PRELIMINARY ESTIMATES OF LOSS OF JUVENILE ANADROMOUS SALMONIDS TO PREDATORS IN JOHN DAY RESERVOIR AND DEVELOPMENT OF A PREDATION MODEL

Interim Report
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by

Bruce E. Rieman,
Raymond C. Beamesderfer,
and
Anthony A. Nigro

Oregon Department of Fish and Wildlife
17330 SE. Evelyn Street
Clackamas, Oregon 97105

Steven Vigg,
Hal C. Hansel,
and
Douglas E. Palmer

U.S. Fish and Wildlife Service
Willard Field Station
Cook, Washington 08605

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ABSTRACT

We made preliminary estimates of the loss of juvenile salmonids to predation by walleye, Stizostedion v. vitreum, and northern squawfish, Ptychocheilus oregonensis, in John Day Reservoir in 1984 and 1985 using estimates of predator abundance and daily prey consumption rates. Preliminary-estimates may be biased and may be adjusted as much as 30%, but indications are that predation could account for the majority of unexplained loss of juvenile salmonids in John Day Reservoir.

Total loss was estimated at 4.1 million in 1984 and 3.3 million in 1985. Northern squawfish consumed 76% and 92% of these totals, respectively. The majority of loss occurred in mid reservoir areas, but loss in a small area, the boat-restricted zone immediately below McNary Dam, was disproportionately large. Peaks in loss in May and July corresponded with peaks in availability of salmonids.

Estimated mortality from predation for April through June in 1984 and 1985 was 9% and 7% respectively. for chinook salmon. Oncorhynchus tshawytscha, and 16% and 15% for steelhead, Salmo qairdneri. Mortality was variable with time but tended to increase over the period of migration. Mortality of chinook was estimated at 26% to 55% during-July and August.

A model of predation in John Day Reservoir is outlined. The model includes a predation submodel that can calculate loss from predator number and consumption rate; a population submodel that can re?ate predator abundance and population structure to recruitment, exploitation, natural mortality and growth; and a distribution submodel that can apportion predators among areas of the reservoir over time. Applications of the mode! are discussed for projecting expected changes in predation over time and identifying management alternatives that might limit the impact of predation.

INTRODUCTION

Construction of dams and reservoirs in the Columbia River basin has had a major adverse effect on survival of juvenile anadromous salmonids migrating through the system (Raymond 1969, 1979; Ebe! 1977). Estimates of mortality range between 15% and 45% (Sims and Ossiander 1981) at individual projects. A significant portion of the estimated mortality can be attributed directly to passage at the dams (Schoneman et al. 1961), but a major portion of the mortality has been unexplained. Predation has been proposed as a significant component of the unexplained mortality (Raymond 1979; Mullan 1980; Uremovich et al. 1980), but has not been previously quantified in any reservoir.

Because of the significance of unexplained loss, the Bonneville Power Administration funded this project to estimate the magnitude of juvenile salmonid loss from predation by resident fish in John Day Reservoir. The project also developed secondary objectives to describe the dynamics of predation and to identify potential measures for controlling predation. The project has been a cooperative effort between the Oregon Department of Fish and Wildlife (ODFW) and the U.S. Fish and Wildlife Service (USFWS). ODFW has been responsible for describing abundance and population dynamics of predators, while USFWS has been responsible for describing food habits and prey consumption rates of the predators. Estimates of salmonids lost to predation are made as the product of predator abundance and consumption rate.

If predation is a major component of salmonid mortality, the dynamics of predation should be an important management concern. A description of changes in predation resulting from changes in predator populations, prey populations, and environmental characteristics could identify alternatives for control. Although uncertainties in the data and estimates may limit our ability to predict actual losses under future conditions, it is possible to examine the dynamics of predation and the relative influence of changes in predator abundance, distribution, population dynamics, and prey consumption on salmonid loss. Modeling provides a means of organizing information developed in this study and available from other sources, to examine the dynamics of predation. A model might, for example, describe the relative magnitude of loss expected if a major predator was eliminated from a part of the reservoir, or the relative change in loss expected over time with fluctuations in year-class strength of predators.

The estimates of loss and the construction of a model require the integration of information from the ODFW and USFWS projects. Detailed annual progress reports are available for these projects (Gray et al. 1984, 1986; Nigro et al. 1985a, 1985b, 1986b; Willis et al. 1985; Palmer et a?. 1986, Poe et al. 1987; Beamesderfer et al.

1987). This report has been prepared to summarize efforts to integrate these data. Objectives are as follows:

1. Describe the methodology for integrating predator abundance and prey consumption data, and provide preliminary estimates of loss and mortality of juvenile salmonids. Describe the temporal and spatial variation likely in loss and mortality.

2. Develop a model to examine the dynamics of predation in John Day Reservoir. Identify submodels to be developed and parameters to be estimated from existing data. Discuss potential application of the model.

3. Identify specific tasks for completion of the model.

Objectives 1 and 2 are addressed in the body of this report. Objective 3 is addressed in Appendix A.

Upon completion of the project, loss and mortality in 1983, 1984, 1985 and part of 1986 will have been estimated. Our final analysis will also describe the relative importance of four predators; walleye, northern squawfish, channel catfish, Ictalurus punctatus, and smallmouth bass, Micropterus dolomieu. At this time data are complete only for walleye and northern squawfish in I984 and 1985. Although total loss will be adjusted by the inclusion of other predator species, walleye and northern squawfish appear to be the most important predators. We anticipate that changes caused by the inclusion of other predators will be minor. Estimates of prey consumption rate also are preliminary and dependent upon completion of evacuation rate-temperature relations. Current approximations of these relations may change, resulting in some adjustment of the loss estimates presented here. However, based on analysis of the assumptions made in calculation changes should not exceed 30% of existing estimates.

METHODS

Estimates of Loss and of Mortality

Loss of juvenile salmonids to predators was calculated as the product of predator numbers, estimated by ODFW, and individual consumption rates, estimated by USFWS as:

$$Z_t = N_t C_t$$

where

Z_t = total number of salmonids consumed by predators during year t,

N_t = numbers of predators in the population during year t (estimated by ODFW), and

C_t = number of salmonids consumed per predator in year t (estimated by USFWS).

Separate estimates of loss were calculated by predator species (i), predator size class (j), month (k) and reservoir area (1), during the period of salmonid outmigration (April-August) to minimize any nonrandom sampling bias and to clarify the temporal and spatial distribution of loss. The separate estimates were summed for an estimate of total loss:

$$Z_t = \sum_i \sum_j \sum_k \sum_l Z_{ijkl}$$

Reservoir-wide predator abundance was estimated for two size classes of walleye and northern squawfish in 1984 and 1985 using a multiple mark and recapture method (Nigro et al. 1985c). Monthly predator abundance was estimated by subtracting removals by sampling and harvest by anglers (Nigro et al. 1985c). Size classes correspond with those used in abundance estimates based on vulnerability to capture (Beamesderfer et al. 1987).

Predator number was apportioned among five reservoir areas (Figure 1) based on differences in catch per unit effort (CPUE) of gear in each month and relative sizes of the reservoir areas. Catch rates were compared statistically among areas to verify that observed differences were not solely due to sampling variation (Beamesderfer et al., 1987). From this analysis the relative densities estimated at Arlington, at Irrigon, and at McNary Dam tailrace were expanded to represent larger sections of reservoir of similar habitat. Sampling in the John Day forebay and the McNary Dam boat restricted zone (BRZ) was considered representative only of those areas (Figure 1). The size of each area, based on reservoir surface area at low pool level, was used to weight the relative

