

MAGNITUDE AND DYNAMICS OF PREDATION ON JUVENILE SALMONIDS  
IN COLUMBIA AND SNARE RIVER RESERVOIRS  
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## ABSTRACT

Three aspects of predation upon juvenile salmonids in the Columbia River are addressed in this report:

1) Indexing predator consumption. During 1989-90, two indices of northern squawfish consumption upon juvenile salmonids were developed for use throughout the Columbia River Basin. The direct Consumption Index (CI) is based upon the concept of meal turnover time and takes into account number of salmonids, temperature, total gut content weight and predator weight. Computing formulae, laboratory methods, sample size requirements and preliminary tests are presented. A Bioenergetics Index (BI) for consumption indexing was also developed to complement the direct CI. In the BI, growth, consumption, excretion/evacuation and respiration processes are modeled to predict the consumption required to produce an observed growth increment. Preliminary parameter estimates are presented and a sensitivity study of the model was done to direct further development.

2) Studies on predator-smolt dynamics. Northern squawfish consumption data were collected in the McNary Dam tailrace during nine days in July, 1988 to improve our understanding of the predator-smolt functional response. Data were summarized and fitted, along with July-August data from 1983-86, to a Type II functional response equation. Maximum consumption experiments with northern squawfish were completed and results appear in Appendix A. Finally, a workshop was held to discuss aspects of predation modeling in the Columbia River. A separate Bonneville Power Administration report that summarizes the workshop has been published.

3) Selective predation by northern squawfish. Laboratory and field protocols were developed to evaluate northern squawfish selection and prey vulnerability. We conducted preliminary selection experiments on three categories of substandard vs. standard juvenile salmonids: live vs. dead; injured vs. non-injured; and stressed vs. unstressed. Results from laboratory studies suggest that northern squawfish prefer dead over live prey and that descaled prey may be more vulnerable to predation than non-descaled prey. Stressed and unstressed prey were consumed in equal proportions when predation occurred for 6 or 24 h. Physiological and behavioral effects of stress on juvenile salmon are presented.

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## BACKGROUND

One of the measures contained in the Northwest Power Planning Council's 1982 Fish and Wildlife Program (Anonymous 1987) called for studies II..... to investigate juvenile salmon and steelhead losses to predators while these fish are migrating through Columbia and Snake River reservoirs." In response to that measure the Oregon Department of Fish and Wildlife (ODFW) and the U.S. Fish and Wildlife Service (FWS), funded by Bonneville Power Administration (BPA), began a cooperative study in 1982 to estimate the number of juvenile salmonids lost to fish predators in John Day Reservoir. Results of the 1983-86 study indicated that fish predation may account for the majority of unexplained losses of juvenile salmonids in John Day Reservoir (Poe and Rieman 1988; Rieman et al. 1988).

Important questions remain to be answered, however, to estimate the system-wide impact of predators on the survival of outmigrating smolts and to determine if predation control is warranted. Although smolt losses to predators were significant in John Day Reservoir, questions remain about the intensity of predation in other Columbia and Snake River reservoirs, cumulative impacts of predators on smolt survival throughout the river system and differential predation-related mortality of healthy versus unhealthy smolts. These questions require a better understanding of predator-prey dynamics at the individual interaction level and at the system level. This project was designed to provide some information on these outstanding questions.

Due to the diverse research objectives in the 1989-90 period, this report is organized into three sections. Section I documents the development of a consumption index, which will be used in conjunction with a predator abundance index (Nigro et al. 1990), to compare the magnitude of predation in reservoirs throughout the Columbia River Basin. Section II describes the development, testing, and refinement of predation

models. Section III documents the development of protocols to determine if predators select dead, physically injured, or stressed juvenile salmonids as opposed to healthy juvenile salmonids.

## SECTION I. PREDATION INDEX

To address the question of system-wide significance of predation, the FWS and ODFW (Poe and Rieman 1988) recommended development of a predation index to estimate the relative magnitude of smolt losses to predators in reservoirs throughout the Columbia River Basin. The index would consist of a Consumption Index, to be developed by FWS, and a Population Abundance Index, to be developed by ODFW. Combination of these indices for an area would yield a Predation Index, similar to a loss estimate. Comparison of Predation Index values among reservoirs would help predict system-wide predation impacts and provide information for directing future predation management decisions.

The FWS objectives were to develop analytical, field and laboratory techniques for a consumption rate index for northern squawfish (*Ptychocheilus oregonensis*), the major fish predator on juvenile salmonids in John Day Reservoir (Rieman et al. 1988). ODFW was to develop corresponding methods for abundance indexing of northern squawfish. After considering numerous approaches for indexing the juvenile salmonid consumption by northern squawfish, two methods were selected for development - a direct, limited sampling method [Direct Consumption Index - CI] supplemented by an indirect method based upon predator growth and fish bioenergetics [Bioenergetics Index - BI]. Each method has advantages and disadvantages that will be discussed below. The two methods would act as checks upon each other and should adequately describe predator consumption at sampling locations. The remainder of this section discusses derivation of consumption indices, data requirements, sampling

requirements and pros and cons of the different methods.

## Direct Consumption Index (CI)

### Backaround

Many methods exist for estimating consumption in fishes (e.g., Bajkov 1935; Swenson and Smith 1973; Elliott and Persson 1978; Eggers 1979; Pennington 1985; Olsen and Mullen 1986; Sainsbury 1986) with little agreement upon the "best" technique (Amundsen and Klemetsen 1986; Boisclair and Leggett 1988). Earlier predation studies in John Day Reservoir used a modification of the Swenson and Smith (1973) technique to calculate consumption of juvenile salmonids by resident predators (Vigg et al. 1988). The modified Swenson and Smith method combines field diet data and laboratory evacuation studies to estimate consumption rates. The method can produce fine-scale temporal estimates of consumption patterns and has been well developed for the existing predator-prey database. Disadvantages of this method are its need for extensive diet data, complex equations with many variables, and the lack of a variance estimate since consumption is calculated only for the "typical" predator in the sample.

Consumption was also calculated for predators in John Day Reservoir by a meal turnover-time method (Rieman et al. 1988) whose main advantages were variance estimation and simplicity. This method integrates meal turnover-time and the number of salmonids found in the gut to calculate consumption for each individual predator (Henchman 1986; Rieman et al. 1988).

Our consumption index is based upon the concept and simple equations of meal turnover-time. Modifications of the basic turnover-time equations were derived and indices computed for the 1983-86 data set. Index values were correlated with corresponding consumption estimates computed with the modified Swenson and Smith method of Vigg et al. (1988). Indices having the highest correlations with the consumption estimates were

chosen for further study. We assumed that the modified Swenson and Smith method was the "best" estimate of consumption for the John Day predator-prey data set. Consumption indices and methods were tested during the 1989 field season. Field and laboratory methods were developed during 1989 to minimize the time and cost of estimating an index.

### Index Derivation

The estimated number of salmonids consumed per day by an individual predator,  $p$ , can be expressed as:

$$C_p = \sum_{i=1}^n 1 / (\text{Evacuation time for prey item } i)$$

or,

$$C_p = \sum_{i=1}^n 1 / D90_i \quad (1)$$

where  $C_p$  is consumption rate (number of salmonids · individual northern squawfish<sup>-1</sup> · day<sup>-1</sup>),  $D90_i$  is number of days to 90% digestion for salmonid prey item  $i$ , and  $n$  is total number of salmonids found in the gut. Using 90% digestion time, rather than 100%, avoids the problem of non-digestible prey parts that may remain in the gut for extended periods. Equation (1) is equivalent to:

$$C_p = \sum_{i=1}^n (24 / T90_i) \quad (2)$$

where  $T90_i$  is number of hours to 90% digestion for the  $i$ th salmonid prey item.  $T90_i$  was calculated by Beyer et al. (1988) and modified by Rieman et al. (1988) to:

$$T90_i = 1147 * M_i^{0.61} * T^{-1.60} * W_p^{-0.27} \quad (3)$$

where  $M_i$  is meal size (g) at time of ingestion of salmonid prey

item  $i$ ,  $T$  is water temperature ( $^{\circ}\text{C}$ ), and  $W_p$  is predator weight (g). Substituting equation 3 into 2 and rearranging gives:

$$C_p = 0.0209 * T^{1.60} * W_p^{0.27} * \sum_{i=1}^n M_i^{-0.61} \quad (4)$$

Equation 4 provides an estimate of daily salmonid consumption per northern squawfish, but still requires estimation of meal size ( $M_i$ ) through intensive gut analysis and complicated data analysis. Equation 4 was, however, used as a starting point to derive a series of test formulae ("indices").

Several modifications of equation (4) were examined, trying different terms for estimating meal size or excluding some terms. The following formula was chosen as a consumption index (CI), based upon simplicity of data required and percent variance explained:

$$CI = 0.0209 * T^{1.60} * MW^{0.27} * [MTsal * MGutwgt^{-0.61}] \quad (5)$$

where  $T$  is water temperature,  $MW$  is mean predator weight (g),  $MTsal$  is mean number of salmonids per predator, and  $MGutwgt$  is mean gut weight (g) per predator. All variables in CI are averaged over all predators in a sample; CI is the consumption index for a collection (sample) of predators. Variance of a CI can be computed by a bootstrap resampling technique (Efron and Tibshirani 1986).

CI was well correlated with the Swenson and Smith estimates of consumption for the John Day pool ( $r=0.89$ ;  $P < .001$ ;  $n=51$ ) and the McNary Boat Restricted Zone ( $r=0.95$ ;  $P < .001$ ;  $n=51$ ). Calculation of actual consumption (prey'predator-'day-'), rather than index units, is possible by using the regression equation shown in Figure 1.

One of the goals of deriving a useful index formula was to include only variables that could be easily measured in the field or in the laboratory; index variables whose measurement

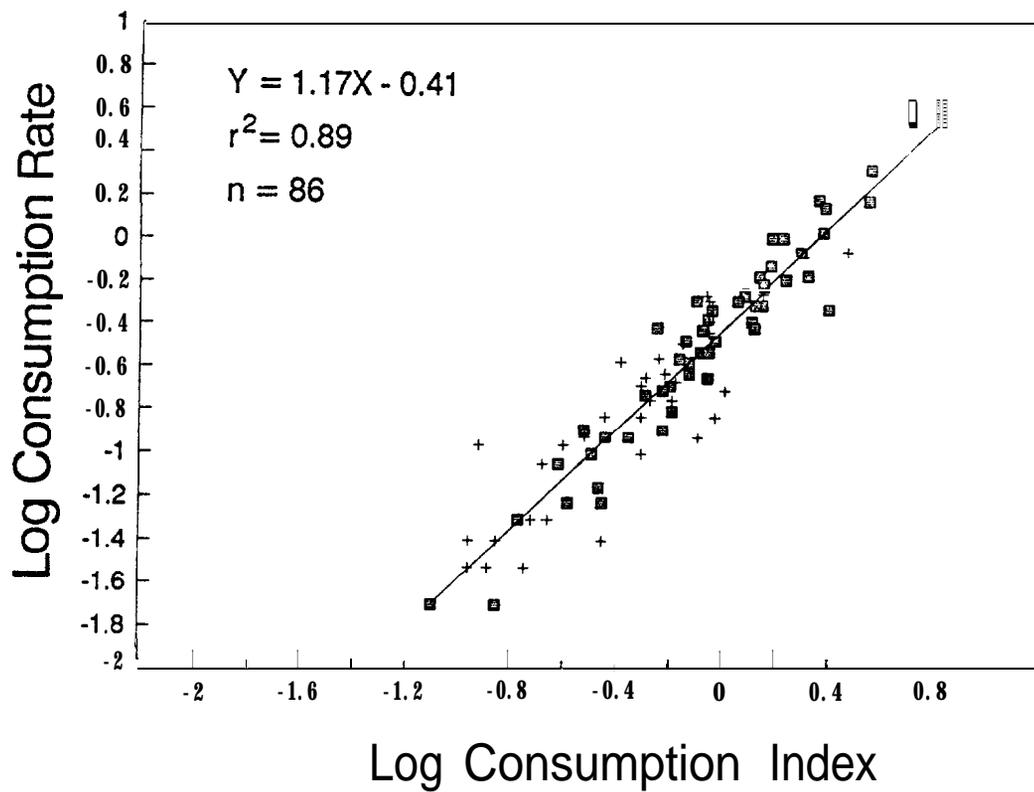


Figure 1. Regression of actual consumption estimates predicted by Consumption Index for McNary BRZ and John Day pool (1983-86). Only days with 15 or more northern squawfish, greater than 250 mm, were used. Squares represent the McNary BRZ (n=51) and crosses represent the John Day pool (n=35); days with a consumption rate of zero were excluded from the regression.

was costly, time consuming or imprecise would defeat the purpose of an index. The only variables needed to calculate CI are predator weight (W), water temperature (T), number of salmonids in the gut (Tsal) and weight of gut contents (Gutwgt). Efficient methods for collecting required data have been developed and are described below.

## Methods

Field methods were developed and tested during 1989. Northern squawfish were sampled at 16 stations associated with four different dams (Bonneville, The Dalles, McNary, and Ice Harbor). Most effort was centered on forebay locations and tailraces, with some sampling in mid-reservoir areas. Predators were collected with an 18 ft, aluminum sled boat equipped with a Smith-Root Type Via electrofishing unit. Pulsed DC (60 and 120 pulses/set) at 700-800 V, drawing 5-6 amps. Electroshocking procedures were similar to those used by Poe et al. (1988) and Vigg et al. (1988).

After capture, northern squawfish were held in an aerated livewell and later placed in water with a lethal dose of ethyl p-aminobenzoate (benzocaine). No stress-induced regurgitation was observed. Predators were measured to the nearest mm (FL), weighed to the nearest 10 g, and scales were collected for age determination. Scales were removed half-way between the posterior base of the dorsal fin and the lateral line. The body cavity of northern squawfish  $\geq 250$  mm was cut open with a knife, and sex and stage of maturity were determined.

After opening the body cavity, the esophagus was checked for food items. Next, the anterior end of the esophagus was pinched shut and cut behind the pharyngeal teeth. The gut was then extended while fat and viscera were removed from the outer gut wall. The anterior, open end of the gut was next placed into a plastic bag. The hindgut was pinched shut near the anus, and, using the thumb and forefinger of the other hand,

gut contents were squeezed into the plastic bag. The foregut was stripped first to prevent large or sharp food items (such as crayfish exoskeleton fragments and prey fish bones) from lodging. Gut contents were labeled, sealed, and frozen. Potential error in field stripping of northern squawfish guts was evaluated by examining a sub-sample of stripped guts for residual food items with a dissecting microscope. Guts of 38 northern squawfish were stripped and also dissected to determine stripping efficiency.

In the laboratory, gut contents were thawed and weighed to the nearest 0.1 g; an empty bag with label was tared to obtain the actual gut content weight. A digestive enzyme technique was developed and tested to speed processing of gut samples. A digestive enzyme solution was prepared using lukewarm tap water, 2% w/w high-strength (8x) porcine pancreatin, and 1% w/w nonahydrate sodium sulfide (Anderson 1965; Dr. Carl Bond, personal communication). The solution was poured into the plastic sample bags until all gut contents were submerged. The bags were sealed and contents were mixed to insure all food was in contact with the solution. Samples were placed in a 40°C desiccating oven for about 24 hr. After all flesh was digested, the contents were poured through a #40 (425 micron) sieve and rinsed with tap water.

Pancreatin digests protein, carbohydrates, lipids, and nucleotides, but not bones, shells, chitin or plant cellulose. Diagnostic bones of prey fish were not affected by enzymatic digestion and were enumerated and identified (Hansel et al. 1988). Other major prey groups (mollusks, crustaceans, insects, and plants) were also identified from undigested hard parts. A magnifying glass and dissecting forceps were used to separate diagnostic bones (primarily cleithra, dentaries, opercles, and hypurals) from other bones. Diagnostic bones were examined under a dissecting microscope, keyed to the lowest possible taxon, paired to enumerate prey fish consumed and preserved in labeled vials with 95% ethanol.

Sample size analyses were performed to demonstrate the relative efficiency of index estimates and to ensure that future efforts would be adequate to accurately evaluate predation intensity. Two components of indexing daily consumption were considered: 1) How many predators must be captured per day to provide an estimate of daily consumption? and 2) How many sampling days are necessary to estimate consumption during a period of time? Data from the 1983-86 Predator-Prey study in John Day Reservoir (Poe and Rieman, 1988) were used in the following analyses.

The effect of the numbers of predators collected upon consumption index (CI) variation was examined using a "bootstrap" resampling method. Bootstrap resampling is a nonparametric technique whose only major assumption is that the original sample is representative of the underlying parameter distribution (Efron 1982; Efron and Tibshirani 1986). Sample size was studied by changing the number of predators selected for each bootstrap sample, generating a CI frequency distribution and examining distribution parameters. Boisclair and Leggett (1988) recently used a similar technique for estimating variation of daily fish ration.

In the following discussion, "sample" will refer to the total number of predators collected and processed during a time period and "resample" will be a randomly selected subset of a sample: a resample may have less than or equal to the number of predators in the sample from which it is drawn.

The data were partitioned into four sets: early (May) and late (July) outmigration periods for the pool and the McNary Boat Restricted Zone (BRZ). Stratification in this manner was similar to previous work (Vigg 1988; Vigg et al. 1988) and gave adequate samples from which to draw bootstrap resamples. Bootstrap resamples of northern squawfish records were generated by randomly selecting, with replacement, records from a data set. For each data set, 250 bootstrap resamples were generated for resample sizes of 5, 15, 30 and 60

predators. Preliminary work indicated that means, coefficients of variation and confidence limits stabilized by taking 250 or more resamples. Resample sizes were chosen since the consumption index was derived from a data set where at least 15 fish per day had been collected and more than 60 fish is difficult to process in one day by a two-person crew. For each resample, a CI was calculated. Percentiles (10th and 90th) of the four CI distributions were plotted and examined: minimum sample size was the point along the plot where increasing sample size did not greatly tighten the confidence bounds.

To estimate the number of sample days, daily consumption indices (CI) were computed for Pool and BRZ areas in John Day Reservoir for the early (April-May) and the late (June-August) smolt migratory periods. Data were pooled over years and months to increase sample size and for other reasons given in Vigg et al. (1988). CI distributions were not significantly different from normal (Kolmogorov-Smirnov tests) so sample-size calculations were based upon the normal distribution. To facilitate comparisons between strata, data were centered to have a mean of 1 by:

$$\text{Standardized CI}_i = \text{CI}_i / \text{Mean}(\text{CI}_i),$$

where  $\text{CI}_i$  was the consumption index on day  $i$ . Power curves were computed using a Type I error (Alpha) = .1 and fixed sample sizes of 2, 4 and 8 days.

