "I" position grow past a certain threshold, they are transferred to the "I+1" position. All or part of the cohort in the lower position can transfer; all those above the threshold will, all those below will not. If some remain, the lower limit of their length distribution remains the same, and the threshold becomes their upper limit. If all transfer, state variables in the "I" position are vacated completely. If the "I+1" position is vacant, upper and lower limits of the transferred animals

are respectively the upper limit of those transferred and the threshold between the positions (if all the cohort transfers from the lower position, the lower limit of the length distribution remains unchanged). If before transfer the "I+1" position is occupied, those segments of the cohort in the "I" position transferring and those in the "I+1" position are combined as described in the previous paragraph. All calculations are based on the length distributions of those in the "I+1" position and those transferring from below.

All positions in the life stage vector are checked for transfer in descending order. This procedure prevents a cohort from transferring into, and out of, a life stage when transfer is to occur among several contiguous positions on the life stage vector on the same date.

Both kinds of transfer, date and growth, can be delayed beyond their respective thresholds. Before transfer into an occupied position occurs, length distributions of those transferring and those there are compared. When length distributions overlap, transfer occurs as described above; if they do not, transfer is halted until either overlap is present or the higher position is vacated. This procedure prevents the evolution through transfer of bimodal length distributions.

J. Reproduction

Reproduction is influenced by environmental and biological factors. Spawning can be triggered by either photoperiod or water temperature (DeVlaming 1972). Fecundity is greatly influenced by size and hence growth in the individual fish (Braun 1971). Survival of eggs to hatching is dependent upon water temperature, wind, currents, and other environmental phenomena (Kramer 1969).

J.1 Spawning

In the model spawning activity is triggered by photoperiod alone. Although some species are more influenced by water temperature (Sundararaj and Vasal 1976), most are not (DeVlaming 1972). Since photoperiod is highly correlated to date, spawning activity is initiated when the simulation passes a given date, SLOVE(1).

In the model relative frequency of spawning, ratio of females in the life stage, and fecundity are used to calculate numbers of eggs spawned and subsequent loss of weight in females. Not all females are forced to spawn during any particular time step. A piece-wise, linear function is used to describe the relative frequency of

spawning (Fig. V). Relative frequency is calculated as a function of date by finding the slope and intercepts for both linear equations. By assuming the area of the enclosed triangle equal to unity, its height can be used in calculations:

$$\text{(ascending slope)} = \frac{2.}{(\text{SLOVE}_2 - \text{SLOVE}_1) \cdot (\text{PLOVE} - \text{SLOVE}_1)} \quad \text{J. 1 (1)}$$

$$\text{(descending slope)} = \frac{2.}{(\text{SLOVE}_2 - \text{SLOVE}_1) \cdot (\text{PLOVE} - \text{SLOVE}_2)} \quad \text{J. 1 (2)}$$

$$\text{(descending intercept)} = \frac{2.}{(\text{SLOVE}_2 - \text{SLOVE}_1)} \quad \text{J. 1 (3)}$$

Current dates are converted to scale before use in the above

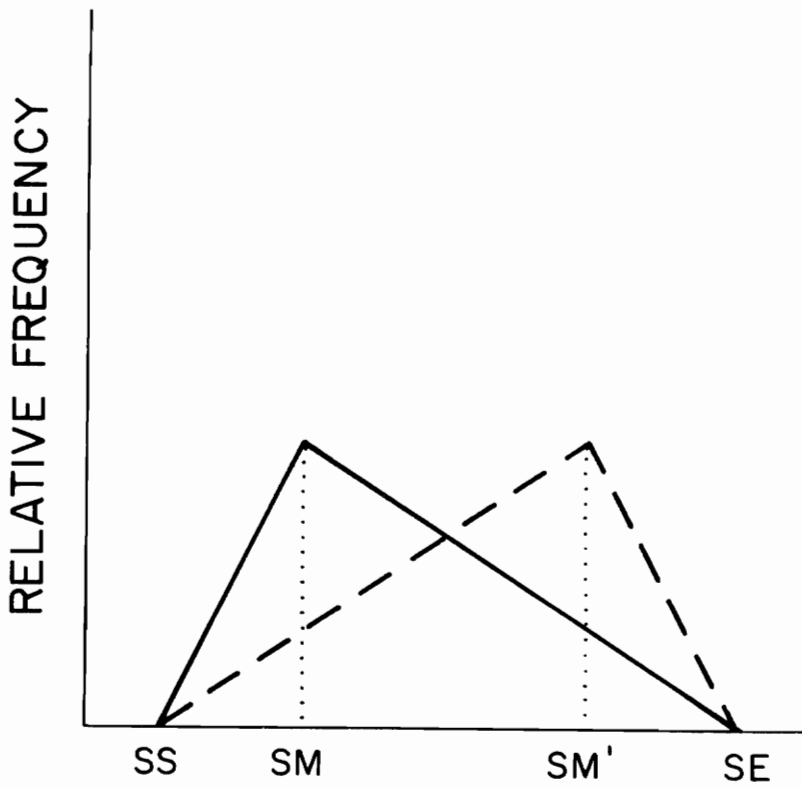


Fig. V. Two possible, piece-wise, linear functions that describe daily relative frequency of spawning for adult fish. Area under each set of lines is unity. SS represents the date of the start of spawning and SE the end. SM represents the date of maximum frequency of spawning.