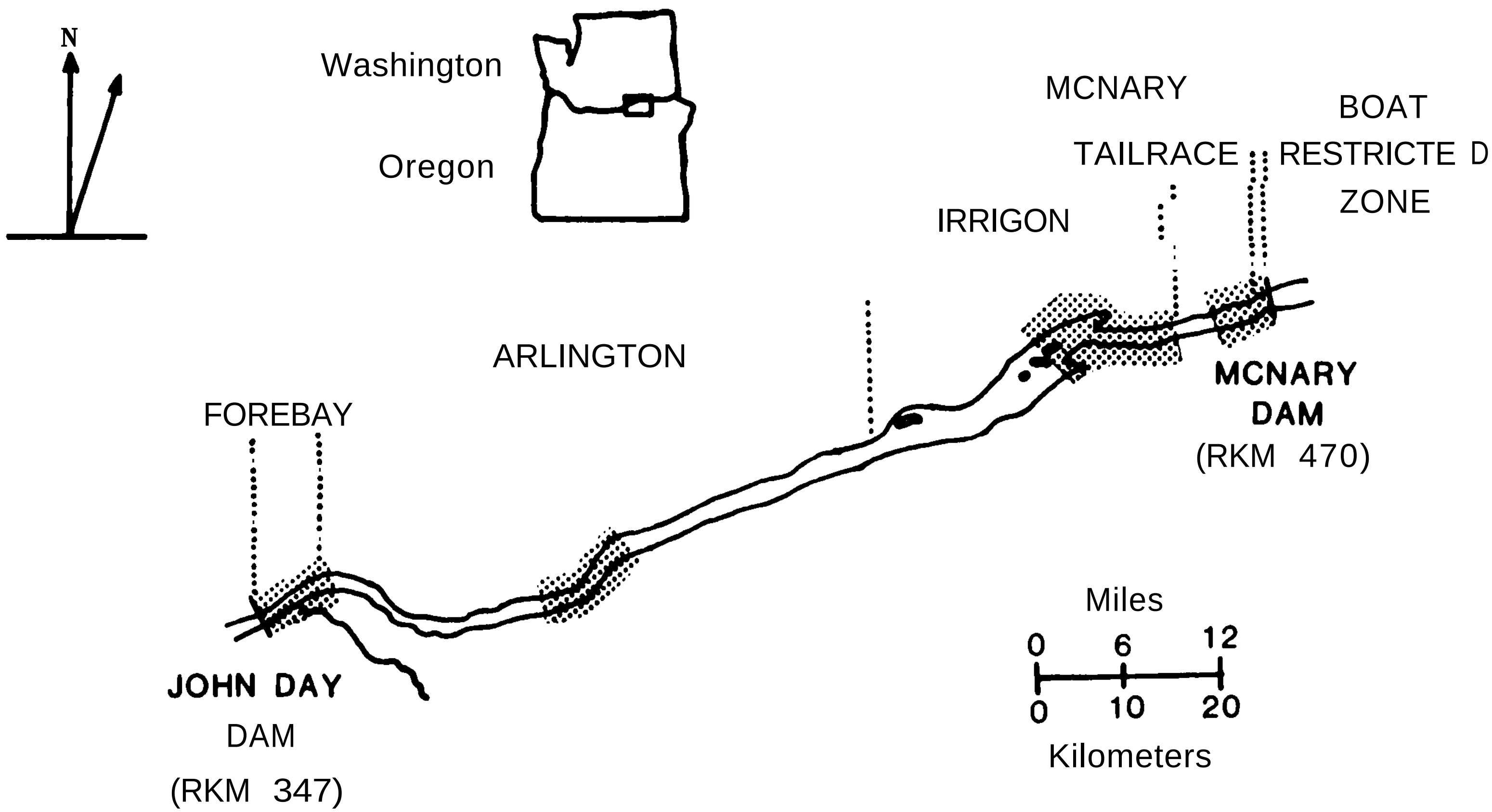

Figure 1. **Sampling areas (shaded) and areas assumed to be represented by sampling in John Day Reservoir in 1984 and 1985.**

density of predators and to calculate the proportion of the population in each area (Appendix B).

Daily consumption of salmonids by predators was estimated empirically based on the technique of Swenson (1972), which integrates stomach content data with the evacuation rate relationship of each predator. The methodology is explained in more detail by Palmer et al. (1986).

Predators of each size class in each reservoir area were sampled in April, May, June, and August. Sampling sufficient to estimate consumption in July was completed only for northern squawfish in 1985. Consumption rate could not be calculated for each size-area cell for each month because many cells included few or no samples. To accommodate this problem, samples from adjacent areas or size classes were pooled when no statistical differences could be detected. Thus, for an estimate of consumption in any area, a combined sample from all adjacent areas in which consumption was not significantly different was used (Appendix Tables C-l and C-Z). Statistical differences in salmonids per predator between areas and between size classes were identified using two-way analysis of variance and Tukey pairwise multiple comparisons (SAS Institute Inc. 1985). Data were log transformed to meet the assumption of normality (Moyle and Lound 1960; Elliott 1977). Direct statistical comparisons of daily consumption rate could not be made, but differences in the occurrence of salmonids in predator stomachs should correspond to differences in daily consumption when evacuation times are similar. Temperature differences between months and the resulting differences in evacuation rate necessitated treating each month separately. Consumption in July of 1984 was approximated by assuming the same proportion between July and a mean of June-August consumption as observed in 1985.

Total estimated loss of juvenile salmonids to each predator species was calculated on a monthly basis and subsequently partitioned among salmonid genera (salmon and trout) based on the proportion of identified prey in the stomach contents (Appendix Table C-3). We assumed that all salmon identified in the stomach samples were chinook and that all trout were steelhead.

Mortality rate of salmonids from predation was calculated from prey-specific estimates of loss and estimates of salmonid numbers passing into John Day Reservoirs as:

$$A_{kp} = \frac{Z_{kp}}{PAS_{kp}}$$

Where

A_{kp} = Total annual mortality rate as a proportion of total abundance of each salmonid (p) in each month (k),

Z_{kp} = The estimated loss of each salmonid prey (p) in each month (k) for a predator, and

PAS_{kp} = The estimated passage of each salmonid prey (p) during each month (k)

Mortality for the entire run of salmonids was estimated in the same fashion using loss and passage estimates totaled for the season.

$$\frac{\sum_{k}\sum_{p} Z_{kp}}{\sum_{k}\sum_{p} PAS_{kp}}$$

To estimate the number of chinook salmon and steelhead that entered John Day Reservoir during 1984 and 1985, we estimated daily passage at McNary Dam using the collection efficiency-powerhouse flow relationships developed by Sims et a!. (1984). The expansion estimates daily passage of age 1 chinook salmon and steelhead at McNary Dam by dividing the number of fish collected at the juvenile salmonid collection facility by the estimated collection efficiency for that species on that day. Collection efficiency was estimated as a function of powerhouse discharge level. We subtracted the number of juvenile salmonids transported from the McNary collection facility on each day from the daily passage estimates to obtain daily estimates of age i salmon chinook and steelhead entering John Day Reservoir. Monthly and annual estimates of chinook salmon and steelhead that entered the reservoir were obtained by summing daily estimates, and adding the number of hatchery fish released directly into the reservoir {Appendix Table d). Passage of age 0 chinook salmon was estimated in the same way. A collection efficiency-powerhouse flow relationship has not been developed for age 0 chinook. We assumed that the relationship for age 1 chinook was apprcpriato. Further work by the National Marine Fisheries Service should clarify the relationship for future estimates. Estimates of sockeye and coho salmon numbers were not included in these preliminary estimates.

To describe the precision of final loss and mortality estimates, we will approximate the standard error of each from variances derived in estimates of abundance, prey consumption, proportions of specific prey in the gut, and passage. The approximations have not been completed for prey consumption rate so preliminary data presented in this report do not include approximations of the standard error associated with each estimate.

The Model

A model of predation and predator populations was conceptualized after Holling (1966) Levins (1966) Orlob (1975), and Overton (1977). Models or protions of models corresonding to each submodel identified in our system were selected (1) to incorporate all regulating factors that could be described to, as realistically as possible, represent the biological processes involved, (2) to be consistent with the method used to estimate losses, (3) to minimize dependence on data from sources other than John Day Reservoir and (4) to be mathematically tractable. The components of each submodel were identified and defined using general mathematical terms.

Activities in constructing the model were detailed following descriptions outlined by Walters (1971), Orlob (1975), and Overton (1977). Tasks in constructing the model include quantifying variables describing the state of the system of interest at any time (state variables), identifying variables affecting but not affected by the system (driving variables), quantifying relationships between state and driving variables, validating each component individually, assembling submodels, and calibrating submodels. Information needs of each activity were compared with data collected by ODFW and USFWS to determine where supplemental information was needed.

RESULTS

Estimates of Loss and of Mortality

Salmonid Loss

Total loss of juvenile salmonids to predation by northern squawfish and walleye was estimated at 4.1 million fish in 1984 and 3.3 million in 1985 (Table 1). We estimated for the April-June period that northern squawfish accounted for 76% of the total loss in 1984 and 92% of the total loss in 1985.

Despite being less abundant large northern squawfish (>375 mm) consumed more salmonids than did small northern squawfish (250-375 mm) because of a higher prey consumption rate. In 1985 we estimated 1.2 million salmonids were lost to small northern squawfish, and approximately 2.0 million were lost to northern squawfish larger than 375 mm. Large walleye (>500 mm) also ate more salmonids than did small walleye (250-500 mm), but this was a result of larger fish being more abundant. Consumption of salmonids by walleye did not differ with predator size.

The estimated loss was unevenly distributed throughout the reservoir in both years (Appendix Tables E-l and E-2). The largest losses were estimated for the mid reservoir areas of Arlington and Irrigon. A disproportionately large part (19%-35%) of the loss caused by northern squawfish occurred in the BRZ, which accounted for only 0.3% of the reservoir area (Appendix Table E-2). On a per mile basis, loss in the BRZ was more than ten times that in all other portions of the reservoir (Figure 2). The higher loss in the BRZ was due to higher concentrations of northern squawfish (relative densities 3 to 30 times that in other areas) and higher consumption rates (4 to 20 times that in other areas) (Appendix Tables B-2 and C-2).

Total loss varied by month in both years. Estimates were low in April,increased in May, and declined in June (Table 1). Loss from April through June was approximately 1 million salmonids in 1984 and 900,000 in 1985. July data, with an actual estimate available only for northern squawfish in 1985, showed a dramatic increase to the highest loss of the season. Estimates of loss declined again in August.

Chinook were the dominant salmonid consumed by predators in 1984 and 1985. During the period April-June, we estimated that five to seven times as many chinook as steelhead were lost to predators (Table 1). Loss of specific prey varied monthly. Loss of chinook in April and May probably included many age 1 fish because they dominated the run during that time (Appendix Table D).

Table 1. Estimated loss of juvenile chinook salmon and steelhead to predation by walleye and northern squawfish in John Day Reservoir, April through August 1984 and 1985.

Year, Month	Chinook Salmon	Steelhead	Total Salmonids
1984			
April	70,000	20,000	90,000
May	55,000	100,000	650,000
June	190,000	40,000	230,000
July	--	0[b]	--
August	440,000	0	440,000
April-June Total	810,000	160,000	970,000
April-Aug Total	3,890,000[a]	160,000	4,050,000
1985			
April	50,000	0	50,000
May	500,000	50,000	550,000
June	220,000	50,000	270,000
July	2,290,000	0[b]	2,290,000
August	110,000	0	110,000
April-June Total	780,000	100,000	880,000
April-Aug Total	3,180,000	100,000	3,280,000

[a]Approximated by assuming July consumption rates similar to 1985.