## Results

Fishing effort for the two-person crew (operator and netter) ranged from 7 to 130 minutes per station. Mean number of salmonids per northern squawfish gut was as high as 5.0 (Table 1). Consumption indices (CI) were highest in July in the McNary Dam tailrace, an area that has been shown to have a high predation rate (Vigg et al., 1988). Although sampling was

not designed for rigorous comparison, CI values were generally lower in May than in July (Table 1).

Of the 38 northern squawfish guts that were stripped to determine stripping efficiency, only four contained prey fish and three of these had residual food items. Food residue, however, average only 0.03% of weight of original gut contents. Of the 34 examined stomachs without preyfish, eight had residual food items (average 0.16% of original gut contents). Most residual food items were sharp crayfish exoskeleton fragments, sharp preyfish bones such as ribs, vertebrae, etc., and minute amounts of plant material. Although few of the examined predators contained preyfish, careful gut stripping removed over 99% of the total gut contents by weight and all diagnostic salmonid bones.

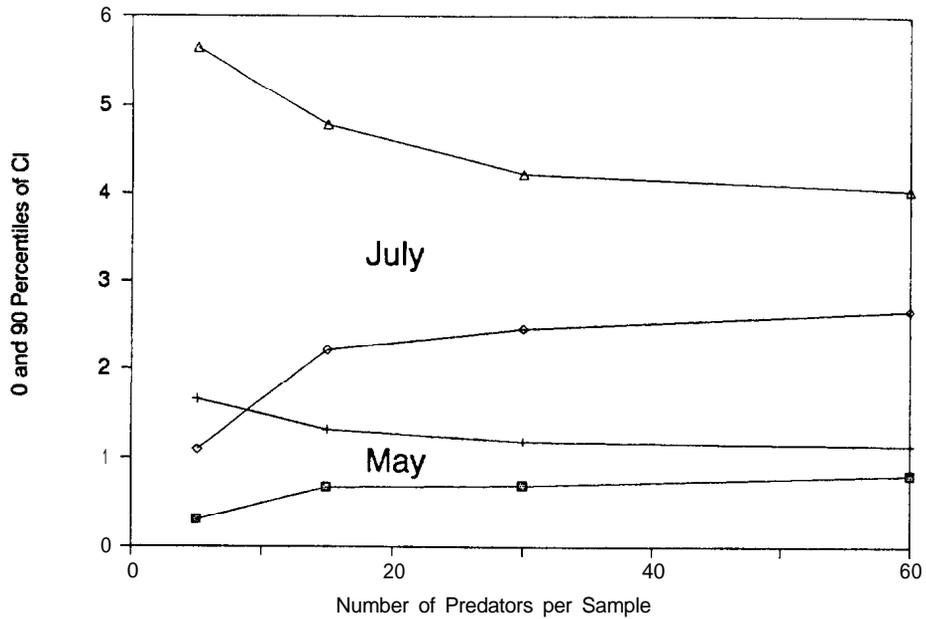
The digestive enzyme method tested greatly reduced the cost and effort required for the laboratory component of the predation index. The gut analysis technique was approximately six times faster (person-hrs) than the analysis method used to process the 1988 samples (see Section II of this report). The digestive enzyme approach yielded less information, but was more cost-effective than traditional methods used to estimate absolute rates of consumption (e.g., Swenson and Smith 1973).

Increasing the number of predators "sampled" by bootstrapping reduced confidence limits of the consumption index (CI), as expected (Figure 2). In May in the Boat Restricted Zone (BRZ), confidence limits were fairly close to the mean and nearly constant for sample sizes of 15 to 60 predators (Figure 2). During July in the BRZ, the mean consumption index was higher but the pattern of change in confidence limits was similar to May. A daily sample minimum of 15 northern squawfish appears sufficient for estimating a consumption index within boat restricted zones. Larger sample sizes do not greatly tighten the confidence interval.

Table 1. Summary of test data from 1989 for northern squawfish consumption index. Consumption Index (CI) was calculated only when sample size (N) of northern squawfish was greater than one.

1989 Date	Sample Location	N	Temp. (°C)	Mean			CI
				SQF Wt (g)	Gut Wt (g)	No. of Salm.	
May 12	Bonneville, mid-reservoir	6	12	527	3.7	0.00	0.00
May 12	Bonneville, mid-reservoir	10	12	894	13.4	0.00	0.00
May 16	The Dalles, mid-reservoir	10	13	1029	14.7	0.10	0.16
May 16	The Dalles, mid-reservoir	13	13	949	7.3	0.00	0.00
May 19	The Dalles, forebay	15	13	897	19.1	0.27	0.35
Jul 07	Ice Harbor, tailrace	45	17	660	4.8	0.04	0.17
Jul 12	McNary, tailrace	23	18	540	7.1	0.87	3.06
Jul 12	McNary, tailrace	77	18	574	8.9	1.29	4.02
Jul 13	McNary, tailrace	25	19	720	7.0	1.52	6.36
Jul 13	McNary, tailrace	4	19	1037	23.2	5.00	11.14
Jul 27	Bonneville I, tailrace	23	20	687	2.1	0.13	1.22
Jul 27	Bonneville I, tailrace	19	20	803	6.1	0.63	3.22
Jul 28	Bonneville II, tailrace	3	19	640	0.5	0.00	0.00
Jul 31	Bonneville I, tailrace	18	20	800	2.6	0.22	1.87
Jul 31	Bonneville I, tailrace	20	20	627	3.0	0.25	1.85
Aug 01	Bonneville II, tailrace	10	20	764	2.9	0.00	0.00

## McNary Boat Restricted Zone



## John Day Pool

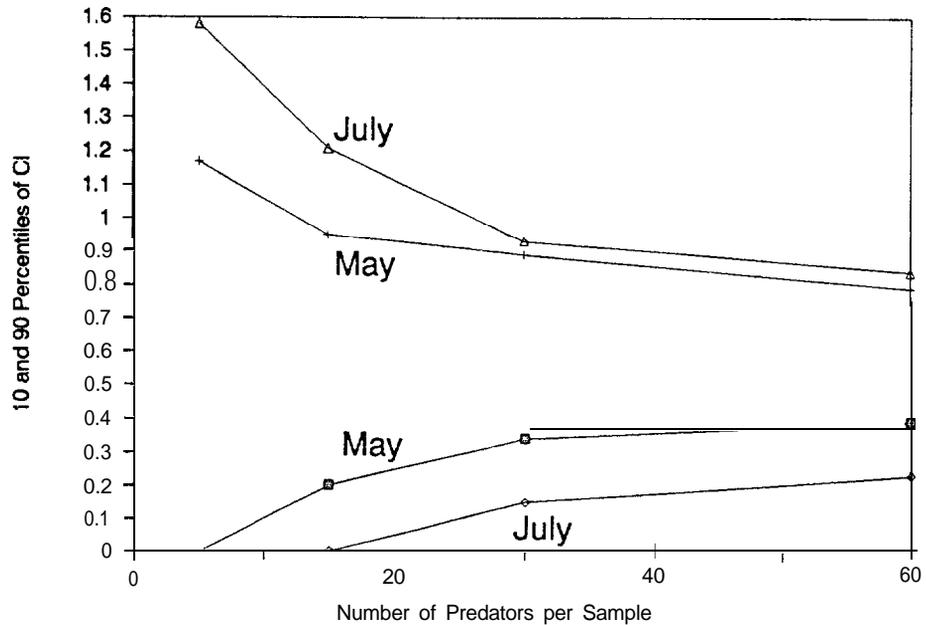


Figure 2. Effect of sample size upon the 10th and 90th percentiles of bootstrapped consumption index distributions. Each distribution had 250 computed consumption indices. The number of original sample days and total predators (days, predators) per strata were BRZ-July (9,589), BRZ-May (12,424), Pool-July (6,243) and Pool-May (15,586).

Slightly larger sample sizes appear necessary for estimating a consumption index within a reservoir pool (Figure 2). Confidence limits did not stabilize for John Day Pool CI distributions until about 30 predators had been sampled. Consumption indexing during the summer period would require the greatest sampling effort. The central 80% confidence interval for July in the pool ranged from 0 to 1.2 index units when 15 fish were sampled (Figure 2); this interval was reduced to 0.15 to 0.9 index units when sample size was increased to 30 predators.

Increasing the number of sample days in an area (Figure 3) increased the probability that two CI samples (called "test" and "control" below for convenience) could be distinguished. With 2 days of spring sampling in the BRZ (Figure 3a), test samples of CI that are two times control or one tenth of control would be detected with about 70% confidence. During the June-August period, samples of 2 days in the BRZ would have low power to distinguish cases when test means were less than twice the control mean (Figure 3b). When test means were triple the control mean, or greater, the probability of falsely rejecting the null hypothesis became very slim in the BRZ (Figure 3b).

Variation of CI's in the pool during April-May were comparable to variation in the BRZ (Table 2), suggesting sampling power would be similar to that described above (see Figures 3a-c). During summer months, however, day-to-day variability increased and the power of a a-day sampling plan thus declines (Figure 3d). Test samples would need to be about three times control samples to have a reasonably high confidence of successful distinction. Sampling on a 4- or 8-day schedule increased statistical power and could be used in specific CI comparisons.

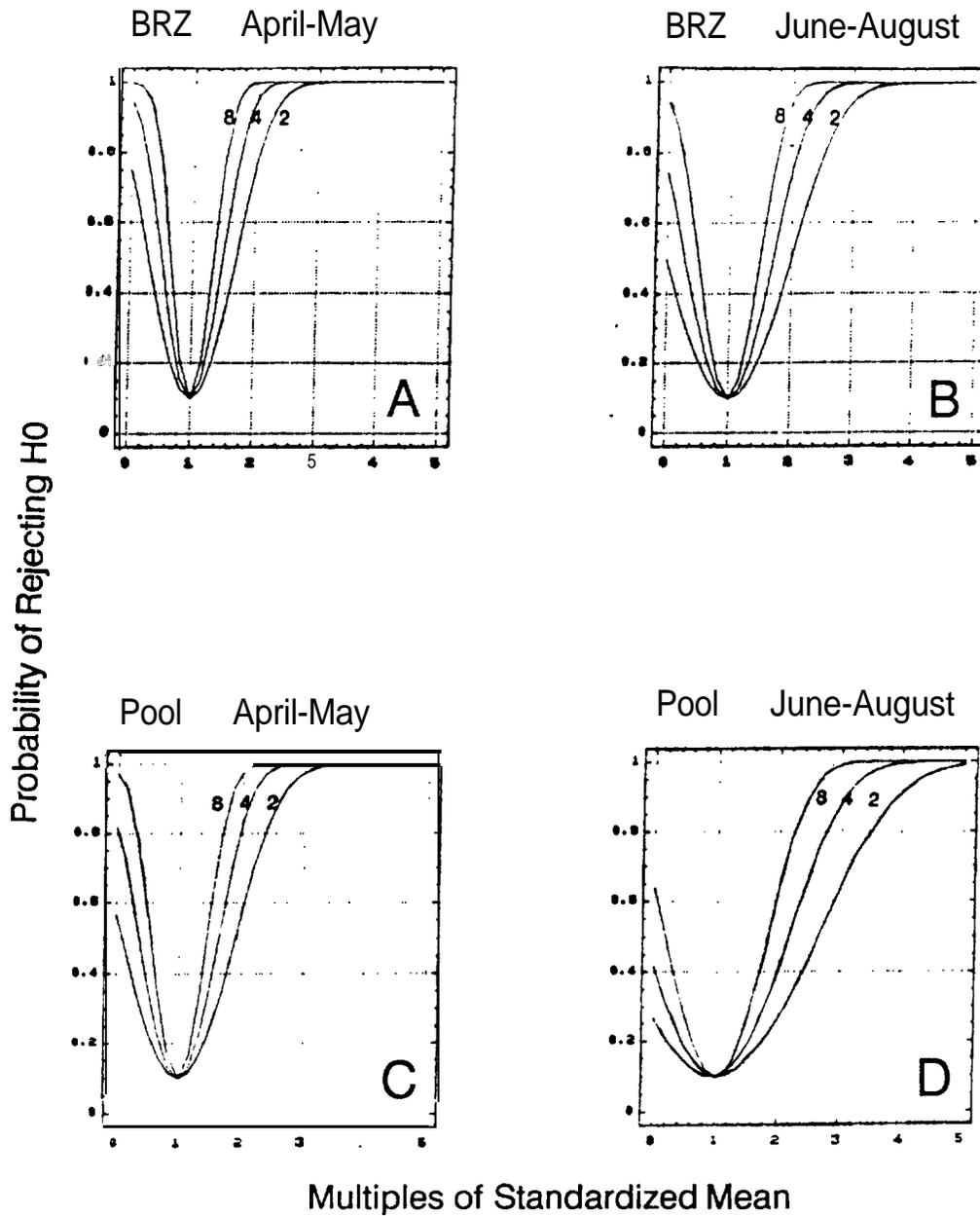


Figure 3. Power of samples of 2, 4 and 8 days of sampling to distinguish test means from a control mean standardized to equal one. The y-axis is the probability of rejecting the null hypothesis when test and control means differ by **some multiple** on the x-axis. Type I error ( $\alpha$ ) was set to .1 and a two-tailed test was specified.

Table 2. Mean Consumption Index for time and location strata used in power analyses for number of days.

Location	Time	Number of Sample Days	Mean Consumption Index	Coefficient of Variation (SD / Mean)
JD Pool	Apr-May	20	0.43	0.78
JD Pool	Jun-Aug	31	0.42	1.41
BRZ	Apr-May	20	0.70	0.61
BRZ	Jun-aug	31	1.31	0.87

### Discussion

Consumption index sampling in 1989 was done primarily to develop methods, test field procedures and resolve problems. Indices measured during 1989 should be considered test data since sampling criteria were not fully developed, geographic location of samples was not systematic and sample timing was not balanced. The consumption indices were, however, highly variable between sample sites suggesting predation intensity may be variable and "hot spots" may be detected with systematic sampling.

The intent in developing the consumption index was to minimize the time and costs associated with sampling the many large reservoirs throughout the Lower Snake and Columbia Rivers. The two components of implementing a system-wide northern squawfish consumption index include the field work required to collect predators and the laboratory work required to process and analyze the gut contents. Both field and laboratory methods were modified in an attempt to reduce the costs associated with traditional food habits studies.

The field collection cost during 1989 predation index testing was roughly the same as past field work conducted in

John Day Reservoir (Poe et al. 1988), since the costs associated with hiring personnel, and procurement and maintenance of vehicles and an electrofishing boat are fixed. Actual field methods using the gut stripping technique required the same amount of time (-2 minutes per predator) as previous food habits methods, thus the only alternative to reduce costs was to reduce sampling effort.

During the 1983-86 predation studies, northern squawfish were collected on at least three consecutive days per month, each day stratified into 6-hour sampling periods (Poe et al. 1988); no specific number of fish was targeted for collection during a sampling period. During 219 total days sampled, the median number of northern squawfish ( $\geq 250$  mm FL) collected and processed per day was 12 (range 1-109 predators). Plans for consumption indexing throughout the Columbia River system involves one year's sampling per reservoir, two days in spring and summer and 15-30 fish per day. Therefore, sampling effort will be reduced from the 1983-86 effort by collecting fish on fewer days per year and during a single year; roughly the same number of fish per sample day will be collected. Also, fewer sites will be sampled, emphasizing "hot spot" areas where predation losses are believed to be high (i.e., tailraces and forebays of dams). An index approach requires less effort since sampling can be less representative than that required for absolute reservoir-wide estimates of mortality.

Selecting appropriate sample sizes requires some a priori definition of the acceptable error levels, which is not usually a straight forward task. The analyses above were meant to describe the confidence in estimating CI's that can be expected with different levels of effort and different sampling scenarios. The general conclusions were that: 1) samples of about 15-30 northern squawfish will be adequate for estimating daily CI's, and, 2) sampling on 2 days will provide a moderately good estimate of the index of consumption for the locations and times studied. Daily variability of CI's within

the pool of John Day Reservoir were high during 1983-86, causing 2-day samples to have only moderate power in distinguishing test from control values. Application of these conclusions to sampling in other reservoirs assumes, of course, that variability will be similar.

## Bioenergetic Consumption Index (BI)

### Backaround

Bioenergetics models have become useful tools for studying various aspects of fish growth and consumption (references in Hewett and Johnson 1987; Hewett 1989). Theoretical, laboratory and field studies of fish physiology have been integrated into flexible models, allowing researchers or fisheries managers to estimate consumption or growth of fish from easily measured field data. One approach to indexing consumption in reservoirs throughout the Columbia River system is to develop a bioenergetics model for northern squawfish and use the model to calculate juvenile salmonid consumption at study sites based upon observed predator growth and water temperature.

A major advantage of bioenergetic indexing is that it uses fish growth to integrate consumption over a period of time, reducing potential sampling problems associated with variable consumption rates. Juvenile salmonid consumption rates are highly variable from day to day, differing by as much as an order of magnitude between successive days (FWS unpublished analyses). Sampling variable consumption patterns with relatively short sample intervals (2-4 successive days) may produce biased estimates if sample dates have particularly low or high consumption. Predators, however, feed throughout the seaward migration period of juvenile salmonids and their growth reflects an integration of daily consumption. Measuring growth rate of predators during the time when juvenile salmonids are passing through a particular reservoir allows estimation of an average daily consumption rate and total consumption for the period.

Two disadvantages of consumption indexing via bioenergetics are no immediate, real-time estimates and no specific model has been developed for northern squawfish. Consumption estimates for a time period of interest cannot be made until

predator growth data have been analyzed at the end of the period. Lack of model development for northern squawfish can be quickly overcome and the remainder of this section describes preliminary development and application of a northern squawfish bioenergetics model. Our general approach is to develop a preliminary model, conduct some test runs of the model, and perform sensitivity analyses upon model parameters. Further development and/or analyses will be recommended based upon results of these test runs and parameter sensitivities.

### Model Development

Hewett and Johnson (1987, 1989) developed a generalized bioenergetics model that contains options for selecting equation forms, changing parameters, output formats, etc. Hewett and Johnson's menu-driven program for microcomputers greatly simplifies model development for new species and was used to begin development of the northern squawfish model. Details of model implementation, data files and program options are not provided here, but are available in Hewett and Johnson (1987).

Fish growth may be described or modeled by a simple energy balance equation:

$$\text{Growth} = \text{Consumption} - (\text{Respiration} + \text{Waste Losses}) .$$

Terms of this equation are expanded based upon data for specific fishes. Computer simulations of the final model may be run to calculate growth, or consumption if the balance equation is rearranged. Many recent studies of fish populations have used this basic modeling approach, successfully predicting growth or consumption (e.g., Kitchell et al. 1977; Kitchell and Breck 1980; Stewart et al. 1983; Rice and Cochran 1984; Stewart and Binkowski 1986).