equations; as an example, during the period described by the ascending equation, SLOVE(1) is used:

$$(\text{fraction spawning}) = \{\text{Eq. J.1(2)}\} \cdot \{\text{ID-SLOVE}_1\} \quad \text{J.1(4)}$$

When time steps are more than a day long, the model will accumulate relative frequencies over the time step and apply their sum. The number of eggs shed per individual female is considered an allometric function of mean length (Bagenal 1971):

$$(\text{fecundity/female}) = \text{PFECND}_1 \cdot \text{X}_3^{\text{PFECND}_2} \quad \text{J.1(5)}$$

Weight of lost reproductive products is the product of the fecundity of the typical female {Eq. J.1(5)} and the weight of a single egg (POVA):

$$(\text{weight lost}) = \{\text{Eq. J.1(5)}\} \cdot \text{POVA} \quad \text{J.1(6)}$$

Current median weight is adjusted for reproduction by subtracting the product of lost weight of reproductive

tissue, the fraction of the females spawning, and the fraction of the life stage female:

$$(\text{adjusted weight}) = X_2 - \{\text{Eq. J.1(4)}\} \cdot \{\text{Eq. J.1(6)}\} \cdot \text{PSEX}$$

J.1(7)

Initial numbers of progeny are calculated as the total number of eggs shed by females within a life stage. Number of eggs from females spawning during a time step is the product of the integral of Eq. J.1(5) over the length distribution, the fraction of the life stage female, and the height of the distribution:

$$(\text{number eggs}) = \left\{ X_6^{\text{PPECND} + 1} - X_5^{\text{PPECND} + 1} \right\} \cdot \text{PSEX} \cdot \text{PPECND}_1 \cdot \{\text{Eq. I. (1)}\} \cdot \{\text{Eq. J.1(4)}\}$$

J.1(8)

Eq. J.1(8) is transferred to a matrix for storage (TXEGGS).

J.2 Hatching

In the model development and hatching of fish eggs are the means by which new year classes enter the model. Upon

spawning, all eggs are placed into a matrix (TXEGGS) whose rows correspond to elements in the life stage vector. All eggs from females in the Ith row of the life stage vector are "deposited" in the Ith row of the egg matrix. Since some life stages represent juvenile fish, some elements in the egg matrix will always contain zero. Upon hatching, surviving eggs are "transferred" to the youngest life stage for their respective species. Numbers are summed directly, current and maximum median weights and mean lengths are as specified in PFRY, and stomach contents are considered non-existent. If the youngest life stage is vacant when transfer occurs, limits of the length distribution are equivalent to mean length (PFRY). If this life stage is occupied, various adjustments are made. The upper limit of the length distribution of current tenants is maintained as the upper limit of the composite cohort after transfer; the lower limit becomes the length of transferring fry (PFRY). Mean length, current and maximum median weights are calculated from this new length distribution as described in the section on transfer (section I.). This procedure creates an initial length distribution. Stomach contents of the composite cohort are reduced proportionately to adjust for the vacant stomachs of newly hatched fry.

Eggs are exposed to a number of causes of mortality.

Fluctuations in water temperature have been shown lethal to eggs of nest-builders (see Fry 1967, Braum 1971); by controlling development, water temperature can prolong or shorten exposure to other causes of mortality for eggs (Johnson 1961, Smith and Kramer 1963, Fry 1967, Kramer 1969). Wind and wave action can cause extensive mortality of eggs of walleye and yellow perch (Johnson 1961, Magnuson and Smith 1963, Forney and Houde 1965, Clady and Hutchinson 1975). Other factors can be important causes of egg mortality under certain circumstances (see Kramer 1969).

Certain biological factors may also have some impact. Commensal spawning, predation, parasites, and diseases are but a few such factors. Still, their separate and combined affects are largely unknown. Kramer (1969) believes that environmental factors are the more important.