[b]Assumed to be zero because few steelhead were believed present in the reservoir.

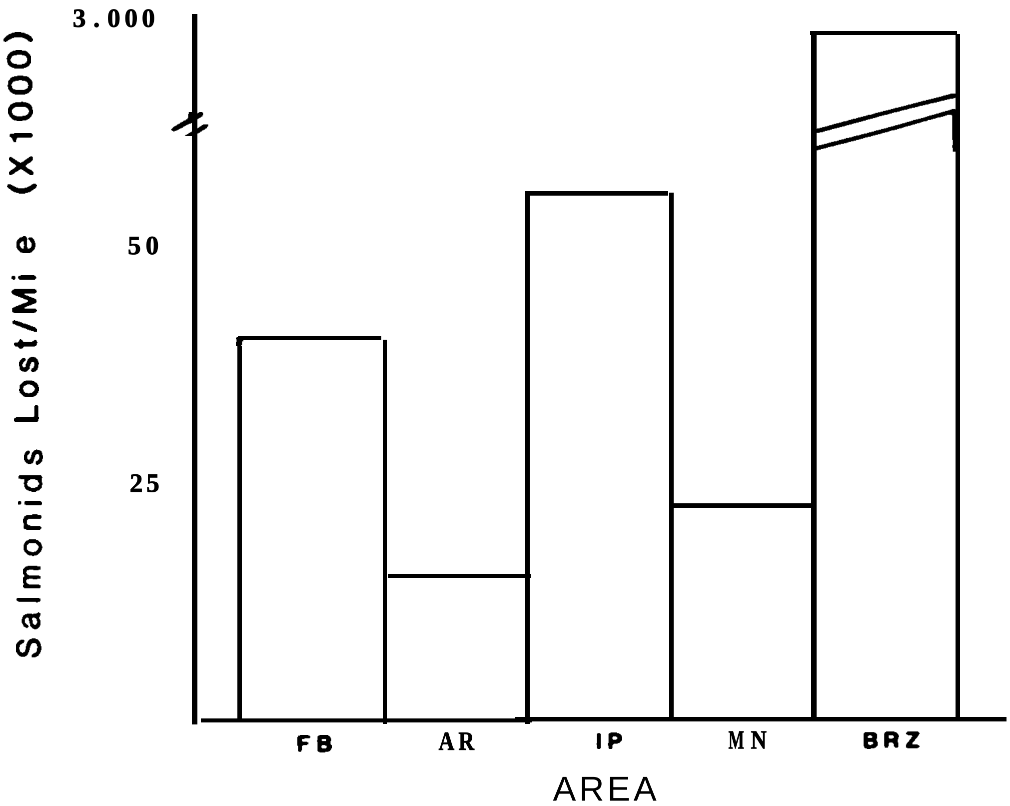

Figure 2. Estimated loss of juvenile salmonids to predators per mile of reservoir in five areas of John Day Reservoir in 1985.

We assumed all loss in July and August was age 0 chinook because few steelhead and age 1 chinook were believed to be in the system during that period.

In general, comparisons of salmonid passage estimates with loss estimates for chinook and steelhead showed that consumption of salmonid prey varied with abundance of prey in the system (Figure 3). Loss of chinook and of steelhead peaked in May coinciding with a peak in passage of age 1 chinook and steelhead. Our July data, limited only to northern squawfish for 1985, showed a second peak in the loss of chinook associated with an increase in passage of age 0 fish.

Salmonid Mortality

Estimates of salmonid mortality ranged from 0.04 to 0.55 for chinook salmon and 0 to 0.50 for steelhead. Estimated mortality for chinook was much higher in July or August than earlier months (Table 2). Estimated mortality of steelhead was highest in June and dropped to 0 in July because few steelhead were present in the reservoir. Estimated mortality of all chinook migrating during the period April-June was similar between years, but total mortality estimated for steelhead was 50% higher in 1985 than 1984 (Table 2).

The Model

A model of the predator prey system was conceptualized in three components or submodels: a predation submodel, a predator population submodel, and a predator distribution submodel.

Predation Submodel

In the predation submodel as in the preliminary estimates loss of juvenile salmonids to predators during a year will be calculated as the product of predator number and prey consumption rate (Figure 4). Separate calculations of loss are made for each predator species, predator size class, area of the reservoir and month. Total loss is estimated as the sum of the cell specific loss estimates. Prey consumption rate for each combination of predator species, predator size-class, reservoir area, and month can be projected as a function of prey abundance and temperature. The form of this functional response is currently being defined from observations in all years of study.

Predator Population Submodel

The population submodel relates predator abundance to regulating factors in a matrix format adapted from the Leslie matrix (Leslie 1945, Vaughan et al. 1983). A new population size

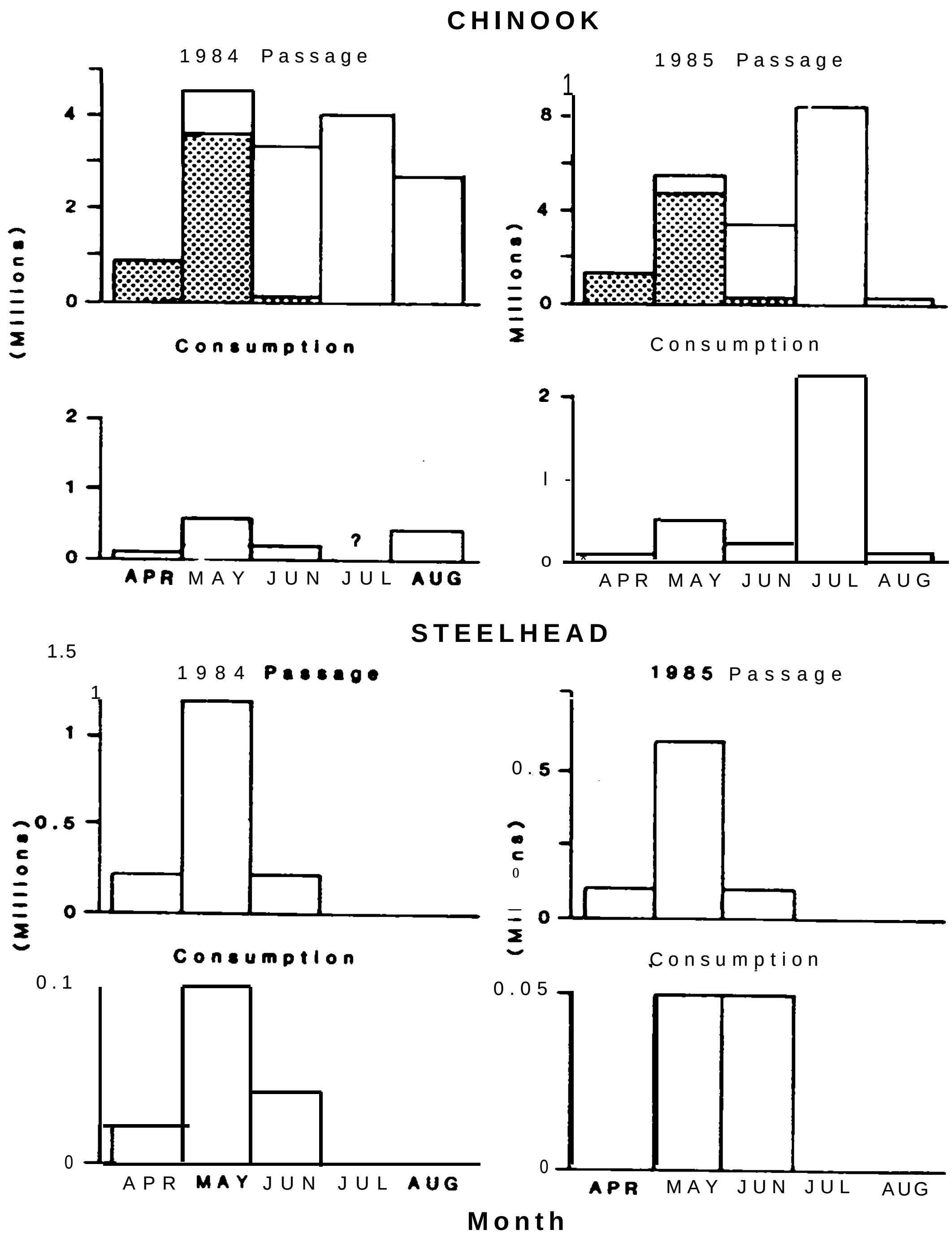

Figure 3. Estimated passage and consumption of juvenile chinook and juvenile steelhead in John Day Reservoir in 1984 and 1985. Passage of age 1 chinook is shown in shaded areas. Note difference in scale between steelhead passage and consumption.

Table 2. Estimated mortality of juvenile salmonids passing McNary Dam[a] resulting from predation by walleye and northern squawfish in John Day Reservoir, April through August 1984 and 1985.

Year, Month	Chinook Salmon	Steelhead
1984		
April	0.07	0.07
May	0.12	0.09
June	0.06	0.19
July	--	0[b]
August	0.26	0
April-June Total	0.09	0.10
1985		
April	0.04	0.02
May	0.09	0.08
June	0.07	0.50
July	0.27	0
August	0.55	0
April-June Total	0.07	0.15
April-Aug Total	0.16	0.15

[a]Passage estimates do not account for losses directly associated with the dam.
[b]Assumed to be zero because few steelhead were believed present in the reservoir.