Growth, the change in weight of predators between two

sampling times, must be known to estimate consumption of juvenile salmonids with a bioenergetics model. Weight of individual, tagged predators could be recorded before and after the juvenile salmonid migration: however, tagging and recapturing adequate numbers of fish in a large system is difficult. Instead, the average weight change of aged cohorts between two sample times are typically used. Estimating growth thus requires data on fish weight and age (from scales or other structures).

Consumption (C), the amount of food consumed by the fish, has the general form:

$$C = C_{\max} * P * F(T)$$

where:

$C_{\max}$  = maximum specific consumption rate ( $g \cdot g^{-1} \cdot d^{-1}$ )

P = proportionality constant

T = temperature ( $^{\circ}C$ )

F(T) = the temperature dependence function.

$C_{\max}$  may be further defined as an allometric function of weight:

$$C_{\max} = a * W^b$$

where:

W = fish weight (g)

a = intercept of the allometric function for consumption, and,

b = slope of the allometric function for consumption.

Several temperature dependence functions [F(T)] have been used in bioenergetic models (Hewett and Johnson 1987). An algorithm by Thornton and Lessem (1978) has been used for northern squawfish (Vigg and Burley MS) and was used below. The Thornton and Lessem (1978) algorithm is essentially the product of two sigmoid curves, one fitting the increasing

portion of the temperature dependence curve (Ki) and one fitting the decreasing portion of the curve (Kd):

$$F(T) = K_i * K_d .$$

The Thornton and Lessem model is best for cool- and cold-water species (Hewett and Johnson 1987) and has been used for alewife (Alosa oseudoharenaus), coho salmon (Oncorhynchus kisutch) and chinook salmon (O. tshawytscha) (Stewart et al. 1981; Stewart and Binkowski 1986). For more details on this function, see Thornton and Lessem (1978) or Hewett and Johnson (1987: Consumption Model 3).

Respiration (R), the amount of energy in weight equivalents necessary to carry out standard and active metabolism, was modeled as:

$$R = a * W^b * F(t) * ACT$$

where:

W = fish weight (g),

a = intercept of the allometric function for respiration,

b = slope of the allometric function for respiration,

F(T) = temperature dependence function, and,

ACT = the increment for active metabolism.

Activity (ACT) is modeled as a constant times the resting metabolism; ACT is also called the "Winberg multiplier" (Winberg 1956). Specific dynamic action (SDA), also required, is calculated separately and added to respiration.

The temperature dependence function for respiration of Kitchell et al. (1977) was used in the northern squawfish bioenergetic model. This function (Respiration Model 2 of Hewett and Johnson 1987) increases from 0 at low temperatures to 1 at the optimum temperature (RTO) and back to 0 at the maximum temperature (RTM).

Waste losses are egestion plus excretion. Egestion is fecal matter and excretion is nitrogenous waste products. The model also considers the caloric density of prey types and predator, weight loss during spawning, and water temperature (see Hewett and Johnson 1987).

## Methods

Growth - Since little is known about the seasonal growth pattern or the cold-water (<10°C, e.g.) physiology of northern squawfish, all growth during a year was assumed to occur at temperatures above 10°C. The greater-than 10°C period at McNary Dam for 1983-86 was between April, 13 - November, 3, which was the period modeled. Carline (1987) also assumed growth only above 10°C when modeling largemouth bass.

Consumption - Vigg et al. (1988) and unpublished FWS analyses have noted increasing ration with increasing predator size for northern squawfish in the BRZ of McNary Dam. Vigg and Burley (MS), however, did not find a significant effect of predator weight upon maximum consumption rate; most variation in their experiments was explained by temperature. We set the allometric consumption slope coefficient (CB) to 0 and the intercept (CA) to 0.4 (Table 3). CA was determined from Figure 4 of Vigg and Burley. Parameters of the temperature dependence function (Table 3) for consumption were fit by Vigg and Burley (MS) to laboratory feeding data with good success ( $R^2 = 0.97$ ).

Respiration - No studies have been done on the metabolic requirements of northern squawfish so data from related species (Sacramento squawfish Ptychocheilus grandis; carp Cyprinus carpio) were used where possible. Parameter values for ACT and SDA are "generic" values used for a variety of predators in previous studies (Hewett and Johnson 1987). Table 4 lists parameters used in initial model exercises.

Waste Losses - Egestion was modeled as a constant proportion of consumption (Kitchell et al. 1977) while

Table 3. Consumption parameters used in bioenergetic modeling of northern squawfish. Parameter names are the same as those used by Hewett and Johnson (1987).

Parameter	Value	Description	Source
CA	0.4	Intercept for max. cons.	Based on Vigg & Burley (MS)
CB	0.0	Coefficient for max. cons.	Based on Vigg & Burley (MS)
CQ	0	Temp. when dep. equals K <sub>l</sub>	Vigg & Burley (MS)
CT0	21.5	Temperature for optimum cons.	Vigg & Burley (MS)
CTM	21.5	Temp. for opt. consumption	Vigg & Burley (MS)
CTL	27	Upper temp.	Vigg & Burley (MS)
CK1	0.001	Temp. depend. lower	Vigg & Burley (MS)
CK4	0.01	Temp. depend. upper	Vigg & Burley (MS)

Table 4. Respiration parameters used in bioenergetic modeling of northern squawfish. Parameter names are the same as those used by Hewett and Johnson (1987).

Parameter	Value	Description	Source
RA	0.0108	Intercept for respiration	Hewett & Johnson (1987)
RB	-0.20	Coefficient for respiration	Basu (1959)
RQ	2.44	Q <sub>10</sub> at 10-25 deg	Calculated from Cech et al. (1990)
RTO	27	Temperature for optimum resp.	Black (1953)
RTM	29	Max. temperature when resp.=0	Black (1953)
ACT	1.0	Activity	Hewett & Johnson (1987)
SDA (S)	0.172	Specific Dynamic Action	Hewett & Johnson (1987)

excretion was considered a constant proportion of consumption minus egestion; egested calories cannot be excreted. Previous studies (Hewett and Johnson 1987; Bartell et al. 1986, e.g.) indicate that proportional descriptions of waste are probably adequate for modeling growth or consumption. The egestion parameter (FA) used was 0.104 (largemouth bass: Hewett and Johnson 1987; Rice et al. 1983) while the excretion parameter (UA) was 0.068 (largemouth bass: Hewett and Johnson 1987).

Northern Squawfish Diet - Four diet categories (salmonids, non-salmonids, invertebrates, and miscellaneous) were considered in the model. For all years (1983-86) and months (April-August) combined, salmonids were 66.7% of the diet, non-salmonid fish were 14.2%, and invertebrates, mostly crayfish, were 16.3% (Poe et al. 1988). A monthly summary of diet categories and caloric densities is provided in Table 5. Diet composition varied by time of year and by predator size (Poe et al. 1988; FWS unpublished data).

An age-at-length key for northern squawfish in John Day Reservoir (Vigg et al. 1988) was used to assign ages to unaged, but measured, fish for diet analyses. Weight (g) was estimated from length (mm), when required, based upon a relationship computed from 5,460 northern squawfish collected in John Day Reservoir and in John Day Dam tailrace:

$$\text{Weight} = 10^{-5.116} * \text{Length}^{3.085} \quad R^2 = 0.98$$

Caloric Density - Caloric density of spring chinook smolts was estimated at selected locations during their outmigration and found to be similar between Priest Rapids Dam and Jones Beach (Rondorf et al. 1985). An energy density of 1,030 calories/g wet weight (Rondorf et al. 1985) was used for juvenile salmonids throughout the simulation period. Energy density of non-salmonid fishes was set to 1,000 Cal/g (Hewett and Johnson 1987). Invertebrates in the diet were primarily amphipods (Corophium) and crayfish (Poe et al. 1988). Amphipods have an approximate energy density of 934 Cal/g and decapods 1,077 Cal/g (Cummins and Wuycheck 1971; Stewart et al.

Table 5. Proportions of major diet categories in northern squawfish guts collected from John Day Reservoir and tailrace during 1983-1986. The "Other" category was plants, detritus and unidentifiable material.

Diet Category	Apr	May	Jun	Jul	Aug
Salmonids	0.676	0.726	0.461	0.810	0.438
Non-salmonids	0.194	0.121	0.166	0.072	0.233
Invertebrates	0.101	0.129	0.322	0.106	0.291
Other	0.026	0.022	0.050	0.010	0.036
N	566	1072	1192	875	1077

1983); the invertebrate food category was assigned an energy density of 1,006 Cal/g. The diet category was assumed to be largely indigestible material (chitin, scales, insects, plant material, etc.) and was given an arbitrary energy density of 500 Cal/g.

Northern squawfish caloric density is not known and was set to 1,000 Cal/g (Hewett and Johnson 1987). Seasonal changes in caloric density of the predator can be modeled, but lack of data prevented such detailed efforts in the present model.

Spawning Losses - Weight loss due to spawning can be accounted for in the northern squawfish bioenergetic model. Jeppson and Platts (1959) estimated fecundity and gonad weight in gravid northern squawfish females in Idaho and found that "In larger female squawfish, eggs may total 100,000 or more, averaging [12.5%] of the body weight". They observed spawning during a one month period in late spring or early summer. In John Day Reservoir, spawning occurred in June through early July, while the gonadosomatic index peaked at about 7% for females and 3% for males (Vigg and Prendergast, unpublished MS). Female northern squawfish in the reservoir lost about 6%

of their body weight between June 9, 1982 and mid-July, 1982. Spawning weight loss in the model was set to 6% of total body weight and occurred on June 15th. All cohorts modeled were assumed to be mature adults.

Temperature - Average monthly temperature was calculated from Army Corps of Engineers data collected at McNary Dam (ACOE 1983-1986).

Sensitivity Analysis - To guide further model development, sensitivity of model output to individual bioenergetic parameters was examined. Simulations were for a single cohort of 0-year old northern squawfish; 8-year old fish were chosen since they weighed about 626-779 g (Vigg et al. 1988), which included the mean weight of all fish captured in John Day Reservoir (772 g; Vigg et al. 1988). Sensitivity was explored by individually varying parameters  $\pm 10\%$  and comparing accumulated smolt consumption (g) with a standard simulation. Temperature parameters were varied by  $\pm 1^\circ\text{C}$ . Parameter values in the standard simulation were described above and are listed in Tables 4-6.

Parameter sensitivity was calculated by the method of Kitchell et al. (1977); this method has also been used in other bioenergetic studies (Bartell et al. 1986; Adams and DeAngelis 1987). Sensitivity values were normalized to the standard simulation by:

$$S(p) = (p * \text{delta } x) / (x * \text{delta } p)$$

where  $S(p)$  = sensitivity for parameter  $p$ ,  
 $p$  = standard parameter value,  
 $\text{delta } p$  = input deviation of parameter  $p$ ,  
 $X$  = standard value of accumulated consumption, and,  
 $\text{delta } x$  = deviation of accumulated consumption due to  $\text{delta } p$ .

A sensitivity of 1.0 means that a parameter change of 10% produces a 10% change in the output variable. Efforts to

improve the bioenergetics model would be focused on parameters with high sensitivities, where small errors could cause the largest change in model output.

Sample Size Requirements - Approximate sample sizes were calculated to answer the question: "How many fish within an age group are required to detect weight changes during spring or summer sampling periods?". Three potential sampling intervals, from May to July, July to September, and May to September, were examined (Table 6). Predicted weights from the simulations on three dates (May 15, July 15 and September 15) were used to calculate sample sizes. Standard deviations of predicted weights, which were necessary for sample size calculations, were estimated using aged northern squawfish (N=266) collected in John Day Reservoir during 1985 (ODFW, data provided by BPA). The mean coefficient of variation for age-specific weights during 1985 (26.7%) was used to compute standard deviations of weights on sample dates. Weights were assumed to be normally distributed about the mean.

## Results

Seasonal Growth - For the period modeled (April 13-November 3), individual predators first showed a gradual weight loss followed by a rapid increase in weight during July, August and September (Figure 4). Spawning in June produced a small weight loss, which was rapidly recovered (Figure 4). This pattern of weight change was probably driven largely by water temperature in the river. Average temperature at McNary Dam during 1983-86 increased from about 9°C in April to over 15°C in June; July through September temperatures were over 19°C (data from ACOE).

Smolt consumption increased rapidly in the spring to a maximum during July (Figure 4), when 5-6 g of juvenile salmonids were consumed in a day by an 8-year-old northern squawfish. The spring outmigration of smolts was not obvious

Table 6. Number of aged northern squawfish necessary to distinguish seasonal weight changes during three periods. Type I error was set to .05, Type II error was .10, and a one-tailed test was specified.

Age	Sample Period					
	May - July		July - September		May - September	
	Sample Size	Percent Weight Change	Sample Size	Percent Weight Change	Sample Size	Percent Weight Change
4	84	8.6	7	30.4	4	41.6
5	89	8.2	8	28.7	4	39.2
6	166	6.1	13	22.3	7	30.0
7	249	5.1	17	19.3	10	25.2
8	274	4.7	18	18.6	11	24.2
9	325	4.3	20	17.5	12	22.6

in the specific consumption curve (Figure 4), possibly because metabolic needs were lower when water was cool.

Ration Comparisons - To make some comparisons of predicted and observed consumption rates, the bioenergetics model was run using data specific to John Day Reservoir during 1983-86. Total ration and salmonid ration for 8-year-old northern squawfish predicted by the model were compared with ration estimates made in the Boat Restricted Zone and the pool of John Day Reservoir by Vigg et al. (1988). Vigg et al. (1988) sampled over 4,700 northern squawfish and estimated consumption by a modification of the Swenson and Smith (1973) technique.

Total ration predictions by the bioenergetic model were fairly close to estimates for the John Day pool, except during May (Figure 5). In May, total ration in the pool ( $18 \text{ mg}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$ ) was over twice that predicted by the bioenergetics model ( $7 \text{ mg}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$ ). During other months, there was less than a  $4 \text{ mg}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$  difference between the model and field data. The

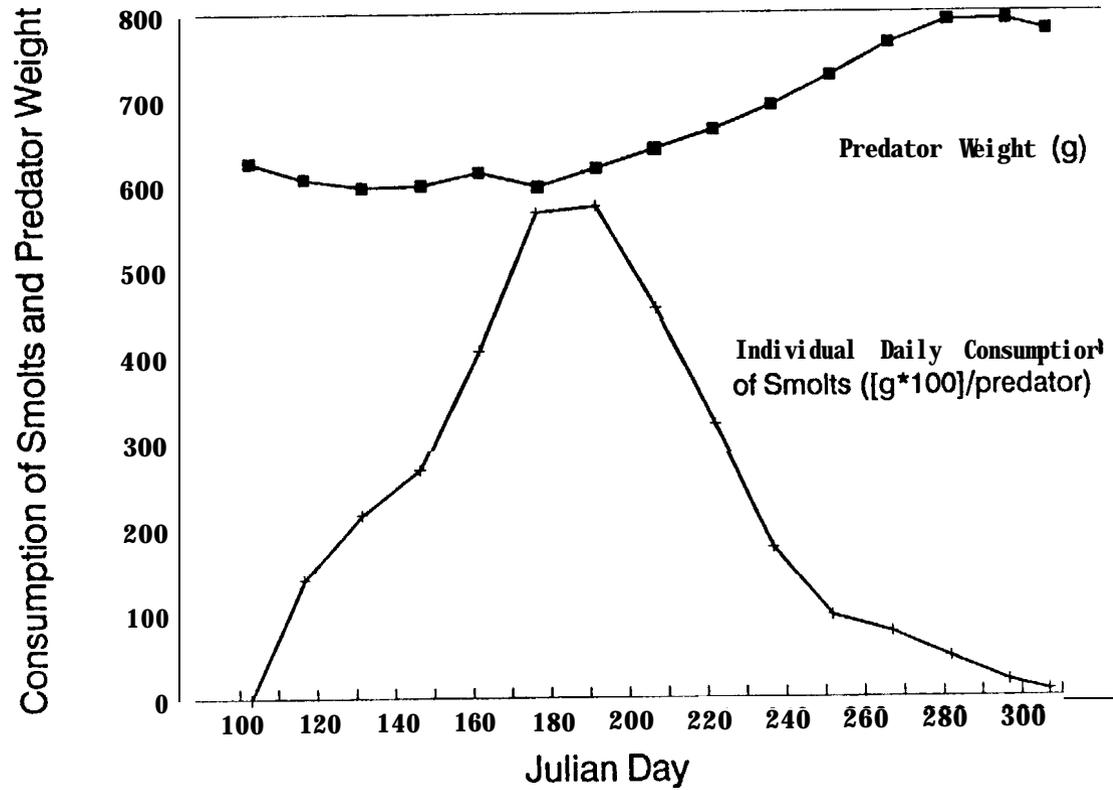


Figure 4. Northern squawfish weight and daily consumption of smolts predicted by the bioenergetics model. Simulation was for an 8-year-old predator and results were plotted for each 15 days between April 13 and November 3 (the greater-than 10°C period).