In the model the only cause of mortality for eggs modeled is wind. Wind is considered to act through wave action to cause physical damage and hence death to eggs. The greater the velocity of such wind, the greater the relative mortality. Obviously, some bodies of water are more exposed to wind than others. Still, above a threshold in wind velocity, mortality is considered as a density-independent function of wind velocity with a linear factor to account for the uniqueness of each body of water modeled:

$$(\text{crude survival rate}) = \text{Exp}\{-\text{PWIND} \cdot X\}$$

2 3

J.2(1)

This factor is expanded to cover the entire time-step for each cohort in the egg vector. Below a threshold of wind velocity, mortality is considered non-existent.

Although water temperature is not a direct cause of mortality in the model, it does control length of development. Hatching occurs when accumulated degree-days (THATCH) for each element of the egg surpasses a given threshold (PHATCH). Cumulative degree-days is a running sum of each day's water temperature expanded by the length of the current time-step (DT).

Several assumptions are made in the construction of routines in the model concerning reproduction. Spawners are assumed to broadcast their eggs and milt. Spawning habitat is not limiting on reproductive success. All eggs from females in a single life stage are assumed to be uniform in size. Obviously, these assumptions will never totally hold. Yet many can be approximated within the context of the model.

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Table V. List of final values of parameters and switches used in the model concerning Oneida Lake, New York. Values were the result of validation on data collected from mid May, 1972, to mid May, 1973. All values are in sequence by life stage from left to right and from top to bottom. Definitions of variables are located in Appendix B. (continued).

(PDIET)	1.	1.	1.	1.	1.	1.	1.
	1.	1.	1.	1.	1.	1.	1.
	.07	.05	.05	.05	.09	.08	.07
(PDIGST)	.8	.8	.8	.8	.85	.9	.9
	.9	.8	.8	.8	.8	.85	.95
	.95	.95	.95	.95			
(PESCAP)	.5	.5	.5	.5	.5	.5	.5
	.5	.5	.5	.5	.5	.3	.3
	.3	.3	.3	.3			
(PEVACT)	.24E-04	.18E-04	.16E-04	.16E-04	.16E-04	.16E-04	.16E-04
	.16E-04	.24E-04	.20E-04	.20E-04	.16E-04	.16E-04	.16E-04
	.16E-04	.16E-04	.16E-04	.16E-04			
(PFASST)	8.	16.	35.	50.	75.	100.	100.
	100.	100.	8.	16.	35.	50.	75.
	100.	100.	100.	100.			

Table VI. List of initial conditions of dependent variables estimated for May 20, 1972. Weights are in gm and lengths are in m.

Life stage	Numbers	Current median weight	Mean length	Weight stomach contents	Lower length	Upper length	Maximum median weight
1	4.6E+09	.008	.01	.001	.0085	.0115	.007
2	0.	0.	0.	0.	0.	0.	0.
3	20.4E+06	14.	.1	.25	.085	.115	13.75
4	6365.E+03	40.	.145	1.25	.115	.175	38.75
5	95.E+03	115.	.21	2.15	.17	.25	122.
6	290.E+03	135.	.225	2.5	.2	.25	150.
7	625.E+03	225.	.265	3.	.24	.29	245.
8	285.E+03	230.	.271	4.	.24	.302	260.
9	405.E+03	230.	.271	4.	.24	.302	260.
10	30.E+06	.008	.01	.001	.0085	.0115	.007
11	0.	0.	0.	0.	0.	0.	0.
12	1.04E+06	34.2	.155	1.2	.145	.165	33.
13	38.02E+04	157.5	.26	2.5	.245	.275	155.
14	4.865E+04	313.5	.33	3.5	.31	.35	320.
15	32.5E+04	420.	.375	4.2	.35	.4	470.
16	2.5E+05	480.	.39	5.	.36	.42	530.
17	1.E+05	565.	.415	6.	.38	.45	635.
18	15.E+04	680.	.46	10.	.38	.54	865.
19	7.87E+13	.8E-05	.25E-03				
20	6.46E+13	.7E-04	.0005				
21	.5E+12	.065	.005				

Table VIII. List of values of dependent variables simulated for May 19, 1973.
Weights are in gm and lengths are in m.