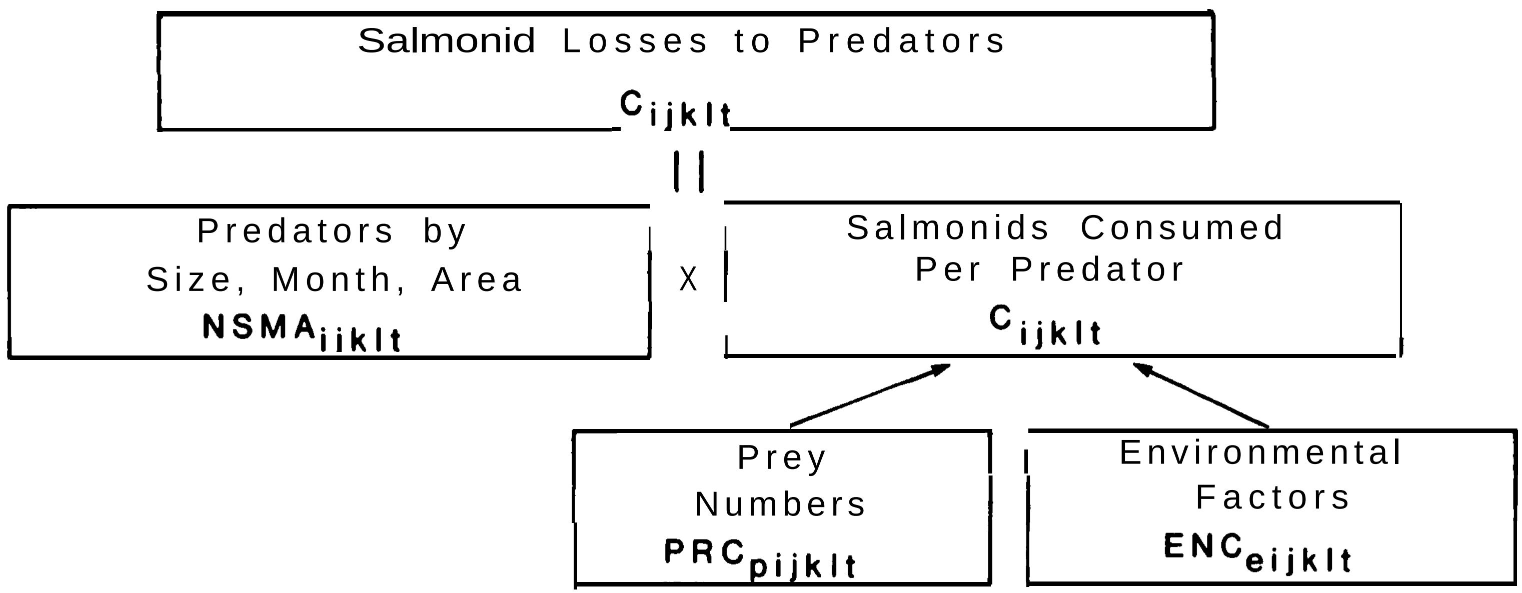

Figure 4. Conceptualization of the predation submodel.

can be calculated from inputs of original abundance, recruitment, and mortality (Figure 5).

The number of predators in each age class at the beginning of any year includes individuals surviving from the preceeding year. Survivors can be estimated as the product of a starting population and an annual survival rate. Both initial predator number and annual survival rate will be age specific and can include harvest by anglers or removals undertaken as part of a predator control program.

In addition to individuals surviving from the previous year, the population will include newly recruited individuals (births). Recruitment to the population is an input but can be calculated as a function of environmental conditions at the start of a year or in the preceding year or as a function of parental stock size. We are currently analyzing data on year-class strength of predators in an effort to identify environmental factors that influence recruitment. If that work does establish any significant relationships, those functions could be incorporated into the model at this level.

The number of predators of each age at the beginning of each month subsequent to the start of the year will include those surviving from the previous months. This number will be estimated as the product of predator number in the preceding month and a month specific survival rate. April through August, the period of salmonid outmigration, will be the period of analysis. Monthly survival, like annual survival, is age specific. In the period April through August, monthly survival will be assumed to be affected solely by exploitation.

Age-specific predator number will be converted to size-specific number with a von Bertalanffy age-length relationship, which describes fork length as a function of age. Average length of each age class will be projected from the relationship and used to place the number of predators in each age class in the appropriate size class.

Predator Distribution Submodel

The distribution submodel will apportion size-specific predator number among subsections of the reservoir in each month of interest. This submodel will connect the population and predation submodels, organizing the population submodel output (size-specific predator numbers) into a form suitable for input into the predation submodel (area-specific predator numbers) (Figure 6). Area-specific numbers will be calculated as the product of size specific numbers and the fraction of predators of a given size that occur in an area. Predator distribution each month can be an input or may be related to predator number, prey number and environmental conditions. We are currently investigating relations that may explain predator distribution and could be used as functions in the model.

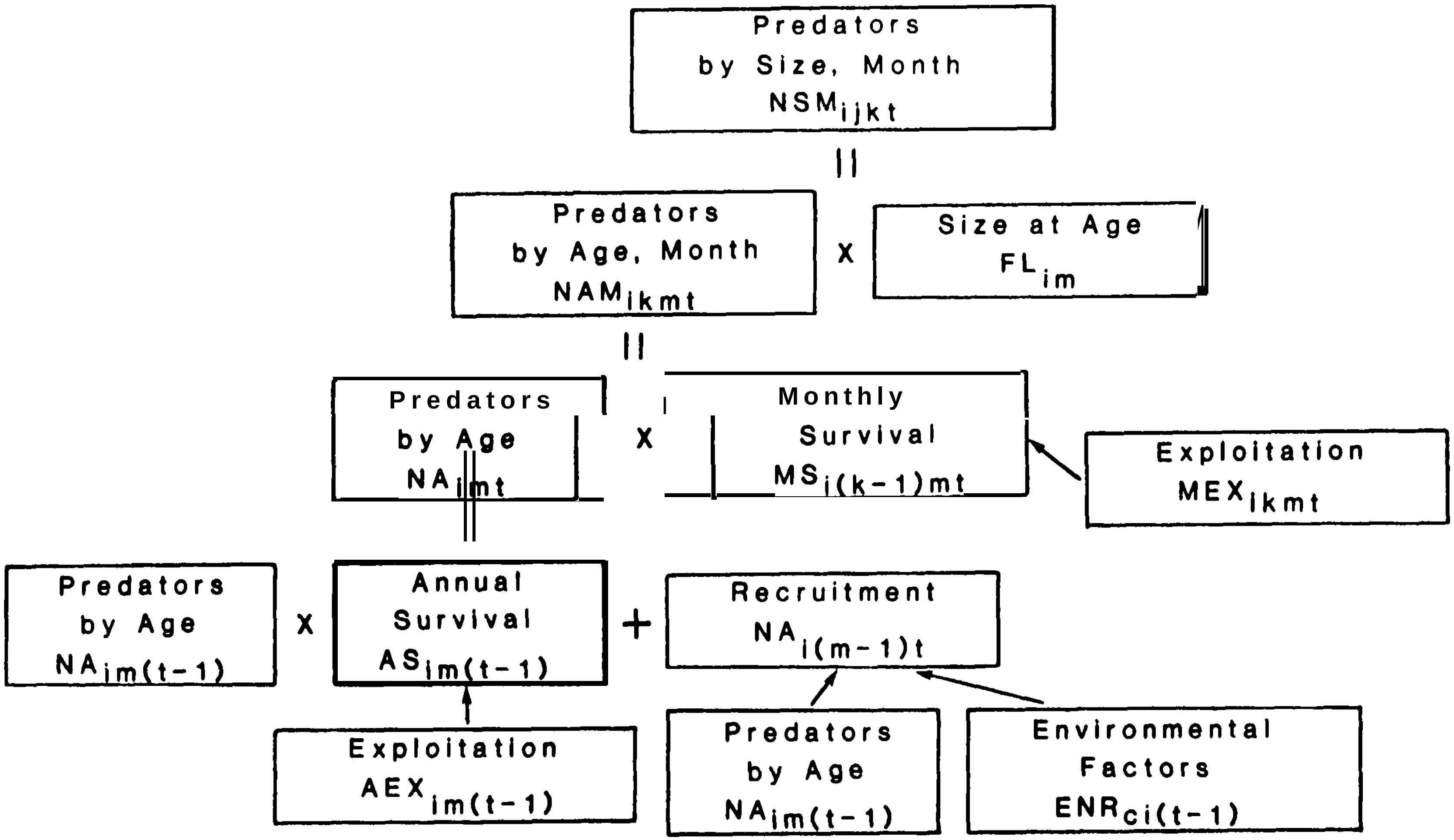

Figure 5. Conceptualization of the predator population submodel.