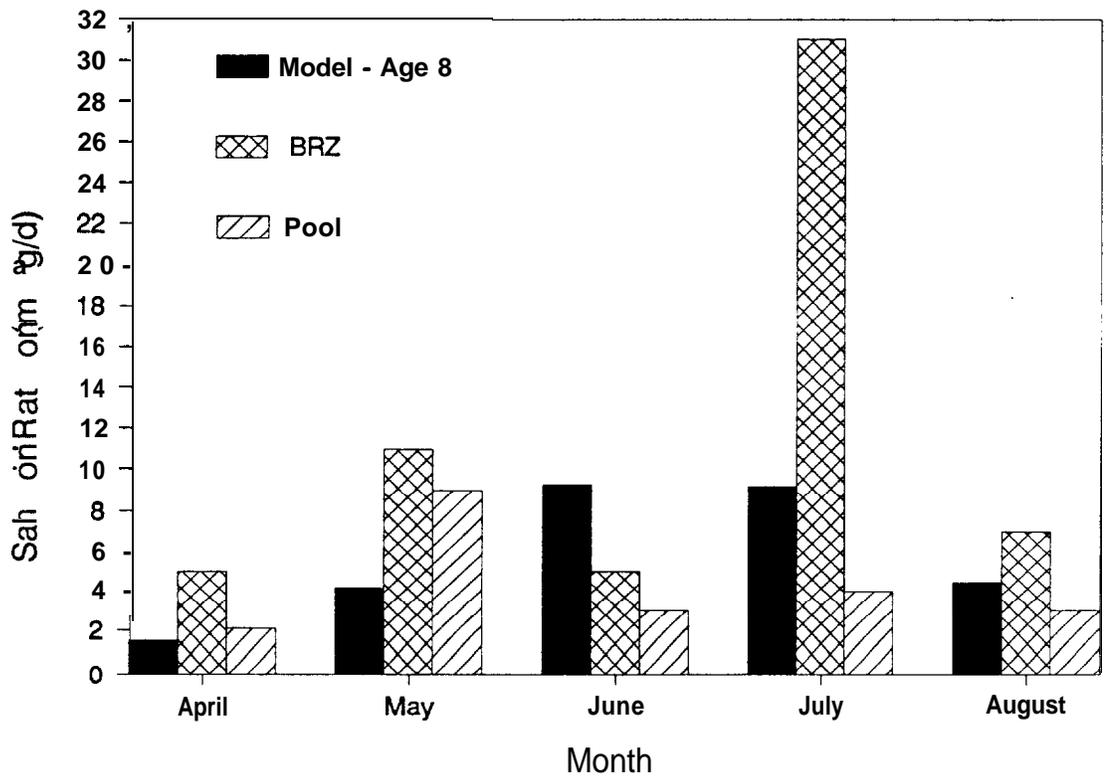
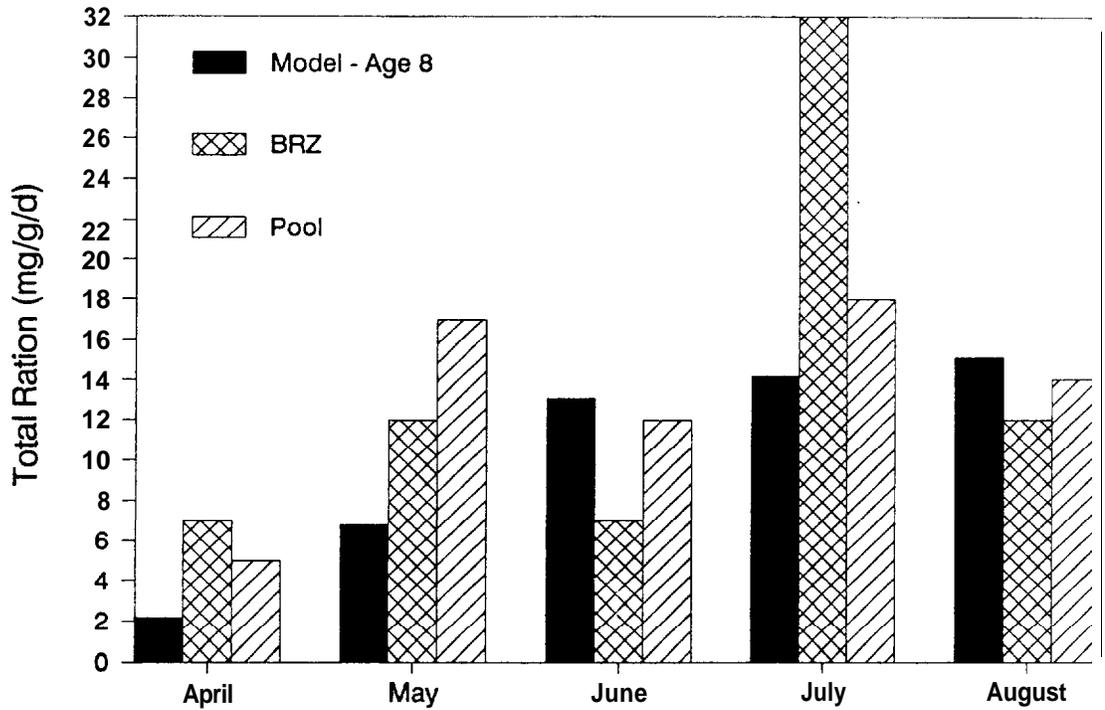


Figure 5. Comparison of rations predicted by the bioenergetics model with data collected in John Day Reservoir during 1983-86. Model predictions were for an 8-year-old fish sampled on the 15th day of the month. Total ration and salmonid ration were taken from Vigg et al. (1988: Figs. 2 and 3). The reservoir was divided into Boat Restricted Zone (BRZ) and Pool.

model was less effective at predicting ration within the BRZ, especially in July when consumption was very high in the Boat Restricted Zone. Salmonid ration predictions and observations were similar to those for total ration, although the June prediction was also higher than observed consumption in both the pool and BRZ (Figure 5).

Sensitivity Analysis - Consumption of juvenile salmonids in the model was most sensitive to respiration parameters (Figure 6). Deviations of several respiration parameters produced relatively large changes in smolt consumption, while variation in maximum consumption, excretion, and egestion parameters produced relatively small changes in the output. Accumulated salmonid consumption was most sensitive to the maximum temperature at which respiration was zero (RTM), where a  $-1^{\circ}\text{C}$  change caused consumption to change by about 25% (Figure 6). Consumption was moderately sensitive to the activity parameter (ACT) and to the caloric density of northern squawfish.

Ageing - Some ageing of northern squawfish in the Columbia River has been done by (Beamesderfer et al. 1987); no ageing was done during the current project. Beamesderfer et al. (1987) found northern squawfish as old as 17 years by counting scale **annuli**. During 1983-86, median age, after adjusting for gear vulnerability, ranged between 4 and 9 years old (Beamesderfer et al. 1987). Reader agreement between separate age determinations was variable but declined with increasing age. Experienced readers had over 50% agreement on age determinations when fish were 9 years old or less.

For bioenergetics modeling, northern squawfish would be categorized into six age groups: 4 years or less, 5, 6, 7, 8, and greater than 8 years. Four-year-old fish are just large enough to consume outmigrating juvenile salmonids (Poe et al. 1988; Vigg et al. 1988). Fish older than 8 years were relatively hard to age by counting scale annuli (Beamesderfer et al. 1987); also, consumption rate differences between older fish are probably small, compared to younger, faster-growing

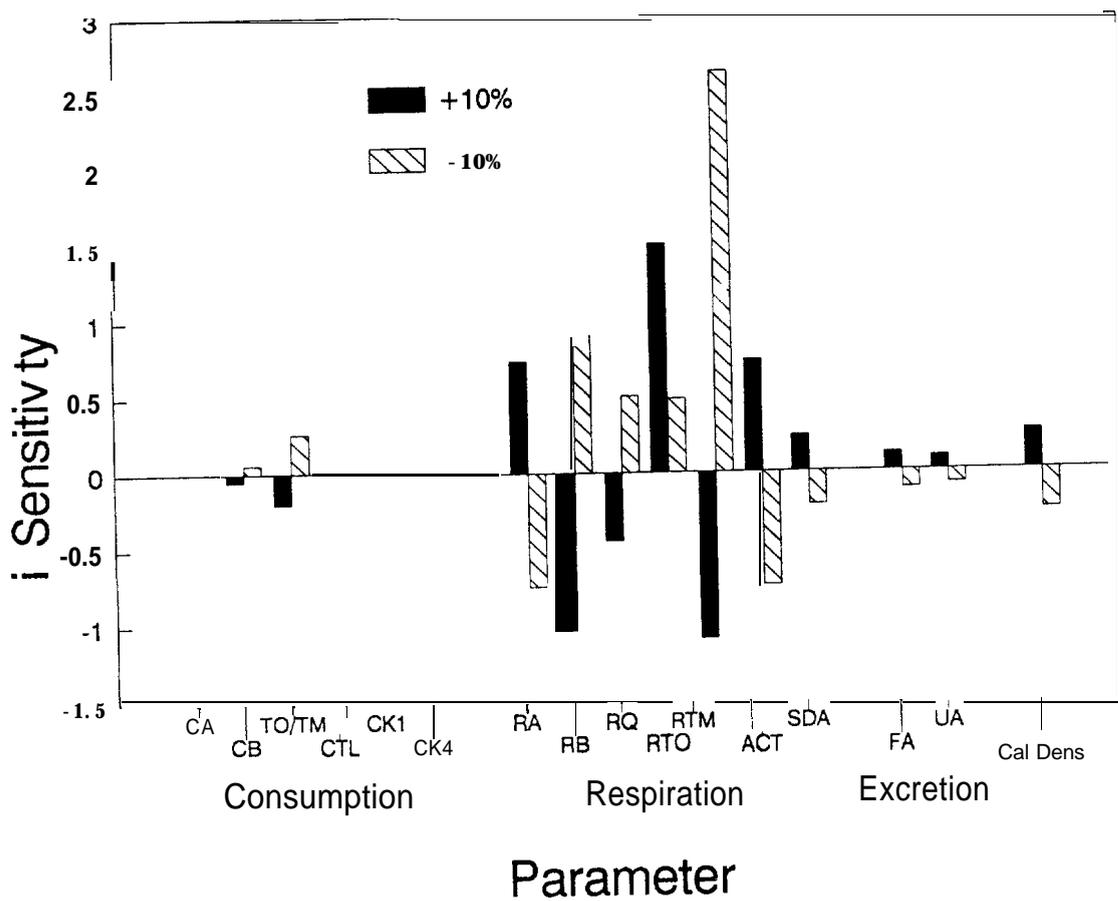


Figure 6. Sensitivity of the northern squawfish bioenergetic model to  $\pm 10\%$  deviation in input parameters. Accumulated **smolt** consumption between April and October was the tested output variable. Temperature parameters were varied  $\pm 1^\circ\text{C}$ , rather than 10%. Parameter names, descriptions and standard values are described in the text. "Cal dens" refers to predator caloric density.

individuals. Grouping age 8 and older fish would also reduce the amount of effort required to age very old fish. Otoliths and other bony structures will be examined for possible use in ageing work and to verify scale-ageing methodology.

Sample Size Requirements - Minimum sample size varied depending upon the growth interval examined (Table 6). The proportional growth of individuals between May and July was relatively low (see Figure 4, e.g.), being about 4-9% depending upon fish age; the sample sizes required to detect this difference were large (Table 6). Between July and September, the percent weight change was much higher (17-30%; Table 6), and fewer individuals would be needed to detect this change, compared to the May-July period. Simulated growth from May to September was greatest and less than 20 fish per age class would be required to detect seasonal growth changes from May to September (Table 6). Older age groups required larger samples since the proportional weight change declined with increasing age.

### Discussion

Ration comparisons of model predictions and field data were meant as a rough guide to potential model performance. A more complete analysis would include all age classes and the proportions of the population within each age class. The above comparisons do, however, suggest that bioenergetic modeling has good potential for estimating consumption, especially within the pool of a reservoir. The slightly poorer performance of the model for predicting salmonid rations suggests that diet proportions and caloric densities of prey types and predator should be re-examined.

Consumption estimation using bioenergetic models has been shown in several studies to be sensitive to respiration parameters, and relatively insensitive to maximum consumption parameters (Kitchell, 1977; Stewart et al. 1983; Cui and

Wootton, 1989). Bartell et al. (1986) concluded that a model of alewife consumption was most sensitive to the temperature dependence of respiration and consumption, requiring accurate data on the thermal history of the fish. Results of our sensitivity analysis, and the shortage of species-specific metabolic data (Table 5), suggest that respiration experiments could improve the bioenergetics model.

Although sample size estimates were approximate, requiring assumptions about seasonal growth patterns and variance about the mean weights, some conclusions could be drawn. The bioenergetics approach would probably not allow separation of consumption into early and late-season components because of sampling considerations. Estimates of consumption for the early smolt outmigration period (April-June) would not be feasible due to slow predator growth and the large sample size needed to detect growth. Bioenergetic-based consumption estimates should be only for spring-fall or summer-fall periods when the growth increment is relatively large and detectable with about 20 fish per age group.

## SECTION II. PREDATOR-SMOLT DYNAMICS

Three aspects of predator-smolt dynamics were included as tasks in the 1989-90 study plan. Additional data were needed on the functional relationship between predators and prey to accurately model and understand the interaction and the influence of physical parameters.

The Columbia River Ecosystem Model (CREM) was developed for John Day Reservoir to explore predation and evaluate predator control efforts. CREM was based primarily upon the functional response of predators to varying prey density. Further data were needed to refine the functional response relationship and to test assumptions of the model. Other modeling approaches were also being considered by researchers in the region and discussion was necessary to resolve problems and plan effective programs. The three parts of this Section address some of these problems.

### Maximum Consumption Experiments

Experiments to measure the maximum consumption rate of northern squawfish within the laboratory were completed and a manuscript (Vigg and Burley MS) has been submitted for publication. See Appendix A.

### Predator-Prey Modeling Workshop

A workshop was held in May, 1989 to discuss modeling approaches and problems related to predator-prey dynamics in the Columbia River. The workshop was coordinated by a steering committee that included Jim Petersen (committee chairman) and Tom Poe of the FWS. Results of the workshop have been published as a separate Bonneville Power Administration report (Fickeisen et al., 1990).

## 1988 Consumption Rate Data

### Introduction

The functional relationship between prey density and predator consumption rate is an important prerequisite to understanding and modeling predator-prey dynamics. Earlier work on juvenile salmonid predation within John Day Reservoir (Poe and Rieman, 1988) provided data on the functional response of predator consumption rates to prey density (Vigg 1988). In general, consumption rates increased in a nonlinear manner as smolt density increased, reaching an asymptotic rate of about five smolts per predator per day when smolt density was very high. The transition and asymptote of the functional response were, however, defined by relatively few data points (Vigg 1988; his Figure 4, e.g.).

Since the functional response of predator consumption rate is central to current predation models and interpretations (Beamesderfer et al. 1988; Poe et al. 1988; Vigg 1988; Fickeisen et al. 1990), definition of the shape and asymptote of this function are crucial. Therefore, we initiated a limited effort to collect data on northern squawfish consumption that would supplement existing data and further define the functional response curve. This section reports our efforts to refine the functional response curve.

### Methods

Northern squawfish were sampled within the McNary Dam boat restricted zone on nine days during July, 1988 (Table 7). Predators were collected through the diurnal period by electroshocking at stations near the navigation lock guidewall, the outlet of the smolt bypass, the spill gates and on the Oregon shoreline. Field methods, laboratory methods, and data analyses were described in earlier predator-prey studies (Poe

et al. 1988; Vigg et al. 1988).

Calculations of consumption by northern squawfish were based upon the method of Swenson and Smith (1973) as modified by Vigg et al. (1988). Calculation of smolt density for the McNary BRZ used Migrational Index (MI) data from McNary Dam (Fish Passage Center, 1988), daily flow at McNary Dam (Koski et al. 1989) and formulae in Vigg (1988). Variability in daily consumption was estimated by the bootstrap resampling technique (Efron 1982; Boisclair and Leggett 1988). Briefly, data sets of daily predator records were resampled by computer to generate new record combinations for consumption calculation. Each resample contained the same number of predator records as the original sample (Efron 1982). The original data were resampled 500 times to produce a frequency distribution of consumption rates for a given day.

## Results

During nine days of sampling, 607 northern squawfish were captured (Table 7). Catch per effort during night (1900-0700 hours) was about 23 predators/hour, compared to 14 predators/hour during the day (0700-1900 hours). Water temperature at McNary Dam increased less than 1°C during the 11-day sampling period (Table 7).

Smolt passage at McNary Dam during the summer of 1988 had several peaks, with the largest occurring in late June (Figure 7). Although our sampling missed the highest passage, fish collected between July 18-20 coincided with a fairly high period of smolt passage (Table 7; Figure 7). Collections made from July 14-16 occurred during a time of intermediate, declining passage and sampling from July 22-24 was during a period of relatively low passage.

Ration and salmonid consumption rate were estimated for each collection day (Table 8); number of fish used in consumption analyses was less than the total catch because of

Table 7. Summary of northern squawfish catch, water temperature and passage index at McNary Dam for sampling dates in July, 1988. Temperature data are from Army Corp of Engineers and juvenile salmonid passage data are from the Fish Passage Center.

Date	Total Catch of Northern Squawfish	River Temperature (°C)	Juvenile Salmonid Passage Index at McNary Dam
7/14/88	104	19.4	164,460
7/15/88	57	19.4	93,160
7/16/88	26	18.9	52,300
7/18/88	78	18.9	163,634
7/19/88	114	18.9	256,900
7/20/88	40	20.0	170,599
7/22/88	58	20.0	29,585
7/23/88	105	20.0	26,133
7/24/88	25	20.0	23,467

size requirements (only predators  $\geq 250$  mm were included) and exclusion of torn or damaged guts. Analyses for daily sample size requirements (see Section I of this report, Direct Consumption Indexing) suggested that 15-30 northern squawfish per day was adequate to describe consumption variation. The minimum number of northern squawfish in a daily sample during July, 1988 was 20, with most sample days having over 40 predators (Table 8).

Salmonids constituted from 73% to 99% (mean 91%) of the northern squawfish diet during the nine sample days in July 1988. During the period of highest consumption (July 18-20), the predator's diet was almost completely salmonids (96-99%). Vigg (1988) also observed a high proportion of smolts in the diet of northern squawfish when density of juvenile salmonids was high.

Total daily ration (Table 8) for northern squawfish varied

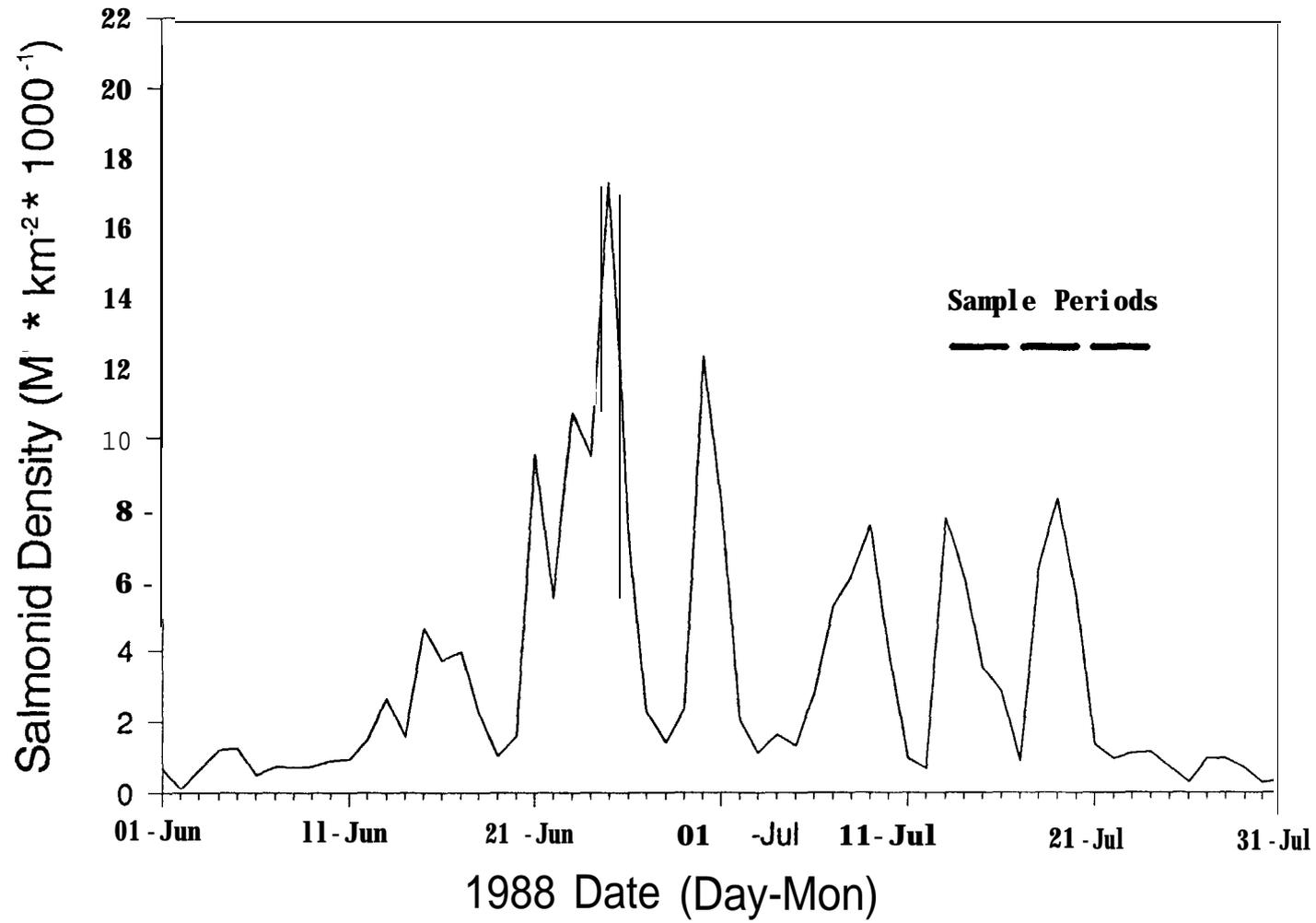


Figure 7. Smolt density in the McNary BRZ during June and July, 1988. The three 3-day sampling periods are also shown.