Life stage	Numbers	Current median weight	Mean length	Weight stomach contents	Lower length	Upper length	Maximum median weight
1	.1416E+10	.7624E-02	.7193E-02	.2178E-02	.7113E-02	.7273E-02	.5446E-02
2	0.	0.	0.	0.	0.	0.	0.
3	.5363E+07	.9564E+01	.9784E-01	.5414	.9203E-01	.1037	.9023E+01
4	.2458E+07	.1044E+03	.1872	.5888E+01	.1798	.1946	.9851E+02
5	.1665E+07	.1240E+03	.2174	.8269E+01	.1982	.2366	.1382E+03
6	.2822E+05	.1216E+03	.2230	.8834E+01	.1959	.2500	.1472E+03
7	.1226E+06	.2420E+03	.2730	.1641E+02	.2435	.3024	.2751E+03
8	.3559E+06	.2475E+03	.2706	.1439E+02	.2451	.2961	.2616E+03
9	.2882E+06	.2188E+03	.2710	.1170E+02	.2400	.3020	.2600E+03
10	.4897E+07	.7920E-02	.7281E-02	.2263E-02	.7162E-02	.7400E-02	.5657E-02
11	0.	0.	0.	0.	0.	0.	0.
11	.1691E+06	.2608E+02	.1360	.1467E+01	.1263	.1458	.2540E+02
12	.2269E+06	.8512E+02	.2172	.4543E+01	.2084	.2259	.9515E+02
13	.1348E+06	.2312E+03	.2916	.8891E+01	.2748	.3085	.2223E+03
15	.1029E+05	.3923E+03	.3726	.1874E+02	.3500	.3952	.4684E+03
16	.1268E+06	.5288E+03	.3892	.1585E+02	.3633	.4151	.5282E+03
17	.8699E+05	.5422E+03	.4132	.1588E+02	.3814	.4449	.6353E+03
18	.5531E+05	.6735E+03	.4600	.1730E+02	.3800	.5400	.8650E+03
19	.9352E+14	.8000E-05	.2500E-03	0.	.2500E-03	.2500E-03	.8000E-05
20	.1028E+15	.7000E-04	.5000E-03	0.	.5000E-03	.5000E-03	.7000E-04
21	.3345E+12	.6500E-01	.5000E-02	0.	.5000E-02	.5000E-02	.6500E-01

VITA

The author of this paper was born in Eldora, Iowa, on March 18, 1949. He was raised on a farm and attended the New Providence Community Schools where he graduated from high school in 1967. The author attended Iowa State University from 1967 to 1971 and received a B. S. degree in Fish and Wildlife Biology in November, 1971. While at this institution, he was a resident advisor in the dormitory system and became members of Gamma Sigma Delta and the American Fisheries Society. On August 16, 1970, the author married the former Miss Arlys Vivian Knowles of Alden, Iowa. From 1972 to 1976, the author attended Utah State University where he became members of Xi Sigma Pi and the American Society of Limnology and Oceanography. He received a M. S. degree in Fisheries Science in May, 1976. From 1976 to the present, the author has been in residence at the Virginia Polytechnic Institute and State University.



David R. Bernard

A TEST OF THE VARIABLE NATURE OF
DENSITY-DEPENDENT MORTALITY IN
FISH POPULATIONS

by

David R. Bernard

(ABSTRACT)

Veracity of past analyses on the impact of impingement and entrainment of fish in power-plant cooling systems was questioned. Density-dependent dynamics were hypothesized as variable, not constant, making previous analyses based on constant density-dependent or density-independent mortality in error. This hypothesis was tested with a simulation model based on complex biological and behavioral mechanisms for individual fish, thereby forgoing the need for assuming the kind of mortality exhibited by a fish community prior to the analysis. Yellow perch and walleye in Oneida Lake, New York, were focal points of this test, and data taken in 1972 from Oneida Lake were used to validate the model. Model experiments consisted of varying turbidity, water temperature, impingement and entrainment, and abundance of young perch and walleye. Under most conditions in the experiments, individual growth was unchanged, and predators

maintained a high frequency of full stomachs. Exceptions were that water temperature influenced growth and that adult walleyes went hungry when fry of both species were limnetic. Mortality of young perch proved depensatory and that of young walleye density-independent. Mortality of walleye fry was inversely influenced by abundance of young perch. High levels of turbidity greatly enhanced fry survival for both species. Impingement and entrainment reduced survival of young perch and young walleye by 43 and 30 percent, respectively. Expected losses due to density-independent impingement and entrainment were 3 and 2 percent. Depletion of young perch occurred because of their depensatory mortality; depletion of young walleye occurred because their survival was related to abundance of young perch. High abundance of young perch and high turbidity dropped mortality to density-independent levels of about 3 percent. These mitigating effects of turbidity and high abundance showed that mortality could shift from density-dependent to density-independent dynamics. The relationship between abundance of young perch and mortality of young walleye meant that no analysis based on a single species could properly assess impacts of impingement and entrainment in Oneida Lake. The conclusion was that density-dependent and density-independent mortality are variable and are

influenced by certain conditions: 1) compensatory mortality is based on density-dependent growth, 2) density-independent and compensatory mortality are based on density-independent growth, 3) density-independent mortality occurs when predation removes insignificant numbers of prey, and 4) compensatory mortality occurs when predators remove large numbers of prey.