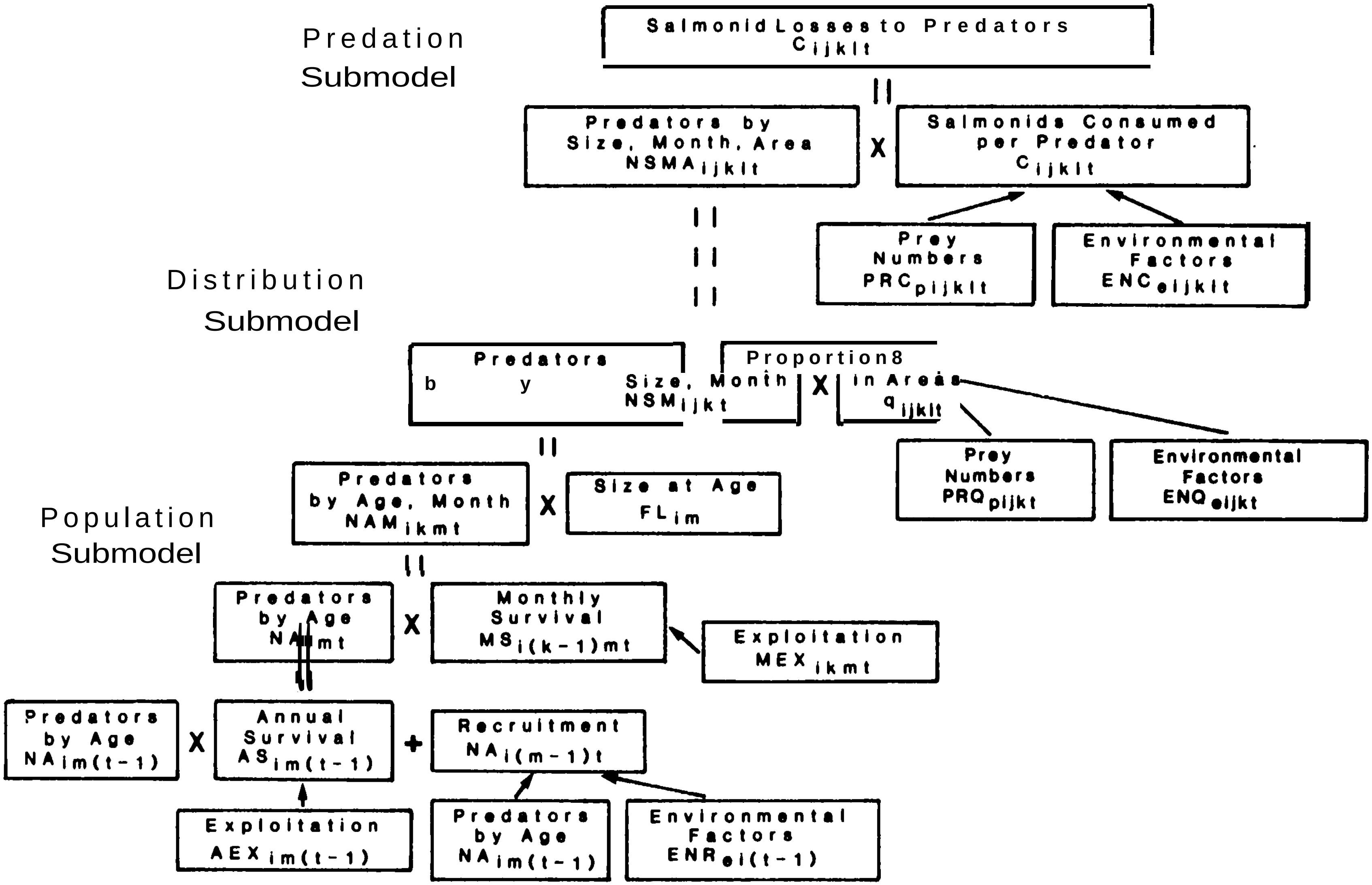

Figure 6. Conceptualization of the distribution submodel linking the predation submodel and and predator population submodel.

DISCUSSIDN

Estimates of Loss and of Mortality

Final loss estimates will differ from those presented here. Consumption estimates, predator population estimates and passage estimates incorporate a number of assumptions. Although we have made an effort to test and support those assumptions (Nigro et al. 1985c USFWS unpublished), some uncertainty remains. Undoubtedly some bias is associated with each of the estimates. Predator population estimates may be biased by assumptions of vulnerability tag mixing, tag loss and delayed handling mortality (Beamesderfer et al. 1987). Consumption estimates may be biased by small sample size in some time periods, assumptions regarding calculation of evacuation rates and assumptions regarding the expansion of samples in a restricted area to represent much larger areas. Passage estimates may be biased by assumptions in collection efficiency, misidentification of age 0 and age 1 chinook and failure to include sockeye and coho salmon. Further work will evaluate the relative influence of each assumption and better define the direction and potential magnitude of each bias (Beamesderfer et a!. 1987).

We do believe the preliminary estimates are conservative. Any consistent bias in both our population and consumption rate estimates should be negative (Beamesderfer et a!. 1987; Poe et a!. 1987). Potential bias in estimates of salmonids exposed to predators is probably oositive; passage estimates at McNary Dam represent numbers of fish arriving at the dam, but do not account for fish lost while passing the dam. Although the magnitude of each bias is uncertain, a significant influence by any one would result in an underestimate of loss and mortality.

Despite the uncertainty associated with these loss and mortality estimates, predation does appear to be important. Tota! mortality has been estimated to range between 15% and 45% for salmonids passing each project (Sims and Ossiander 1981). Approximately half of that can be attributed directly to the dams while remaining mortality within each reservoir is unexplained Our data show that predation could account for much, if not most, of the unexplained loss.

Our work also suggests that losses and mortality are dynamic. Because consumption rate by northern squawfish increased with size, the relative size structure of the northern squawfish population may have a significant influence on the magnitude of loss. Previous results have shown that year-class strength of northern squawfish may vary several fold (Nigro et a!. 1985c). As strong and weak year classes move through the population, relative abundance of small and large fish will vary. Loss of salmonids will also vary from year to year as the relative abundance of small and large northern squawfish changes.

In addition to variation in loss likely with variation in predator recruitment, we found the loss was unevenly distributed throughout the reservoir. The large loss associated with the BRZ may represent an opportunistic response by predators that have concentrated in an area where prey are particularly vulnerable. The more subtle weighting of loss to the upper and mid reservoir is probably related to distribution of predators in favorable habitat. John Day Reservoir tends to grade from a complex system of embayments, shoals, and cover in mid reservoir reaches to a relatively simple, deep channel in the lower reservoir (Hjort et al. 1981). Progressing downstream, availability of preferred habitat, and consequently abundance of predators, appears to decline. The implication is that mortality from predation is not strictly a function of reservoir size, but rather the quality and distribution of habitat. Other reservoirs in the Columbia River system, even though smaller than John Day Reservoir, may have predation losses of similar a magnitude if the distribution of predators associated with the dam, the habitat availability, and prey availability are also similar.

Loss also varied by month, and tended to vary with prey availability. The increase in loss with increased prey availability suggests that the predators exhibited a functional response (Holling 1965; Murdoch and Oaten 1975; Peterman and Gatto 1978). The nature of that response could explain relative differences in loss between years. Consumption of prey may increase with availability of prey but often at a decreasing rate (Peterman and Gatto 1978). As a result predators could consume a smaller proportion of the total when abundance is high and a larger proportion when abundance is low. Mortality from predation may be depensatory. Our data for 1984 and 1985 are consistent with such a phenomenon. Estimated mortality of steelhead in 1984 was 10% with an estimated passage of 1.6 million fish, and 15% in 1985 with passage of 0.6 million fish. Loss of chinook salmon showed a similar trend though relative differences were less. If predators do impose a depensatory mortality in John Day Reservoir, mortality could increase substantially as run size declines or increasing numbers of fish are transported. Conversely, enhanced runs may experience a decline in mortality.

In general mortality was much higher late in the season than early. Although our data is limited for July it does indicate that predation is much more important for age 0 chinook than age 1 chinook or any group of fish moving after May. Rising temperature and corresponding increase in evacuation rate and energy demand of the predators accounts for some of the increased consumption. As the water warms predators become more active, grow faster, and require more food (Webb 1978). This implies that any delay in migration could subject fish to higher predatory mortality. Reservoirs high in the system may also have lower mortality than lower reservoirs because of the seasonal difference in passage.

Seasonal differences in the stocks and behavior of salmonids passing through the reservoir may also have contributed to seasonal differences in mortality. The age 1 chinook salmon and steelhead that predominate early in the year migrate through the reservoir quickly (McConnaha et al. 1985) traveling offshore near the surface (Smith 1974). The age 0 chinook that comprise virtually all of the salmonids after June, travel more slowly (Miller and Sims 1984) and spend more time near shore where vulnerability to predators may be higher.

Modeling Approach

To describe the dynamics of a predator population it is useful to incorporate functions of growth, mortality and recruitment. This task has been approached using bioenergetics models, surplus production models, dynamic pool models, stock recruitment models, Leslie matrixes and combinations of all of these (Dickie 1979; Stewart 1980; Vaughan et al. 1983). Selection of an approach depends on whether it is desirable to incorporate the functions independently or integrate them as a single population response; to consider the population in discrete age groups or integrate all ages; and to incorporate or ignore density dependent responses.

Only the dynamic pool and Leslie matrix models allow growth, recruitment and mortality to be considered independently, and both allow age structuring of a population. Neither model requires density dependent functions though both can easily incorporate stock-recruitment relationships or density-related growth rates. The matrix provides a simple, tractable format consistent with our method of loss estimation. The matrix also allows the consideration of populations over discrete time intervals, and allows the consideration of unstable population structure. The dynamic pool model assumes the population to be stable. For these reasons we chose a matrix approach for the population submodel. The standard Leslie approach was modified slightly by input of recruitment independent of parental stock size and age structure, though separate functions can be used to relate driving variables to survival and recruitment rates.