Table 8. Total daily ration, salmonid ration and salmonid consumption rate for northern squawfish in the McNary Dam tailrace during July, 1988. Bootstrap analyses were done on each sample date to estimate standard deviations, which are shown in parentheses.

Date	# of Predators	Total Ration (mg·g <sup>-1</sup> ·d <sup>-1</sup> )	Salmonid Ration (mg·g <sup>-1</sup> ·d <sup>-1</sup> )	Salmonid Rate (smolts' predator <sup>-1</sup> ·d <sup>-1</sup> )
7/14/88	94	19.4 ( 3.7)	18.5 ( 3.8)	1.27 (0.28)
7/15/88	50	30.3 ( 8.3)	28.4 ( 8.0)	1.84 (0.58)
7/16/88	21	12.0 ( 6.2)	8.8 ( 5.6)	0.40 (0.27)
7/18/88	53	74.6 (12.9)	73.9 (12.9)	4.39 (0.90)
7/19/88	98	78.8 ( 7.3)	75.9 ( 7.7)	4.20 (0.59)
7/20/88	47	42.7 ( 6.1)	42.3 ( 5.9)	2.24 (0.41)
7/22/88	52	12.9 ( 4.5)	11.3 ( 4.3)	0.55 (0.21)
7/23/88	95	13.4 ( 2.8)	10.4 ( 2.7)	0.42 (0.10)
7/24/88	20	15.5 ( 4.5)	14.9 ( 4.9)	0.69 (0.21)

Table 9. Functional response parameters for data (n=32) from late June through August of 1983-86 and July, 1988. Parameters were fit by nonlinear, least-squares regression.

$$\text{Equation: Consumption} = C_{\max} / [1 + (a * \exp(b * \text{Smolt Density}))]$$

Parameter	Estimate	Standard Error
C <sub>max</sub>	3.915	0.664
<b>a</b>	10.951	4.828
<b>b</b>	-0.618	0.194

from 12 mg prey per g predator (July 16) to over 78 mg prey per g predator (July 19). Daily variation in salmonid ration and number of salmonids consumed per day was closely correlated with total daily ration (Table 8). Variability of the bootstrap distributions was also similar for the three estimated rates (Table 8); coefficient of variation of the mean was less than 40%, except for July 16 when the coefficient of variation was as high as 67%. Bootstrap distributions of total ration, salmonid ration and salmonid consumption rate were tested for normality by chi-square tests. About half (12 of 27) of the tested distributions were significantly different from a normal distribution, being skewed toward low rations or rates.

A functional response curve was fit to consumption rates estimated during July, 1988 and late June-August, 1983-86. All sample dates later than June 20 with 15 or more predators ( $\geq 250\text{mm}$ ) were selected from the 1983-86 database. Most dates were in July or August, but four days in late June (23-26) of 1986 were also included. A total of 32 daily consumption estimates were analyzed. Data were fit to an exponential sigmoid function of the form:

$$\text{Consumption} = C_{\text{max}} / [1 + (a * \exp(b * \text{Smolt Density}))] \quad (1) .$$

Equation parameters are given in Table 9 and data are plotted in Figure 8. Analysis of variance for the regression was highly significant ( $F=41.6$ ;  $df\ 3,29$ ;  $P < .001$ ) and about 66% of the variation was explained.

### Discussion

The maximum rations and rates observed on July 18-19 were comparable to maximums estimated in predator-prey studies for 1983-1988 (Vigg et al. 1988; Vigg 1988). During the earlier studies, maximum salmonid consumption rate was about 5 smolts .

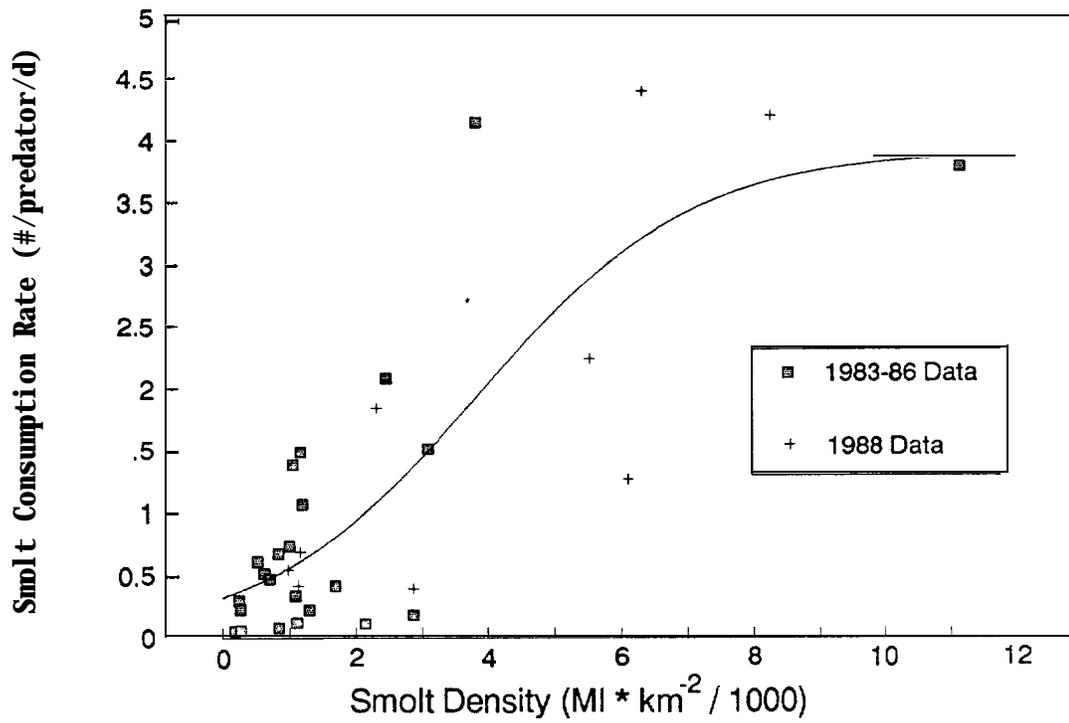


Figure 8. Smolt consumption rate by northern squawfish as a function of smolt density in the McNary BRZ. Data are from late June through August of 1983-86 and July 1988. The functional response curve was fitted to the data using an exponential sigmoid equation (see text and Table 9).

northern **squawfish**<sup>-1</sup> · **d**<sup>-1</sup> and maximum salmonid ration was roughly 65 mg salmonid · g northern **squawfish**<sup>-1</sup> · **d**<sup>-1</sup> (Vigg 1988, his Figure 4). During 1988, maximum consumption rate was 4.4 smolts · northern **squawfish**<sup>-1</sup> · **d**<sup>-1</sup> and maximum salmonid ration was 76 mg salmonid · g northern **squawfish**<sup>-1</sup> · **d**<sup>-1</sup> (Table 8). The lower consumption rate but higher ration in 1988, compared to Vigg's (1988) results, suggest that the juvenile salmonids during 1988 were slightly larger than those consumed during 1983-86.

Consumption data from 1988 refined the shape and asymptote of the functional response curve, particularly at intermediate and high juvenile salmonid densities (Figure 8). At low salmonid densities, the 1988 results were similar to earlier data. Between smolt densities of 3000-6000 MI/km<sup>2</sup>, consumption estimates were fairly scattered, as might be expected since consumption changes rapidly within this range. Four estimates of consumption, over a broad range of prey densities, were near 4 smolts · northern **squawfish**<sup>-1</sup> · **d**<sup>-1</sup>, apparently representing maximum daily consumption for "average" predators. Addition of July, 1988 data for this analysis provides two new values to define the asymptote of consumption and, also, a couple of values in the mid-density range. Future analyses of functional response relationships of northern squawfish should also benefit from the July, 1988 data set.

### SECTION III. SELECTIVE PREDATION

The U.S. Fish and Wildlife Service (FWS) and the Oregon Department of Fish and Wildlife (ODFW) recently completed a six year study to determine the significance of predation on juvenile salmonids in John Day Reservoir. Study results indicated that predation may account for the majority of previously unexplained smolt mortality and that northern squawfish was the dominant predator (Poe and Reiman 1988). Northern squawfish consumption rates on juvenile salmon were significantly greater and their abundance was from 12 to 18 times higher in the boat restricted zone (BRZ) below McNary Dam than in other areas of the reservoir (Beamesderfer and Rieman 1988; Vigg et al. 1988). These results suggest that northern squawfish may be selecting smolts that are killed, injured, stressed, or disoriented as a consequence of dam passage. If northern squawfish are selective for certain types of prey or substandard (*sensu* Temple 1987) prey are more vulnerable to predation, the overall significance of predation, as a mortality factor must be reassessed.

Studies of feeding preferences are fundamental to understanding basic trophic relationships and can help define the functional role of predaceous fishes. Selective predation occurs when the relative frequencies of prey types in the predator's diet differ from the relative frequencies in the environment (Chesson 1978). Prey vulnerability, as an adjunct to selective predation, may be the primary determinant of what actually is eaten (Allen et al. 1987).

There is substantial literature on selective predation by fish, with the emphasis on prey size (Wright 1970; Werner and Hall 1974; Post and Evans 1989) or species selection (Espinosa and Deacon 1973; Hargreaves and Le Brassuer 1985; Wahl and Stein 1988). Several investigators have found that various stressors, including exposure to temperature shock or contaminants (Hatfield and Anderson 1972; Coutant 1973; Coutant

et al. 1974) handling (Olla and Davis 1989), and crowding (Congleton et al. 1985) increased the vulnerability of prey to predators. Out-migrating juvenile salmonids exhibit a variety of physiological and morphological conditions due to disease, stress, and physical injury (Maule et al. 1988; Koski et al. 1989; Rondorf et al. 1989). Dam passage related and multiple cumulative stresses have been shown to maximally stress salmonids (Barton et al. 1986; Maule et al. 1988), perhaps rendering them unable to cope with subsequent stresses such as predation. Although the theory of selection upon substandard individuals is widely accepted, evidence supporting such a theory is scarce (Temple 1987).

The objectives of this work were to develop the laboratory and field protocols necessary to evaluate predator selection and prey vulnerability. To address these objectives, we designed and constructed laboratory systems and conducted preliminary experiments on selective predation by northern squawfish on three categories of substandard vs. standard juvenile salmonids: dead vs. live; injured vs. non-injured; and stressed vs. unstressed. To conduct selective predation experiments in a more realistic environment, we planned some experiments using net pens anchored in backwaters of the Columbia River. Although we obtained net pens and located potential test sites, subsequent agency review precluded us from conducting any field experiments.

## Methods

Test fish. -Northern squawfish (>275 mm FL), collected from the Columbia River by electroshocking, were used as predators for all experiments. Fish were acclimated in the wet laboratory (described below) for 3 weeks prior to experiments. During the acclimation period and between experiments, northern squawfish were fed a maintenance diet of live juvenile coho salmon Oncorhynchus kisutch from the Willard National Fish

Hatchery.

Subyearling spring chinook salmon O. tshawytscha (average weight 10.8 g  $\pm$  0.2 g SE; average length 96.0 mm  $\pm$  0.6 mm SE) from the Little. White Salmon National Fish Hatchery were used as prey in all experiments and as test fish in stress evaluations (see below). Fish were maintained in either the wet laboratory or in outside circular tanks receiving well or river water. Both chinook and coho salmon were fed a maintenance diet (0.7% body weight/day) of BioMoist feed.

Variable derivation. -Several variables are important to selective predation experiments, including water temperature, photoperiod, numbers of predators and prey, experiment duration, and predator starvation period. This section briefly describes the derivation of variables for our selective predation experiments; unless noted, the values stated below were used in all experiments.

We used water temperatures of 15-17°C for all experiments. Beyer et al. (1988) reported that northern squawfish feed well at these temperatures and the range approximates Columbia River water temperatures during early to mid-summer periods. Photoperiod for all experiments was set at 15-h-daylight and 9-h-darkness. We used relatively low light levels (3.2 lux) during daylight periods because preliminary experiments revealed northern squawfish did not feed well in bright light. Either two or three predators were used in experiments conducted in circular tanks (see below); we noted in earlier trials that northern squawfish appear to be rather social and do not feed well in isolation. The number of prey offered to predators was set at 10 of each treatment group per predator. This number is twice the maximum consumption rate reported for northern squawfish (Appendix A) and would prevent any problems with prey depletion or total prey consumption. We typically allowed predation to proceed for 24 h, a time frame covering the diel cycle and often used in other studies (Congleton et al. 1985; Wahl and Stein 1988). We chose 48 h for our predator

starvation period to ensure high feeding motivation. This period was based upon maximum prey intercapture times of northern squawfish calculated from field data (USFWS, unpublished data).

### Live vs. Dead Selection Experiments

Experimental apparatus. -All experiments were carried out in 1.5 m diameter flow-through circular tanks receiving an input flow of 19 L/min. Water was recirculated by two centrifugal pumps, heated by an electric heater, and sterilized by ultraviolet light. Water was also passed through a bio-filter to remove ammonia and other particulate waste. Lighting was provided by six 50-W incandescent lights set on timers to control photoperiod. Lights were aimed toward the ceiling to provide indirect light intensities of 3.2 lux at mid-water level. A complete description of this laboratory is given by Lucchetti and Gray (1988).

Experimental design. -To begin an experimental trial, three northern squawfish were stocked in each of six circular tanks and allowed one week to acclimate. On the morning following predator starvation, 180 chinook salmon were killed by a blow to the head and given an adipose fin clip to distinguish them from live prey should any live prey die during the experiment. Live and dead prey (30 of each) were then introduced simultaneously into each tank and predation allowed to proceed for 24 h. All remaining prey were identified and enumerated at the end of each trial. Each tank was considered a replicate; we conducted 3 trials of this experiment, each with 6 tanks, for a total of 18 replicates. For each trial, either new predators were used, or fish were moved among tanks to minimize habituation or learning. Experiments were conducted from July to September, 1989.

A one-way analysis of variance failed to reveal any time or tank effects during the experiments, therefore all data were

combined for analysis. A 2 x 2 contingency test of proportions (z) using arc sine transformed data (Snedecor and Cochran 1980) was used to test the hypothesis that the proportions of dead and live prey consumed were equal.

#### Injured vs. Non-injured Selection Experiments

The same laboratory as described above was used to conduct these experiments. We used descaling to injure prey because descaling is widespread in out-migrating juvenile salmon and its effects on their vulnerability to predation are unknown. Because of the amount of time required to manually descale fish, we reduced the number of predators to two per tank and therefore used fewer prey fish.

We conducted three different trials of this experiment: 50% descaling with a 1 h recovery; 50% descaling with a 24 h recovery; and 20% descaling with a 1 h recovery. We replicated the 50% descaling trials three times and the 20% trials four times. To begin a trial, 20 prey (per tank) were anesthetized in 50 mg/L MS-222 and descaled on both sides of the body using a soft-blade stainless steel spatula to achieve the required scale loss. Fish were returned to the circular tanks for the appropriate recovery period. Equal numbers of control fish were placed in the anesthetic, allowed the appropriate recovery period, and received no further disturbance. Following recovery, both groups were rapidly transferred from the recovery tank to the experimental tank. After 24 h, surviving prey were netted from the tanks and identified. Because these experiments were very preliminary, the results will be presented in a qualitative context.

#### Stressed vs. Unstressed Selection Experiments

Experimental apparatus. -We constructed a rectangular, completely recirculating fiberglass raceway to conduct these

experiments (Figure 9). Our intentions with this system were to create a large, flowing water environment in which to conduct experiments. The raceway measures 7.6 m long, 1.2 m wide, and 1.2 m deep; total volume was 11,326 L. Water flow was produced by a 450 gal/min centrifugal pump. The pump intake was a 15 cm diameter port, reduced to flow through 10 cm diameter PVC pipe, and ultimately discharged into the raceway through a 10 cm diameter port. A butterfly valve was installed in the PVC pipe to control flow. Water level was maintained by a standpipe in the downstream end; makeup water was added at approximately 1.0 L/min. Water was also passed through a mechanical filter and ultraviolet light sterilizer by a separate pump unit. After leaving the filtration unit, water passed through an electrical heating unit and a cracking column before being discharged into the raceway and a prey holding tank (see below). Lighting, comprised of three 50-W incandescent lights evenly spaced above the raceway, was controlled by a timer to simulate ambient photoperiod. Plexiglas windows covered with nylon screen were inserted at even intervals along the side of the raceway and curtains erected around the perimeter to permit observation without disturbing the fish. An aluminum tank (1.2 m long, 0.7 m wide, 0.6 m deep) was installed at the upstream end above the raceway to hold juvenile salmon prior to predation trials. The tank could be partitioned into two equal size compartments with a removable divider and received raceway water that re-entered the raceway via standpipes. Fish were released into the raceway by removing the standpipes. Screening covered the tank and raceway to prevent fish from jumping out.

To facilitate fish observations, we installed a video system consisting of two cameras, one underwater and the other above the raceway (Figure 9). The underwater camera was mounted on a PVC frame at mid-water level in the downstream end of the raceway. The above tank camera was mounted on rafters above the raceway towards the downstream end. Both cameras

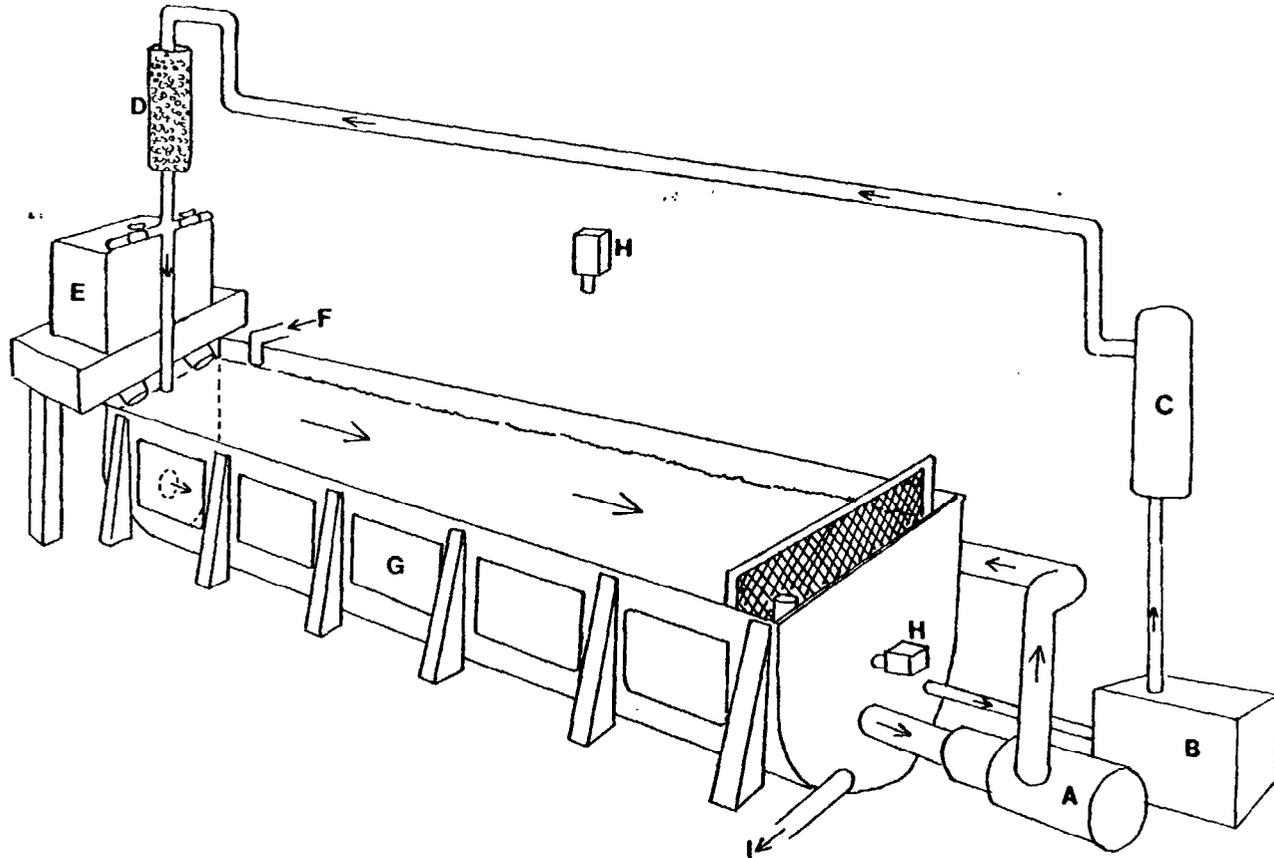


Figure 9. Diagram of the raceway used for selective predation experiments. Arrows indicate direction of water flow. A = recirculation pump; B = filtration unit; C = heater; D = cracking column; E = prey holding tank; F = makeup water inlet; G = Plexiglas window; H = video cameras; I = outflow drain.

could be connected individually to a time lapse video recorder and monitor. To clarify images and estimate northern squawfish reaction distance, we analyzed and image enhanced video tapes using JAVA video analysis software (Jandel Scientific, Corte Madera, California).

Experimental design.-We evaluated the efficacy of the raceway system by conducting a series of preliminary selective predation trials using stressed and unstressed juvenile spring chinook salmon. These trials allowed us to evaluate the conduct of predation experiments in this type of system, assess the relative importance of several variables (e.g. starvation period, experiment duration, etc.), and refine experimental designs for future, more rigorous tests.

Experiments were conducted from August to October, 1989. Prior to all trials, chinook salmon were graded by size, cold branded on either the right or left side, and held separately in 0.6 m diameter, 100 L tanks for at least two weeks to allow recovery. For each trial, 10 northern squawfish were transferred from the circular tanks to the raceway; 50 chinook salmon from each cold branded group were transferred to and held separately in the holding tank. One group of right- or left-branded prey was randomly designated as the treatment (stressed) group; the other group served as controls. All fish were held for at least 1 week to acclimate to the new environs and maintained as described previously. Individual northern squawfish were used for a maximum of two trials.

To begin a trial, predators were starved for 24 h prior to introducing the prey. At 0700 h on the morning following predator starvation, the group of prey designated as treatment fish were subjected to three acute handling stresses separated by 1 h, a procedure modified after Barton et al. (1986). Our objective was to use a stressor severe enough to elicit physiological stress responses similar to those obtained by Maule et al. (1988) for chinook salmon subjected to the bypass, collection, and handling procedures at McNary Dam. The

handling stress consisted of netting the fish out of the aluminum tank, holding them in the air for 30 s, and returning them to the tank for recovery. At 0.5 h following the third stress, 10 fish from each group were netted and immediately placed in a lethal dose of MS-222 (200 mg/L). The fish were then removed from the anaesthetic and bled into an ammonium heparinized capillary tube after severance of the caudal peduncle. Plasma was obtained by centrifugation and stored at -15°C for future assay of physiological indicators (see below). Immediately following removal of fish for blood samples, we removed the tank divider and allowed the remaining control and treatment fish to mix for 5 min; they were then released into the raceway by removing the standpipes. Predation was allowed to proceed for 6 or 24 h (three replicates each): all surviving prey were netted from the raceway and identified and enumerated.

We used the depredation ratio (dp: Barns 1967; Coutant 1973) to assess predator preference:

$$dp = i_t/i_c$$

where  $i_t$  and  $i_c$  are the instantaneous mortality rates for treatment and control fish, respectively;  $i = -\log, S$ , where  $S$  is the survival ratio, i.e. the number of fish at the end/number at start. A dp value of 1 indicates equal susceptibility to predation of treatment and control fish. Chi-square analysis was used to test for differences in survival rate between treatment and control groups.

### Stress Evaluations

To document the effects of the multiple handling stress used in the selective predation experiments, we conducted experiments on chinook salmon to assess the dynamics of plasma cortisol (a primary physiological indicator of stress) and the

behavioral reaction to a negative stimulus. These experiments were relevant because the stress response can be extremely polymorphic due to genetics, rearing history, species, etc. and would provide objective measures of the severity of the stress.

Physiological experiments. -Fifty juvenile spring chinook salmon were maintained in each of eight 0.6 m diameter circular, flow-through tanks receiving 4 L/min heated well water (12-14°C). The fish were fed a maintenance diet of BioMoist feed, held under natural photoperiod, and acclimated for at least two weeks before experimentation.

Tanks were randomly assigned to one of four treatments: (1) a single handling; (2) two handlings separated by 1 h; (3) three handlings, each 1 h apart; or (4) undisturbed controls. This design resulted in two replicate tanks per treatment. The handling stress was as described previously. Blood samples were collected from 5 fish just before each stress, and at 0.5, 1, 3, 6, 12, 24, and 168 h after the final stress. The experiment was conducted on August 7-8, 1989.

Plasma was obtained and stored as previously described. Plasma cortisol was determined by <sup>3</sup>H-radioimmunoassay (Foster and Dunn 1974), as modified by Redding et al. (1984) for use with salmonid plasma. All data were tested for homogeneity of variance (Bartlett's test, Sokal and Rohlf 1981). Those found to be homogenous were treated by analysis of variance followed by Fisher's Least Significant Difference Test at the 5% probability level (Ott 1977). Data with heterogeneity among the means were either transformed to stabilize the variance or subjected to a Kruskal-Wallis One-Way Analysis by Ranks (Sokal and Rohlf 1981).

Behavioral experiments. -As a behavioral indicator of the effects of stress, we determined the response times for individual fish by exposing them to a sudden, continuous light and measuring the time it took for each fish to swim to cover, as in the protocol of Sigismondi and Weber (1988). Juvenile spring chinook salmon used in these experiments were maintained

as described for the physiological experiments. Behavioral experiments were carried out in two "Living Stream" systems (Frigid Units, Inc., Toledo, Ohio) each 2.13 m long, 0.60 m wide, and 0.56 m deep. Water was completely recirculated by an electric pump, maintained at 10-12°C by a cooling unit, and passed through a two-stage filtering system. Divider screens were used to partition the tank into one large (1.1 m x 0.6 m) and one small (0.5 m x 0.6 m) compartment. Fitted over the large compartment was a permanent black plastic cover mounted on a wooden frame; the cover extended 0.45 m from a screen shielding the pump and then angled (90°) down into the water before stopping approximately 10 cm from the bottom. A 75-W incandescent light was positioned 40 cm above the small compartment. The small compartment, and the remaining open area of the large compartment, were fitted with a removable black plastic sheet mounted on a wooden frame.

Fish were exposed to one of three treatments: (1) three handling stresses separated by 1-h; (2) an agitation stress; and (3) undisturbed controls. The agitation stress consisted of filling a 19 L bucket approximately 1/3 full with water, netting fish from the experimental tank to the bucket, and pouring the fish into another bucket located on the floor; water fell a distance of about 1.0 m. The buckets were then switched and the process continued for 4 min before returning the fish back to the experimental tank. The behavioral response was then measured immediately or after a 1, 3, 6, or 24 h recovery period. The treatments were randomly assigned to consecutive days, with tanks serving as replicates on any given day.

To conduct a test, six fish were introduced into the small compartment of each tank and allowed to adjust overnight. The lights were off and covers in place. The next morning, all fish (except controls) were rapidly netted out of the tank and subjected to either the handling stress or the agitation stress. After the stress, fish were returned to the small

compartment and the cover replaced until the next stress or until the appropriate recovery time had elapsed. After the recovery period, the cover was removed while simultaneously removing the divider screen and switching on the light. We switched off the pump/chiller unit 0.5 h before application of the stimulus to reduce disturbance to the fish. The time taken for each fish to swim under the permanent cover was recorded using an event recorder. A test ended when the last fish reached cover or after 30 min, whichever came first. General notes on the behavior of the fish were also recorded, such as whether fish moved in and out of cover and their degree of excitability. On each day, the initial stress was applied at 0800 h for fish in one tank and 0.5 h later in the second tank; data from the six fish in each replicate tank were pooled for analysis.

The median response time was calculated for each pooled sample because the data were not distributed normally. Within each recovery period, we used a nonparametric Kruskal-Wallis test to determine whether the medians differed among the treatment groups. When medians differed significantly, a nonparametric Tukey-type multiple comparison procedure was used to determine where differences actually existed (Zar 1984).

## Results

Although we present some results in a statistical context, we considered the use of statistics only another part of developing protocols. We reiterate that the results should be considered preliminary and caution readers to interpret them as such.

Live vs. Dead Experiments. -Northern squawfish consumed significantly more dead than live chinook salmon ( $z = 6.28$ ,  $P < 0.001$ ). Overall, 65% of the prey consumed were dead. In only 4 of 18 replicates were live prey consumed at a higher frequency than dead prey (Figure 10). Dead prey typically sank

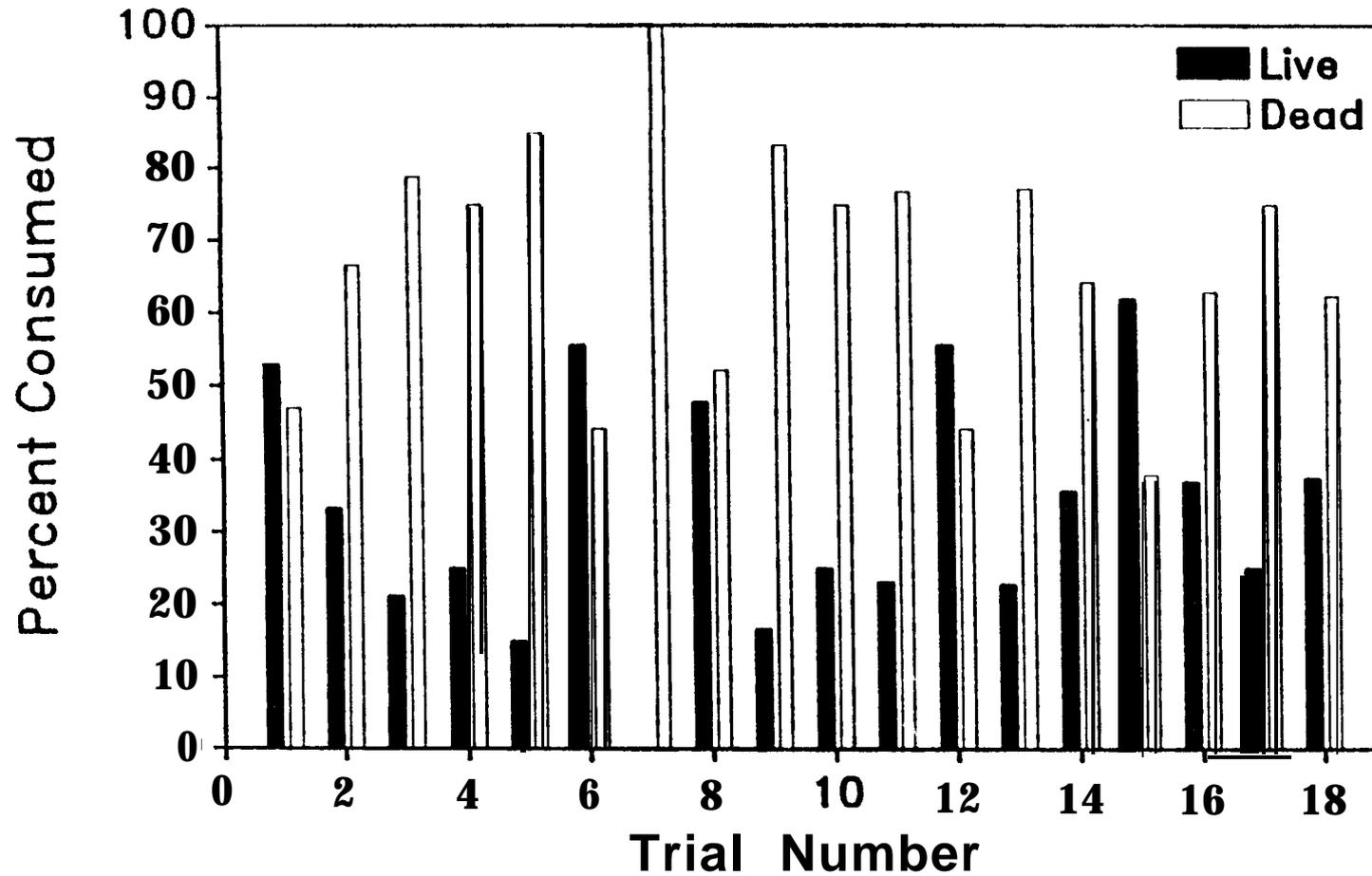


Figure 10. Percent of live or dead spring chinook salmon consumed by northern squawfish during selection experiments. Bars are the values for 18 replicates.

to the bottom of the tank within 1 min of release.

Injured vs. Non-injured Experiments.-In all trials, northern squawfish consumed more descaled than non-descaled chinook salmon (Table 10). Overall, > 80% of all prey consumed were descaled. During all trials, there was a high rate of regurgitation (Table 10), with more descaled fish regurgitated than controls. Of all prey attacked and ingested, almost 60% were regurgitated.

Stressed vs. Unstressed Experiments.-There was little evidence for northern squawfish selection of either stressed or unstressed prey, regardless of experiment duration. For both the 6 and 24 h experiments, the survival rate of stressed and control prey did not differ (6 h:  $\chi^2 = 1.275$ ,  $P > 0.05$ ; 24 h:  $\chi^2 = 0.6976$ ,  $P > 0.05$ ). The depredation ratios of fish in the 6 and 24 h experiments were 1.075 and 0.949, respectively, indicating that both stressed and control groups were equally susceptible to predation. Plasma cortisol in stressed fish was significantly higher than controls for all trials (Figure 11).

Physiological experiments.-Plasma cortisol responded in a cumulative manner with each application of an additional acute disturbance (Figure 12). For all groups, cortisol peaked at 0.5 h after the final stress and returned to control levels by 6 h.

Behavioral experiments.-The median response times of stressed fish were significantly greater than those of controls immediately after the stress and at 1 and 6 h post stress (Figure 13). Control fish typically darted to cover within 10 s. Fish receiving the agitation stress showed the longest response time immediately after the stress but responded similarly to controls for other recovery periods. The response times in fish receiving the handling stresses showed a somewhat inconsistent pattern, being high at 0, 1, and 6 h and low at 3 and 24 h after the final stress. Response times of all fish were highly variable, as indicated by the range of times for each group (Table 11).

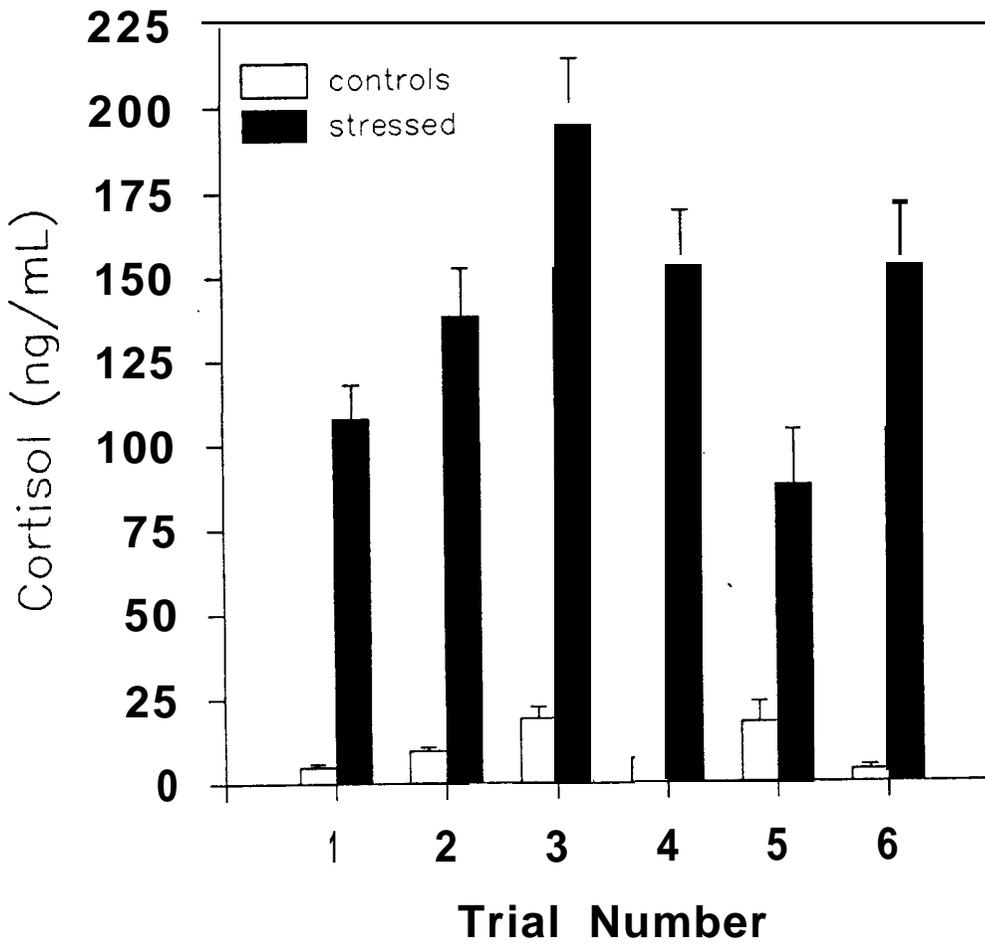


Figure 11. Mean (and SE) plasma cortisol titers of juvenile spring chinook salmon (N = 10) subjected to three 30-s handling stresses separated by 1 h relative to unstressed controls prior to being exposed to predation.