We chose to consider population rate functions as independent variables to aide analyses of potential management strategies. For instance, by varying predator mortality in the model, we can simulate the influence of harvest or management control actions. By varying recruitment, we can examine potential control actions as well as the influence of random or environmental factors that may influence predator year class strength and total abundance. Available data allow us to characterize total, fishing, and natural mortality, growth, recruitment, and relative year class strength for three predators in John Day Reservoir during the period of study (Beamesderfer et al. 1987).

Consideration of discrete age groups in a model allows the stratification of populations into size groups consistent with observations of consumption. From preliminary estimates we found that consumption of prey was not uniform for all sizes of northern squawfish. Detailed size stratification was not considered important in estimates of salmonid loss since both consumption and population estimates were from the same populations, and weighted similarly by size. Size stratification could be important for any simulation, however, since a change in the size structure of the predator population may have a dramatic influence on the magnitude of prey consumption.

As yet we have no evidence that density dependent or stock recruitment processes are important in the dynamics of John Day Reservoir predator populations. Although compensation has been suggested for the predator species (Colby et al. 1978, Rieman 1987), population densities in John Day Reservoir appear to be low relative to other observations (Beamesderfer et al. 1987). It is likely that compensation, at least, will be unimportant without substantial increases in predator numbers (Colby et al. 1978, Rieman 1987).

A routine necessary for describing prey consumption rate for individual predators is currently being developed. Preliminary consumption estimates vary with temperature, and may vary with size of predator, reservoir area and prey availability. We are using a regression approach in an effort to describe consumption as a function of those interacting variables.

The submodel necessary for predicting predator distribution through time (month) has not been developed. We have described the relative distribution of predators during our sampling. We have not determined whether distribution of predators has occurred in a consistent or predictable fashion among sampling periods and years. If statistical analyses reveal no differences in relative distribution of predators with time, the observed distribution will serve as the submodel for partitioning predators in our simulation. If significant differences are found, an attempt will be made to explain differences in distribution based on independent environmental variables including flow, temperature and prey availability.

Application of the Model

The model could have useful application in two areas, these include a description of expected changes in predation over time with normal variation in the system, and identification of management alternatives that might limit predation.

As a first step we believe it is important to examine the loss and mortality estimated during our study in relation to variation and extremes possible in the reservoir. We know that year class strength and recruitment of predators has varied five fold or more over recent time (Nigro et al. 1985c). We expect that abundance and relative age or size structure of each predator population has also varied in response. At the same time we recognize that prey consumption rate will change with abundance of prey available to predators. The number of juvenile salmonids passing McNary Dam has varied from year to year. As a result, we expect that loss and mortality due to predation will also vary. A model incorporating these kinds of variation will help describe the ranges of loss and mortality possible and the full significance of predation.

We can incorporate variation in prey abundance and in predator populations based on historic information for each. Projections of expected loss will be best for years when conditions in prey abundance were similar to those when our data were collected. To generalize beyond our range of observation we must assume system components continue to interact in a similar manner or that differences in behavior are predictable. For instance, preliminary data show that a predator's consumption rate increases with salmonid number. This is consistent with other observations and theory that also predict that consumption rate increases to some maximum (Holling 1965, Murdoch and Oaten 1975) which is a function of handling time, hunger or maximum meal size. By assuming a maximum meal from laboratory observations or the literature, we may extend our relationship of consumption rate and prey abundance to an asymptote at that point. In that manner consumption rate would be predicted at any level of prey abundance. Obviously there will be some increased uncertainty for total loss projections made in this way. The effort should still be useful, however, as a generalization of system dynamics.

General strategies for controlling loss of juvenile salmonids to predators in John Day Reservoir can also be identified using the model. A number of specific control measures have already been identified and reviewed based on application in other areas (Gray et al. 1986). Other potential strategies might emerge from the modeling process. For example, factors that influence predator numbers or prey consumption rates would obviously influence loss to predation. Predator abundance can be changed by altering survival or recruitment. The relative influence of fishing mortality on survival and population structure or the influence of variables (such as flow) on recruitment could be large enough to influence loss. Specific fisheries or flow manipulation at the dam might emerge as potential management strategies. The apparent depensatory response in predation may result in large differences in proportions of prey consumed with changing prey numbers. Holding several days passage at the dam and then "pulsing" migrants through the reservoir might significantly reduce mortality. The release of hatchery fish to boost the apparent abundance of prey might similarly emerge as an alternative to reduce effects of predation on specific stocks. The model might be used to examine salmonid protection measures. Transportation, for example, is known to improve survival of some stocks (Park 1980, Matthews et a?. 1985). Our data suggest, however, that reduction of migrant numbers could significantly increase mortality experienced by untransported fish. The model could be used to weigh that tradeoff.

Application of a model of the John Day Reservoir predator-prey system will provide some insight regarding predation. Although this effort will provide new information, it may not be representative of conditions outside John Day Reservoir. Our data describing the temporal and spatial distribution of loss and the distribution of predators suggest that the importance of predation on juvenile salmonids could differ substantially in other reservoirs. Although the approach used to characterize predation in John Day Reservoir might be used for other reservoirs, several components of the model would have to be requantified.

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APPENDIX A

Tasks, Activities, Data Requirements and References for Completing a Model of Predation and a Predator Population in John Day Reservoir

Appendix Table A. Tasks and activities for constructing a model of predation and a predator population in John Day Reservoir. Mathematical terms are included for model components addressed by each activity.

Submodel	Task	Activity	Component
1. Predation	A. Quantify state variables.	1. Estimate species, size, month, and area specific predator numbers.	$NSMA_{ijklt}$
		2. Estimate species, size, month, and area specific per predator consumption rate.	C_{ijklt}
		3. Estimate predation loss from numbers and consumption rate.	Z_{ijklt}
	B. Validate estimates of state variables.	1. Compare estimated predator density with that for the same species in other systems.	$NSMA_{ijklt}$
		2. Compare estimated consumption rate with that estimated by others and projected consumption based on growth.	C_{ijklt}
		3. Compare estimated predation loss with known losses based on salmonid counts at McNary and John Day dams.	Z_t
	C. Identify driving variables.	1. List aspects of prey abundance and environmental conditions that could affect consumption rate.	PRC_{pijklt} ENC_{eijklt}
		2. Gather all available data on factors potentially affecting consumption rate.	
		3. Select driving variables by correlating with consumption rate and by using information from similar systems.	

Appendix Table A. Continued.

Submodel	Task	Activity	Component
	D. Validate identification of driving variables.	1. Compare factors affecting consumption rate with those identified in other systems.	PRC_{pijklt} ENC_{eijklt}
	E. Quantify functional relationships between state and driving variables.	1. Select forms of functions relating consumption rate to driving variables using regression techniques and information from other systems.	$C_{ijklt}=F\{\}$
	F. Validate functional relationships between state and driving variables.	1. Compare function relating consumption rate to driving variables with similar relationships from other systems.	$C_{ijklt}=F\{\}$
	G. Assemble submodel.	1. Express loss in terms of predator numbers and factors affecting consumption rate.	
	H. Calibrate submodel.	1. Using the assembled submodel, predict loss with varying inputs of predator numbers, prey numbers, and environmental factors.	
		2. Compare predicted loss with estimated loss.	
		3. Return to task C. if predictions do not correspond with known levels.	
II. Population	A. Quantify state variables.	1. Estimate age- and month-specific predator numbers.	NAM_{ikmt}
		2. Estimate size- and month-specific predator numbers.	NSM_{ikmt}
		3. Estimate average length at each age.	FL_{imt}
		4. Estimate age-specific annual survival rate.	AS_{imt}
		5. Estimate age-specific monthly survival rate.	MS_{ikmt}

Appendix Table A. Continued.

Submodel	Task	Activity	Component
	B. Validate estimates of variables.	1. Compare estimated age distribution with that for the same species in other systems.	NAM_{ikmt}
		2. See I.B.1 for validation of predator number estimates.	NSM_{ikmt}
		3. Compare estimated average size at each age with that for the same species in other systems.	FL_{im}
		4. Compare estimated annual survival rate with that for the same species in other systems.	AS_{imt}
		5. Investigate assumption that natural mortality is negligible.	$MS_{ikmt} = f\{MEX_{ikmt}\}$
	C. Identify driving variables.	1. List aspects of predator abundance and environmental conditions that could affect recruitment.	$\left\{ \begin{matrix} NA_{imt} \\ ENR_{eit} \end{matrix} \right\}$
		2. Gather all available data on factors potentially affecting recruitment.	
		3. Select driving variables by correlating with recruitment by using information from similar systems.	
	D. Validate identification of driving variables.	1. Compare factors affecting recruitment with those identified in other systems.	$\left\{ \begin{matrix} NA_{imt} \\ ENR_{eit} \end{matrix} \right\}$
	E. Quantify functional relationships between state and driving variables.	1. Select form of function relating recruitment to driving variables using regression techniques information from other systems.	$NA_{i(m=1)t} = f\{\ \}$

Appendix A. Continued.

Submodel	Task	Activity	Component
	F. Validate functional relationships between state and driving variables.	1. Compare function relating recruitment to driving variables with similar relationships from other systems.	$NA_{i(m=1)t} = f\{\}$
	G. Assemble submodel.	1. Express size-specific predator numbers in terms of starting population size, exploitation, and factors affecting recruitment.	
	H. Calibrate submodel.	1. Using the assembled submodel, predict predator numbers with varying inputs of predator numbers, exploitation, and environmental conditions.	
		2. Compare predicted predator numbers with estimated predator numbers.	
		3. Return to task C if predictions do not correspond with known levels.	
III. Distribution	A. Quantify state variables.	1. Estimate size-, month-, and area-specific predator numbers.	$NSMA_{ijklt}$
		2. Estimate size- and month-specific predator numbers.	NSM_{ijkt}
		3. Calculate the proportions of the predator populations of each size in each area for each month.	q_{ijklt}
	B. Validate estimates of state variables.	1. See I.B.1 for validation of predator number estimates.	$NSMA_{ijklt}$

Appendix Table A. Continued.