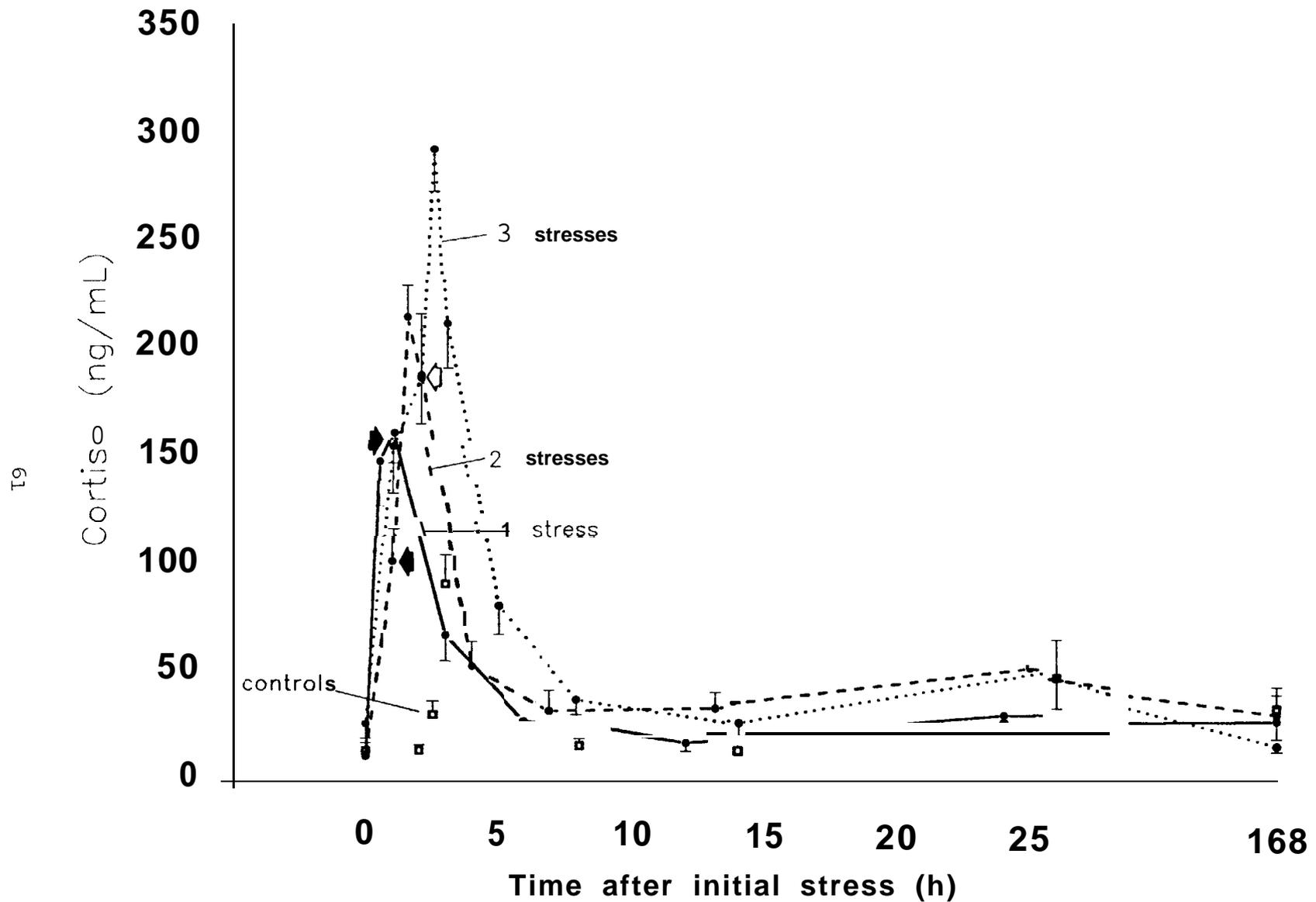


Figure 12. Mean (and SE) plasma cortisol dynamics of juvenile spring chinook salmon (N = 10) subjected to either one, two, or three 30-s handling stresses separated by 1 h. Solid arrows indicate application of the second stress and the open arrow indicates application of the third.

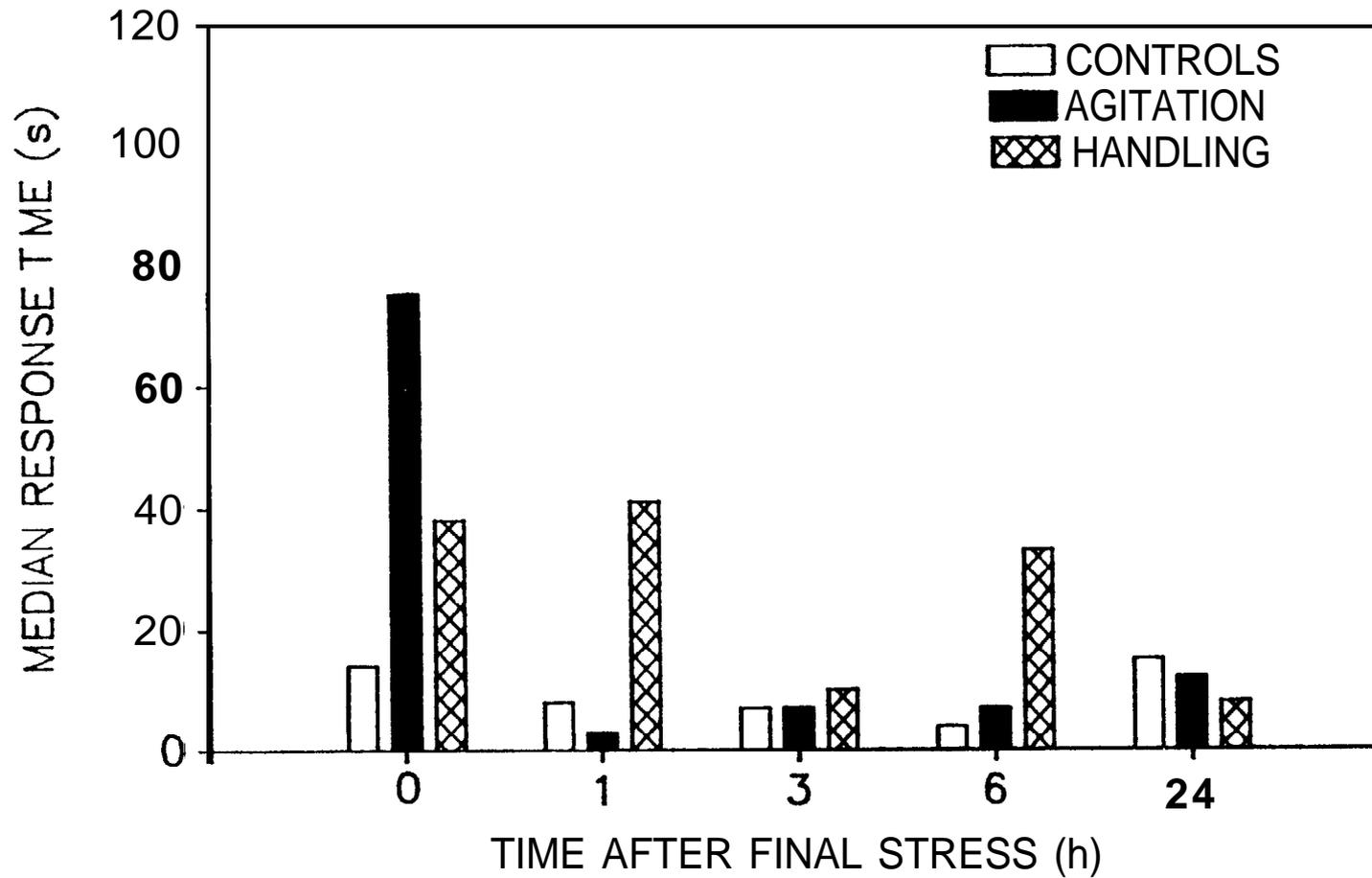


Figure 13. Median response times to swim to cover after exposure to a continuous bright light for juvenile spring chinook salmon subjected to three 30-s handling stresses separated by 1 h, an agitation stress, or unstressed controls.

Table 10. The number of prey available, eaten, and regurgitated in selective predation experiments using descaled and non-descaled prey. Data are from all replicates of an experiment combined. DSC = descaled fish; CON = controls.

Experiment description	Prey					
	Available		Eaten		Resurgitated	
	DSC	CON	DSC	CON	DSC	CON
50% descale 24 h recov.	60	60	8	0	17	0
50% descale 1 h recov.	60	60	13	2	14	2
20% descale 1 h recov.	60	60	10	1	7	4

Table 11. Range of times (s) for juvenile spring chinook salmon to swim to cover after exposure to a sudden bright light for fish subjected to an agitation stress, three handling stresses, or unstressed controls. Recovery time is the time (h) allowed after application of the stress before testing.

Recovery Time (h)	Response Time (s)		
	Controls	Agitation Stress	Handling Stress
0	0.4-35.7	7.5-1070.8	2.6-140.8
1	2.3-331.9	0.3-327.5	2.4-682.2
3	0.4-182.8	0.2-568.1	1.0-38.6
6	0.4-41.7	0.2-1535.1	0.4-167.1
24	3.3-679.2	5.6-237.0	1.4-90.4

Upon exposure to the light, control fish were typically very excited and swam erratically around the tank before seeking cover. It was common, however, for stressed fish to remain motionless or swim slowly on the bottom. When stressed fish finally sought cover, they typically did so in a smoother, less erratic fashion. Several fish in all groups repeatedly darted in and out of cover.

### Discussion

The primary objective of this work was to develop the laboratory and field protocols necessary to evaluate selective predation and prey vulnerability. The laboratory we used for live vs. dead and injured vs. non-injured selection experiments has been in use since 1985 (Lucchetti and Gray 1988). Several key attributes were addressed in the design of this laboratory, including disease control, water quality, temperature control, and efficiency and ease of operation. Lucchetti and Gray (1988) successfully held northern squawfish for up to 6 months with no disease or water quality problems and Beyer et al. (1988) conducted northern squawfish consumption rate experiments in this laboratory. Because of the history of this wet laboratory, little modification was necessary and we believe it worked well in allowing us to evaluate selective predation under the simplest of conditions.

Our results revealed that northern squawfish preferred dead over live prey by almost a 2 : 1 ratio. In contrast, Irvine and Northcote (1983) found that underyearling rainbow trout Oncorhynchus mykiss preferred live over dead prey and concluded that body movement was an important prey characteristic to stream rearing trout. Also, Howick and O'Brien (1983) noted that prey movement increased reaction distance and probability of attack in largemouth bass Micronterus salmoides. We believe our results may provide some insight into the functional role of northern squawfish as a predator. If, for example, northern

squawfish prefer dead over live prey, these fish may be more of a scavenger than an active predator. This information would question the overall impact northern squawfish have as predators on juvenile salmonids. Assuming that food quality (Krebs and Davies 1978) of live and dead prey are similar, selecting dead prey may be energetically most efficient. As Stein (1977) points out, predators should minimize costs associated with locating, pursuing, capturing, and ingesting prey while maximizing benefits from prey consumption in terms of energy gained. Of course, more research is needed to determine whether this situation occurs in the natural environment.

Our results suggested that descaled prey were more vulnerable to predation than non-descaled prey. Scales are usually lost when smolts are trapped and transported around dams or when they pass through turbines and spillways. The importance of the integument complex in maintaining ionic and osmotic balance is well known (Van Oosten 1957) and the effects of descaling on fish mortality have received much attention. Kostecki et al. (1987) noted that scale loss was greater in Atlantic salmon Salmo salar that had died within 48 h after passage through a turbine than in fish that survived longer or controls. Gloss and Wahl (1983), assessing the mortality incurred by migrating Atlantic salmon passing through turbines, found a significant relationship between fish size and mortality. Bouck and Smith (1979) found that experimental removal of 25% of slime and scales from coho salmon caused no deaths in fresh water but 75% mortality within 10 d in sea water. In this study, we held 27 fish that had been descaled 20% to evaluate delayed mortality. Within 2 h, 5 fish had died and others were showing abnormal swimming behavior. Within 24 h, 44% of the fish had died and some abnormal swimming behavior was still present. The results of these studies suggest that descaling per se may contribute little to mortality and that physical trauma may be more important, as stated by Kostecki et

al. (1987). It is possible that short term behavioral and physiological effects of descaling and physical trauma may affect the performance of juvenile salmon, thereby rendering them more vulnerable to predation. More research is needed to fully evaluate this hypothesis.

We constructed the raceway tank to create a larger, more realistic environment in which to conduct selection experiments. Several investigators have used large, flowing systems to study the ecology and behavior of stream fish (Mason and Chapman 1965; Reeves et al. 1983; Fausch and White 1983; Congleton et al. 1985). From an operational standpoint, we encountered few problems and the system was virtually maintenance free. Water velocity varied throughout the length of the raceway (Table 12) with a turbulent surface flow created in the most upstream 2.5 m and flow smoothing out further downstream. Because of the single discharge port, two large back eddy areas were created that provided refuge for both northern squawfish and juvenile salmon. Some improvements to be made in the future would include developing an easier way to collect fish out of the raceway, producing more uniform, laminar flow, and using screens to partition the tank into smaller areas.

We encountered several problems with our video system which must be solved if video is to be used for behavior observations. Although several investigators have successfully used video as an aid in the study of fish behavior (Rand and Lauder 1981; Webb 1984a; Blaxter and Batty 1987; Lawrence and Smith 1989), such filming was often done using small aquaria where the logistical difficulties were reduced. The sheer size of the raceway created field of view problems for both the overhead and underwater cameras. The overhead camera field of view covers only a small fraction of the length of the raceway; wide angle lenses or multiple cameras could be

Table 12. Water velocities at selected distances from the upstream end of the fiberglass raceway used for selective predation experiments. Surface, mid, and bottom refer to the position in the water column where the measurement was taken.

Distance (m)	Water velocity (cm/s)			
	Surface	Mid	Bottom	
Upstream	1	12.2	73.2	18.3
	2	15.2	67.1	36.6
	3	21.3	42.7	18.3
	4	9.1	6.1	12.2
	5	15.2	9.1	3.1
	6	6.1	3.1	6.1
Downstream	7	9.1	6.1	9.1

used to overcome this problem. It was common for predator-prey interactions to occur very close to the underwater camera and out of the field of view, thereby precluding them from being recorded on tape. Recent work in the raceway has shown that partitioning off the area around the camera and using brighter lights provided underwater videotape of much better quality. Water turbulence and surface glare were additional difficulties to overhead filming. Blaxter and Batty (1985) used a raft of transparent Perspex set at an angle to eliminate light reflection during overhead filming: it is possible that a modification of that method could reduce turbulence and glare in the raceway. Perhaps the largest filming obstacle to be overcome is the ability to film in the dark. Although infra-red-sensitive TV cameras have been used successfully to study fish behavior in the dark (Blaxter and Batty 1985, 1987), the filming was done over relatively small areas. Our preliminary

experiments in the raceway indicated that much of the feeding activity of northern squawfish occurred at night. Indeed, Congleton et al. (1985) were unable to observe northern squawfish behavior in feeding experiments due to the nocturnal activity of the fish. Clearly, a more thorough understanding of northern squawfish behavior may be possible if we can solve the problems involved with filming in the dark.

Although northern squawfish did not show selection for stressed prey, conclusions based on this would be premature because these experiments have not been fully completed. Our intentions in conducting these experiments were to learn about the operation of the raceway, evaluate and manipulate important variables, observe fish behavior, and refine experimental designs; generating rigorous data from these experiments was of secondary importance. We used multiple acute handling stresses to produce a stress response similar to that obtained by Maule et al. (1988) for fish passing through the collection system at McNary Dam. Maule et al. (1988) noted three characteristics of the collection system: the system was stressful, the stresses were acute, and each element of the collection system had cumulative effects on the fish. Our multiple stress protocol could be described in a similar manner. Our peak cortisol values were similar to those obtained by Maule et al. (1988) and lower than those for fall chinook salmon used by Barton et al. (1986). One major difference in the three studies was recovery dynamics--our fish required 6 h for cortisol to return to control levels versus a recovery period of 12-48 h for fish used by Maule et al. (1988) and Barton et al. (1986). We believe that our multiple stress protocol, although physiologically disturbing to the fish, **was** probably missing some stressful elements that contribute to changes in prey vulnerability, notably physical trauma, disorientation, and fatigue. Future research will attempt to address this question.

The effects of stress on fish become apparent as sublethal

changes in a variety of blood constituents (see Mazeaud et al. 1977 and Schreck 1981 for reviews) and as general lethargic behavior (Bouck and Ball 1966; Sigismondi and Weber 1988). Sigismondi and Weber (1988) stated that a likely consequence of these effects is increased exposure and vulnerability to predation. Indeed, several investigators have found that exposure to temperature shock or contaminants increased the vulnerability of prey to predators (Hatfield and Anderson 1972; Coutant 1973; Coutant et al. 1974). Olla and Davis (1989) found that coho salmon stressed by 60 s of handling showed a decreased ability to avoid predators, but recovered from this effect in 90 min. Congleton et al. (1985) reported that vulnerability to rainbow trout and northern squawfish predation increased in several stocks of spring chinook salmon subjected to chronic crowding stresses.