Submodel	Task	Activity	Component
	C. Identify driving variables.	1. List aspects of predator abundance, prey abundance, and environmental conditions that could affect predator distribution.	$NSMA_{ijkt}$ PRQ_{pijkt} ENQ_{eijkt}
		2. Gather all available data on factors potentially affecting predator distribution.	
		3. Select driving variables by correlating with predator distribution by using information from similar systems.	
	D. Validate identification of driving variables.	1. Compare factors affecting predator distribution with those identified in other systems.	$\left\{ NSM_{ijkt}, PRQ_{pijkt}, ENQ_{eijkt} \right\}$
	E. Quantify functional relationships between state and driving variables.	1. Select form of function relating predator distribution to driving variables using regression techniques information from other systems.	$q_{ijklt} = f\{\ \}$
	F. Validate functional relationship between state and driving variables.	1. Compare function relating predator distributions to driving variables with similar relationships in other systems.	qijklt'f $\{\ \}$
	G. Assemble submodel.	1. Express predator numbers of each size, month, and area in terms of month- and size-specific numbers and factors affecting distribution.	

Appendix Table A. Continued.

Submodel	Task	Activity	Component
	H. Calibrate submodel.	1. Using the assembled submodel, predict predator numbers of each size, month, and area with varying inputs of month- and size-specific numbers and driving variables.	
		2. Compare predicted distributions with estimated distributions.	
		3. Return to Task C if predicted and estimated distributions do not correspond.	

APPENDIX B

Estimated Abundance of Predators in Portions of John Day Reservoir Used for Calculations of Loss

Appendix Table B-1. Estimated number of walleye in four areas of John Day Reservoir used for calculations of salmonids lost to predators in 1984 and 1985.

Year, Predator Size, Area	Month				
	April	May	June	July	August
1984					
250-500mm					
John Day Forebay	0	0	0	0	0
Arlington	0	200	500	800	0
Irrigon	700	700	500	400	1,100
McNary Tailrace	800	600	600	300	400
>500mm					
John Day Forebay	0	0	0	0	0
Arlington	0	300	800	2,300	7,400
Irrigon	10,300	10,600	11,200	10,400	3,800
McNary Tailrace	3,600	3,000	1,800	1,200	2,600
1985					
250-500mm					
John Day Forebay	0	0	0	100	0
Arlington	900	300	1,400	900	3,000
Irrigon	800	1,400	700	2,000	0
McNary Tailrace	1,800	1,800	1,400	500	500
>500mm					
John Day Forebay	0	100	0	0	0
Arlington	0	1,200	0	3,100	4,300
Irrigon	5,200	8,600	12,200	9,500	7,500
McNary Tailrace	7,300	2,700	400	0	700

Appendix Table B-2. Estimated number of northern squawfish in five areas of John Day Reservoir used for calculations of salmonids lost to predators in 1984 and 1985.

Year, Predator Size, Area	Month				
	April	May	June	July	August
1984					
250-375mm					
John Day Forebay	2,700	3,300	2,100	5,700	3,000
Arlington	35,000	33,200	28,900	24,800	19,000
Irrigon	10,100	9,100	12,100	13,100	23,200
McNary Tailrace	1,300	3,000	4,000	5,400	2,800
BRZ	900	1,500	2,800	800	1,500
>375mm					
John Day Forebay	1,100	1,800	800	2,600	900
Arlington	14,000	12,200	11,200	15,000	11,000
Irrigon	12,100	9,600	8,000	7,900	12,400
McNary Tailrace	1,700	3,200	4,000	2,800	1,600
BRZ	1,300	3,300	5,900	1,400	3,700
1985					
250-375mm					
John Day Forebay	5,300	3,700	3,000	3,100	2,300
Arlington	22,400	18,500	13,600	15,200	23,900
Irrigon	21,500	23,500	26,500	27,700	21,200
McNary Tailrace	3,500	6,500	8,800	3,700	2,200
BRZ	500	700	400	1,900	1,700
>375mm					
John Day Forebay	2,100	2,100	3,300	1,200	2,600
Arlington	10,800	9,400	10,600	7,400	18,100
Irrigon	22,200	20,500	18,100	24,000	13,100
McNary Tailrace	4,000	4,800	4,300	9,800	600
BRZ	3,200	5,200	5,000	7,100	6,100

APPENDIX C

Estimated Prey Consunption Rates and Prey Composition for Predators in John Day Reservoir Used for Calculations of Loss

Appendix Table C-l. Estimated daily consumption of juvenile salmonids by walleye in John Day Reservoir used for calculations of salmonids lost to predators in 1984 and 1985.[a]

Year	Month				
	April	May	June	July	August
1984	0.037	0.310	0.138	--	0.510
1985	0	0.610	0.088	--	0.000

[a]Estimates are pooled among all reservoir areas and among all size classes of walleye because of no stastical differences among individual sampling strata as described in text.

Appendix Table C-2. Estimated daily consumption of juvenile salmonids by two size groups of northern squawfish in five areas of John Day Reservoir used for calculations of salmonids lost to predators in 1984 and 1985.

Year, Predator Size, Area	Month				
	April	May	June	July	August
1984					
250-375mm					
John Day Forebay	0	0.053	0.061	--	0.058
Arlington	0	0.053	0.061	--	0.058
Irrigon	0	0.051	0.061	--	0.058
McNary Tailrace	0	0.131	0.061	--	0.058
BRZ	0	0.178	0.140	--	0.410
>375mm					
John Day Forebay	0.133	0.358	0.061	--	0.058
Arlington	0.076	0.358	0.061	--	0.058
Irrigon	0.076	0.388	0.061	--	0.058
McNary Tailrace	0.076	(1.614	0.061	--	0.058
BRZ	0.063	0.681	0.140	--	0.410
1985					
250-375mm					
John Day Forebay	0.010	0.007	0.063	0.546	0.032
Arlington	0.010	0.007	0.063	0.546	0.032
irrigon	0.010	0.007	0.063	U.546	0.032
McNary iailrace	0.010	0.007	0.063	0.546	0.032
BRZ	0.207	0.250	0.426	3.235	0.136
>375 mm					
John Day Forebay	0.010	0.315	0.063	0.546	2.032
Arlington	0.010	0.315	0.063	0.546	0.032
Irrigon	0.010	0.315	0.063	0.546	0.032
McNary Tailrace	0.010	0.315	0.063	0.546	0.032
BRZ	0.207	0.861	0.426	3.235	I). 136

[a] Estimates are pooled among reservoir areas and among size classes of northern squawfish when statistical differences were not found among those sampling strata as described in the text.

Appendix Table C-3. Proportions of juvenile salmon and steelhead identified in stomachs of walleye and northern squawfish from John Day Reservoir used for calculations of salmonids lost to predators in 1984 and 1985. The number of salmonids identified is also shown.

Predator, Year, Salmonid	Month				
	April	May	June	July	August
Walleye					
1984					
Salmon	1.00	0.90	1.00	--	1.00
Steelhead	0.00	0.10	0.00	--	0.00
N	6	30	14	--	4
1985					
Salmon	1.00[a]	0.86	1.00	--	0.00
Steelhead	0.00	0.14	0.00	--	0.00
N	0	7	2	--	0
Northern Squawfish					
1984					
Salmon	0.69	0.84	0.76	--	1.00
Steelhead	0.29	0.15	0.24	--	0.00
N	17	131	38	--	57
1985					
Salmon	0.97	0.91	0.79	1.00	1.00
Steelhead	0.03	0.09	0.21	0.00	0.00
N	61	129	62	134	14

[a] Value assumed from 1984 observations.

APPENDIX D

Estimated Passage and Release of Hatchery Produced Juvenile Salmonids into John Day Reservoir Used for Calculations of Loss

Appendix Table D. Estimated passage (X 1000) and hatchery releases[a] (X 1000) of juvenile salmon and steelhead into John Day Reservoir used for calculations of salmonids lost to predators in 1984 and 1985.

Year, Salmonid, Passage, Release	Month				
	April	May	June	July	August
1984[b]					
Age 0 Salmon					
Passage	0	900	2,700	3,300	1,700
Release	0	0	500	700	0
Age 1 Salmon					
Passage	900	3,600	100	0	0
Release	0	0	0	0	0
Steelhead					
Passage	200	1,100	200	0	0
Release	0	100	0	0	0
1985					
Age 0 Salmon					
Passage	0	200	2,900	5,400[c]	200
Release	0	500	300	3,000	0
Age 1 Salmon					
Passage	1,300	4,800	300	0	0
Release	0	0	0	0	0
Steelhead					
Passage	100	500	100	0	0
Release	0	100	0	0	0

[a]Releases made directly to John Day Reservoir and to tributaries.
[b]Collection of data for passage was not initiated until April 13.
[c]Release was made the last week of June, we assume movement into the reservoir occurred in July.

APPENDIX E

Estimated Number of Juvenile Salmonids Lost to Predators in John Day Reservoir

Appendix Table E-l. Estimated number (X 1000) of juvenile salmonids lost to predation by walleye in four areas of John Day Reservoir in 1984 and 1985.

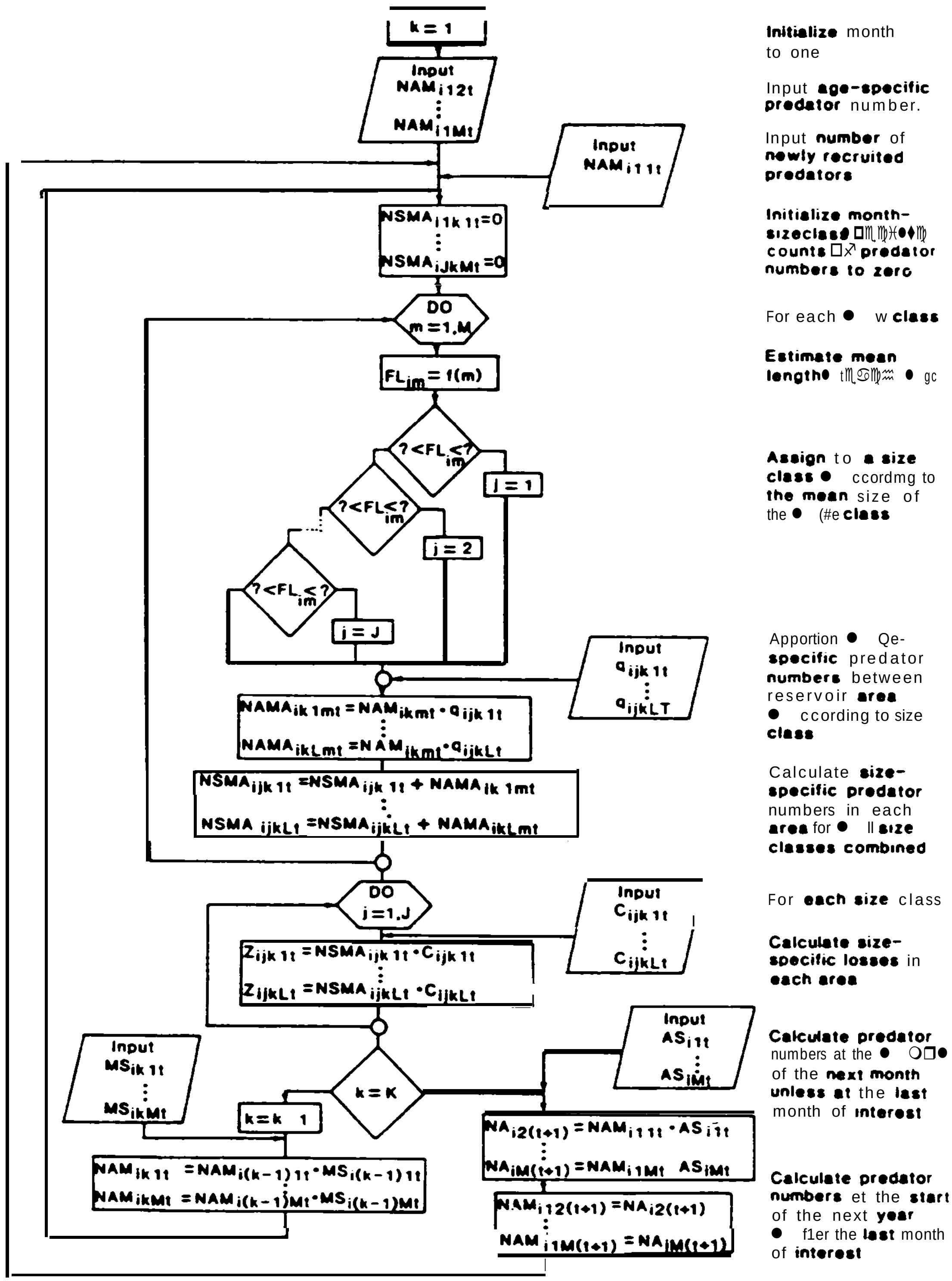
Year, Area	April	May	June	July	August
1984					
John Day Forebay	0	0	0	--	0
Arlington	0	19	3	--	117
Irrigon	12	71	46	--	78
McNary Tailrace	5	59	15	--	46
1985					
John Day Forebay	0	0	0	--	0
Arlington	0	3	4	--	0
Irrigon	0	19	34	--	0
McNary Tailrace	0	8	5	--	0

Appendix Table E-2. Estimated number (X 1000) of juvenile salmonids lost to predation by northern squawfish in five areas of John Day Reservoir in 1984 and 1985.

Year, Area	Month				
	April	May	June	July	August
1984					
John Day Forebay	4	26	5	--	7
Arlington	32	190	73	--	54
Irrigon	28	130	37	--	64
McNary Tailrace	4	73	15	--	8
BRZ	3	78	36	--	66
1985					
John Day Forebay	2	21	12	77	5
Arlington	10	96	46	380	40
Irrigon	13	205	84	873	32
McNary Tailrace	2	49	25	78	7
BRZ	22	145	68	878	30

APPENDIX F.

Model Algorithm and Definitions



Appendix Figure F-1. Algorithm of calculations for a model of Predation and a predator population in John Day Reservoir.

Appendix Table F-1. Definitions of terms used in a model of predation and a predator populations in John Day Reservoir.

Term	Definition
$AEX_{im}(t)$	- Annual exploitation of a predator age class.
$AS_{im}(t)$	- Fraction of a predator age class at the start of a year that survives to the start of the next year (annual survival).
$C(t)$	- Salmonids consumed per predator during year t.
$C_{ijkl}(t)$	- Salmonids consumed per predators in a given size class, month and reservoir area. (consumption rate)
e	- Subscript referring to an environmental condition.
E	- Total number of environmental conditions of interest (e = ones,...,E).
$ENC_{eijkl}(t)$	- Environmental condition affecting consumption rate by predators in a given size class, month, and reservoir area.
$ENQ_{eijk}(t)$	- Environmental condition affecting distribution of predators of each size class, each month.
$ENR_{ei}(t)$	- Environmental condition affecting recruitment of a predator (i).
f	- "is a function of"
FL_{im}	- Mean fork length of a predator age class.
i	- Subscript referring to a predator species.
I	- Total number of predator species of interest (i = 1,...,I).
j	- Subscript referring to a predator size class.
J	- Total number of predator size classes of interest (j = 1,...,J).
k	- Subscript referring to a month.
K	- Total number of months of interest (k = 1,...,K).
l	- Subscript referring to a reservoir area.
L	- Total number of reservoir areas of interest (l = 1,...,L).
m	- Subscript referring to a predator age class.
M	- Total number of age classes of interest (m = 1,...M).
$MEX_{ikm}(t)$	- Monthly exploitation rate of a predator age class.
$MS_{ikm}(t)$	- Fraction of a predator age class at the start of a month that survives to the start of the next month (monthly survival).
$N(t)$	- Estimated predator numbers at the start of year t.
$NA_{im}(t)$	- Number of predators in an age class at the start of the year.
$NA_{i1}(t)$	- Number of predators in the age class of recruitment at the start of each year.
$NAM_{ikm}(t)$	- Number of predators in each age class at the start of each month.
$NAMA_{iklm}(t)$	- Number of predators in each age class at the start of each month in each reservoir area.
$NAS_{ijm}(t)$	- Size specific numbers of predators affecting annual survival of an age class.

Appendix Table F-l. Continued.

Term	Definition
NSM_{ijkt}	- Number of predators in each size class at the start of each month.
$NSMA_{ijklt}$	- Number of predators in each size class and reservoir area at at the start of each month.
p	- Subscript referring to a prey species.
P	- Total number of prey species of interest ($p = 1,...,P$).
PRC_{pijklt}	- Prey species numbers affecting consumption rate by a predator size class in a month and reservoir area.
PRQ_{pijkt}	- Prey species numbers affecting distribution by predators of each size class each month.
q_{ijklt}	- Proportion of a size-specific predator population during each month in each reservoir area.
t	- Subscript referring to a year.
T	- Total number of years of interest ($t = 1,...,T$).
$Z(t)$	- Losses of salmonids during year.^{t}
Z_{ijklt}	- Losses of salmonids to a predator species and size class in a month and reservoir area.

Appendix Table F-2. Functional relationships between terms used in a model of predation and a predator population in John Day Reservoir.

Relationship	Equation Number
$Z_{ijklt} = N_{ijklt} C_{ijklt}$	(1)
$C_{ijklt} = f\ [PRC1_{1jklt},\ldots,PRC_{pijklt}; ENC1_{1jklt},\ldots,ENC_{eijklt}]$	(2)
$NA_{imt} = NA_{im}^{(t-1)} \quad AS_{im}^{(t-1)}$	(3)
$NAM_{ikmt} = NAM_{i(k-1)mt} MS_{i(k-1)mt}$	(4)
$AS_{imt} = f\ [AEXm_t; NAS_{i1mt},\ldots,NAS_{ijmt}; ENAS_{1imt},\ldots,ENAS_{eimt}]$	(5)
$MS_{ikmt} = f\ [MEX_{ikmt}]$	(6)
$NA_{i(m-1)t} = f\ [ENR_{1i}^{(t-1)},\ldots,ENR_{ei}^{(t-1)}; NA_{i1}^{(t-1)},\ldots, NA_{im}(t-1)]$ (7) $FL_{im} = f\ (m)$	(8)
$NSMA_{ijklt} = NSM_{ijkt}\ q_{ijklt}$	(9)
$Q_{ijklt} = f\ [NSM_{ijkt}; PRQ_{1ijkt},\ldots,PRQ_{pijkt}; ENQ_{1ijkt},\ldots,ENQ_{eijkt}]$	(10)