The lack of northern squawfish selection for stressed prey may have been due to complications in experimental design and behavior of the juvenile salmon. For example, when predation was allowed to proceed for 24 h, almost all prey were eaten and the effects of stress were probably much reduced as time elapsed. Reductions in prey availability and consumption of all prey are important considerations in selectivity experiments (Barns 1967; Coutant et al. 1974). A more complicated problem, however, was the schooling behavior of the juvenile salmon. Just after release, salmon were scattered randomly throughout the raceway. After predator attacks started, most salmon would group together, move to the top of the water column, and remain tightly schooled. The advantages of schooling fish in countering predators has been well documented (see Pitcher 1986 for a recent discussion). We believe that stressed fish gained benefits from the school, even though on an individual basis performance capacity (*sensu* **Schreck 1981**) may be reduced; the end result is apparent random feeding by northern squawfish. Changes in experimental design, such as introducing groups separately or using shorter

experiment durations, may clarify selective predation on stressed fish and should provide needed insight into the relative vulnerability of stressed fish to predation.

Results of both the physiological and behavioral tests indicate that treatment fish exposed to predation were stressed. In the behavioral response test, although we adapted our procedures after Sigismondi and Weber (1988), the results were clearly different. Sigismondi and Weber (1988) reported median response times commonly  $> 1$  min and ranges that often spanned to 30 + min; we rarely achieved response times  $> 1$  min and our ranges were much smaller. There are several possible explanations for these discrepancies, including use of different strains and sizes of fish, different experimental systems, and our handling stresses separated by 1 h instead of 3 h. Nevertheless, we agree with the conclusion of Sigismondi and Weber (1988) that likely consequences of a large response time latency and lethargic behavior are increased vulnerability to predation or other environmental hazards. Given that predators attack using acceleration fast-starts that take  $< 1$  s (Webb 1976, 1984b) even slight changes in behavior could adversely affect fish survival.

We believe our laboratory experiments have provided some interesting results to test in the field, although the results should be considered preliminary and some experiments are not yet fully complete. The advantages of laboratory experiments are relative simplicity, and the ability to manipulate important variables and have adequate replication. Although the realism of laboratory experiments has often been questioned, Diamond (1986) noted that in some instances, particularly physiological or behavioral ecology, laboratory experiments can be quite realistic. We believe our results demonstrated that we have the facilities and experimental designs necessary to perform selective predation and prey vulnerability experiments. Future experiments will be aimed at a more rigorous evaluation of selective feeding of northern

squawfish, both in the laboratory and field, and evaluating how stress, injury, etc. might affect the relative vulnerability of juvenile salmon to predation.

## LITERATURE CITED

- Adams, S. M. and D. L. DeAngelis. 1987. Indirect effects of early bass-shad interactions on predator population structure and food web dynamics. In: Predation: Direct and Indirect Impacts on Aquatic Communities. W. C. Kerfoot and A. Sih (eds). University Press of New England, Hanover, NJ.
- Allen, J.D., A.S. Flecker, and N.L. McClintock. 1987. Prey preference of stoneflies: sedentary vs. mobile prey. *Oikos* 49:323-331.
- Amundsen, P. and A. Klemetsen. 1986. Within-sample variabilities in stomach contents weight of fish - implications for field studies of consumption rate. In: Contemporary Studies in Fish Feeding: the Proceedings of gutshop '84. Developments in Environmental Biology of Fishes 7. (C. A. Simenstat and G. M. Caillet, eds.). pp. 307-314. Boston, Dr. W. Junk.
- Anderson, R. M. 1965. Methods of collecting and preserving vertebrate animals. Bulletin No. 69, National Museum of Canada.
- Anonymous. 1987. Columbia Basin Fish and Wildlife Program. Northwest Power Planning Council, Portland, Oregon. 246 p.
- Bajkov, A. D. 1935. How to estimate the daily food consumption of fish under natural conditions. *Trans. Am. Fish. Soc.* 65:288-289.
- Barns, R. A. 1967. Differences in performance of naturally and artificially propagated sockeye salmon migrant fry, as measured with swimming and predation tests. *J. Fish. Res. Bd. Canada* 24:1117-1153.
- Bartell, S. M., J. E. Breck, R. H. Gardner, and A. L. Brenkert. 1986. Individual parameter perturbation and error analysis of fish bioenergetics models. *Can. J. Fish. Aquat. Sci.* 43:160-168.
- Barton, B.A., C.B. Schreck and L.A. Sigismondi. 1986. Multiple acute disturbances evoke cumulative physiological stress responses in juvenile chinook salmon. *Trans. Am. Fish. Soc.* 115:245-251.
- Basu, S. P. 1959. Active respiration of fish in relation to ambient concentrations of oxygen and carbon dioxide. *J. Fish. Res. Bd. Canada.* 16:175-212.

- Beamesderfer, R. C., R. E. Rieman, J. C. Elliott, A. A. Nigro and D. L. Ward. 1987. Distribution, abundance and population dynamics of northern squawfish, walleye, smallmouth bass, and channel catfish in John Day Reservoir, 1986. Annual Progress Report. Bonneville Power Administration, Portland, OR.
- Beamesderfer, R. C. and B. E. Rieman. 1988. Predation by resident fish on juvenile salmonids in a mainstem Columbia Reservoir: Part III. Abundance and distribution of northern squawfish, walleye, and smallmouth bass. In: Poe, T. P. and B. E. Rieman (eds.), 1988. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-86. Final Report, (Contracts DE-A179-82BP34796 and DE-A179-82BP35097) Bonneville Power Administration, Portland, OR.
- Beamesderfer, R. C., B. E. Rieman and S. Vigg. 1988. Simulation of predation by a resident fish on juvenile salmonids in a Columbia River reservoir. In: Poe, T. P. and B. E. Rieman (eds.), 1988. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-86. Final Report, (Contracts DE-A179-82BP34796 and DE-A179-82BP35097) Bonneville Power Administration, Portland, OR.
- Beyer, J. M., G. Lucchetti, and G. Gray. 1988. Digestive tract evacuation in northern squawfish (Ptychocheilus oregonensis). Can. J. Fish. Aquat. Sci. 45:548-553.
- Black, E. C. 1953. Upper lethal temperature of some British Columbia freshwater fish. J. Fish. Res. Bd. Can. 10:196-210. [Cited by Xi He, unpublished MS].
- Blaxter, J.H.S., and R.S. Batty. 1985. Herring behaviour in the dark: responses to stationary and continuously vibrating obstacles. J. Mar. Biol. Ass. U.K. 65:1031-1049.
- Blaxter, J.H.S., and R.S. Batty. 1987. Comparisons of herring behaviour in the light and dark: changes in activity and responses to sound. J. Mar. Biol. Ass. U. K. 67:849-860.
- Boisclair, D. and W. C. Leggett. 1988. An in situ experimental evaluation of the Elliott and Persson and the Eggers models for estimating fish daily ration. Can. J. Fish. Aquat. Sci. 45:138-145.
- Bouck, G.R. and R.C. Ball. 1966. Influence of capture methods on blood characteristics and mortality in the Rainbow Trout (Salmo aairdneri). Trans. Am. Fish. Soc. 95(2):170-176.

- Bouck, G. R. and S. D. Smith. 1979. Mortality of experimentally descaled smolts of coho salmon (Oncorhynchus kisutch) in fresh and salt water. Trans. Am. Fish. Soc. 108:67-69.
- Carline, R. F. 1987. Simplified method based on bioenergetics modeling to estimate food consumption by largemouth bass and northern pike. Trans. Am. Fish. Soc. 116:224-231.
- Cech, J. J., Jr., S. J. Mitchell, D. T. Castleberry, and M. McEnroe. 1990 (In Press). Distribution of California stream fishes: influence of environmental temperature and hypoxia. Environ. Biol. Fish.
- Chesson, J. 1978. Measuring preference in selective predation. Ecology 59:211-215.
- Congleton, J.L., T.C. Bjornn, B.H. Burton, B.D. Watson, J.I. Irving, R.R. Ringe. 1985. Effects of handling and crowding on the stress response and viability of chinook salmon parr and smolts. Completion Report to Bonneville Power Administration, Portland, Oregon, (contract number DE-AC79-83BP11196).
- Coutant, C. 1973. Effect of thermal shock on vulnerability of juvenile salmonids to predation. J. Fish. Res. Bd. Can.. 30:965-973.
- Coutant, C.C., H.M. Ducharme Jr. and J.R. Fisher. 1974. Effects of cold shock on vulnerability of juvenile channel catfish (Ictalurus punctatus) and largemouth bass (Micropterus salmoides) to predation. J. Fish. Res. Bd. Can.. 31: 351-354.
- Cui, Y. and R. J. Wootton. 1989. Bioenergetics of growth of a cyprinid, Phoxinus phoxinus (L.): development and testing of a growth model. J. Fish Biol. 34:47-64.
- Cummins, K. W. and J. C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. International Association of Theoretical and Applied Limnology, No. 18:1-158, Stuttgart, Germany.
- Diamond, J. 1986. Overview: laboratory experiments, field experiments, and natural experiments. Pages 3-22 in Diamond, J. and T.J. Case, eds. Community Ecology. Harper and Row Publishers, New York.
- Efron, B. 1982. The Jackknife, the Bootstrap and Other Resampling Plans. Society for Industrial and Applied Mathematics, Philadelphia, Pennsylvania. No. 38.

- Efron, B. and R. Tibshirani, 1986. Bootstrap methods for standard errors, confidence intervals, and other measures of statistical accuracy. *Statistical Science*, 1:54-77.
- Eggers, D. M. 1979. Comments on some recent methods for estimating food consumption by fish. *J. Fish. Res. Bd. Can.* 36:1018-1019.
- Elliott, J. M. and L. Persson. 1978. The estimation of daily rates of food consumption for fish. *J. Animal Ecol.* 47:977-991.
- Espinosa, F.A. Jr. and J.E. Deacon. 1973. The preference of largemouth bass (*Micronterus salmoides* Lacepede) for selected bait species under experimental conditions. *Trans. Am. Fish. soc.* 103:355-362.
- Fausch, K.D., and R.J. White. 1983. Sinuous stream aquarium to simulate lotic fish habitat. *Prog. Fish-Cult.* 45:113-116.
- Fickeisen, D. H., D. D. Dauble, and D. A. Neitzel. 1990. Proceedings of the predator-prey modeling workshop, Friday Harbor, Washington, May 16-19, 1989. Final contract (DE-AC06-76RLO-1830) completion report to Bonneville Power Administration, Portland, Oregon.
- Fish Passage Center. 1988. Weekly Reports.
- Foster, L.B., and R.T. Dunn. 1974. Single-antibody technique for radioimmunoassay of cortisol in unextracted serum or plasma. *Clinical Chemistry* 20: 365-368.
- Gloss, S. P. and J. R. Wahl. 1983. Mortality of juvenile salmonids passing through Ossberger crossflow turbines at samll-scale hydroelectric sites. *Trans. Am. Fish. soc.* 112:194-200.
- Hansel, H. C., S. D. Duke, P. T. Lofy, and G. A. Gray. 1988. Use of diagnostic bones to identify and estimate original lengths of ingested prey fishes. *Trans. Am. Fish. Soc.* 117:55-62.
- Hargreaves, N.B., and R.J. LeBrasseur. 1985. Species selective predation on juvenile pink (*Oncorhynchus sorbuscha*) and chum salmon (*O. keta*) by coho salmon (*O. kisutch*). *Can. J. Fish. Aquat. Sci.* 42:659-668.
- Hatfield, C.T., and J.M. Anderson. 1972. Effects of two insecticides on the vulnerability of Atlantic salmon (*Salmo salar*) parr to brook trout (*Salvelinus fontinalis*) predation. *J. Fish. Res. Bd. Can.* 29:27-29.

- Henchman, T. R. 1986. Distribution and food habits of northern squawfish, Ptychocheilus oregonensis (Richardson), and estimates of their consumption of migrating juvenile salmonids in John Day Reservoir and tailrace during the spring and summer, 1983. MS Thesis, University of Washington, Seattle.
- Hewett, S. W. 1989. Ecological applications of bioenergetics models. American Fisheries Society Symposium, 6:113-120.
- Hewett, S. W. and B. L. Johnson. 1987. A generalized bioenergetics model of fish growth for microcomputers. University of Wisconsin Sea Grant Institute, Report No. WIS-SG-87-245.
- Hewett, S. W. and B. L. Johnson. 1989. A general bioenergetics model for fishes. American Fisheries Society Symposium, 6:206-208.
- Howick, G.L., and W.J. O'Brien. 1983. Piscivorous feeding behavior of largemouth bass: an experimental analysis. Trans. Am. Fish. Soc. 112:508-516.
- Irvine, J.R., and T.G. Northcote. 1983. Selection by young rainbow trout (Salmo gairdneri) in simulated stream environments for live and dead prey of different sizes. Can. J. Fish. Aquat. Sci. 40:1745-1749.
- Jeppson, P. W. and W. S. Platts. 1959. Ecology and control of the Columbia squawfish in northern Idaho lakes. Trans. Am. Fish. Soc. 88:197-202.
- Kitchell, J. F. and J. E. Breck. 1980. Bioenergetics model and foraging hypothesis for sea lamprey (Petromyzon marinus). Can. J. Fish. Aquat. Sci. 37:2159-2168.
- Kitchell, J. F., D. J. Stewart and D. Weininger. 1977. Applications of a bioenergetics model to Yellow Perch (Perca flavescens) and Walleye (Stizostedion vitreum vitreum). J. Fish. Res. Bd. Can. 34:1922-1935.
- Koski, C. H., S. W. Pettit and J. L. McKern, 1989. Fish Transportation Oversight Team Annual Report-FY 1988; Transport Operations on the Snake and Columbia Rivers. NOAA Technical Memorandum NMFS F/NWR-25.
- Kostecki, P. T., P. Clifford, S. P. Gloss and J. C. Carlisle. 1987. Scale loss and survival in smolts of Atlantic salmon (Salmo salar) after turbine passage. Can. J. Fish. Aquat. Sci. 44: 210-214.

- Krebs, J.R., and N.B. Davies. 1978. Behavioural ecology an evolutionary approach. Sinauer Associates, Inc. Sunderland, Massachusetts.
- Lawrence, B.J., and R.J.F. Smith. 1989. Behavioral responses of solitary fathead minnows, Pimphales promelas, to alarm substance. J. Chem. Ecol. 15:209-219.
- Lucchetti, G.L., and G.A. Gray. 1988. Ptototype water reuse system. Prog. Fish Cult. 50:46-49.
- Mason, J.C., and D.W. Chapman. 1965. Significance of early emergence, environmental rearing capacity, and behavioral ecology of juvenile coho salmon in stream channels. J. Fish. Res. Bd. Can. 22:173-190.
- Maule, A.G., C.B. Schreck, C.S. Bradford, and B.A. Barton. 1988. Physiological effects of collecting and transporting emigrating juvenile chinook salmon past dams on the Columbia River. Trans. Am. Fish. Soc. 117: 245-261.
- Mazeaud, M.M., F. Mazeaud, and E.M. Donaldson. 1977. Primary and secondary effects of stress in fish: some new data with a general review. Trans. Am. Fish. Soc. 106:201-212.
- Nigro, A. A., S. Vigg and C. Burley. 1990. Development of a system-wide predator control program: Stepwise implementation of a predation index, predator control fisheries, and evaluation plan in the Columbia River Basin. Annual Progress Report, August 1988 - September 1989, Project Summary. Project Number 82-028, Bonneville Power Administration.
- Olla, B.L., and M.W. Davis. 1989. The role of learning and stress in predator avoidance of hatchery-reared coho salmon (Oncorhynchus kisutch) juveniles. Aquaculture 76:209-214.
- Olson, R. J. and A. J. Mullen. 1986. Recent developments for making gastric evacuation and daily ration determinations. Environ. Biol. Fishes 16:183-191.
- Ott, L. 1977. An introduction to statistical methods and data analysis. Duxbury Press, North Scituate, Massachusetts.
- Pennington, M. 1985. Estimating the average food consumption by fish in the field from stomach contents data. Dana 5:81-86.

- Pitcher, T.J. 1986. Functions of shoaling behaviour in teleosts. Pages 294-337 In: T.J. Pitcher, ed. The Behaviour of Teleost Fishes. The Johns Hopkins University Press, Baltimore, MD.
- Poe, T. P., H. C. Hansel, S. C. Vigg, D. E. Palmer and L. A. Prendergast. 1988. Predation by resident fish on juvenile salmonids in a mainstem Columbia River Reservoir: Part I. Feeding ecology during the salmonid out-migration. In: Poe, T. P. and B. E. Rieman (eds.), 1988. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-86. Final Report, (Contracts DE-A179-82BP34796 and DE-A179-82BP35097) Bonneville Power Administration, Portland, OR.
- Poe, T. P. and B. E. Rieman (eds.). 1988. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-86. Final Report, (Contracts DE-A179-82BP34796 and DE-A179-82BP35097) Bonneville Power Administration, Portland, OR.
- Post, J.R., and D.O. Evans. 1989. Experimental evidence of size-dependent predation mortality in juvenile yellow perch. Can. J. Zool. 67:521-523.
- Rand, D.M, and G.V. Lauder. 1981. Prey capture in the chain pickerel, Esox niser: correlatons between feeding and locomotor behavior. Can. J. Zool. 59:1072-1078.
- Redding, J.M., C.B. Schreck, E.K. Birks, and R.D. Ewing. 1984. Cortisol and its effects on plasma thyroid hormone and electrolyte concentrations in fresh water and during seawater acclimation in yearling coho salmon, Oncorhvnchus kisutch. Gen. and Comp. Endocrin. 56: 146-155.
- Reeves, G.H., F.H. Everest, and C.E. McLemore. 1983. A recirculating stream aquarium for ecological studies. USDA Forest Service Research Note PNW-403. Pacific Northwest Forest and Range Experiment Station, Portland, OR. 8 p.
- Rice, J. A., J. E. Breck, S. M. Bartell and J. F. Kitchell. 1983. Evaluating the constraints of temperature, activity and consumption on growth of largemouth bass. Environ. Biol. Fish. 9:263-275.
- Rice, J. A. and P. A. Cochran. 1986. Independent evaluation of a bioenergetics model for largemouth bass. Ecology. 65:732-739.

- Rieman, B. E., R. C. Beamesderfer, S. Vigg and T. P. Poe. 1988. Predation by resident fish on juvenile salmonids in a mainstem Columbia Reservoir: Part IV. Estimated total loss and mortality of juvenile salmonids to northern squawfish, walleye, and smallmouth bass. In: Poe, T. P. and B. E. Rieman (eds.), 1988. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-86. Final Report, (Contracts DE-A179-82BP34796 and DE-A179-82BP35097) Bonneville Power Administration, Portland, OR.
- Rondorf, D. W., M. S. Dutchuk, A. S. Kolok and M. L. Gross. 1985. Bioenergetics of juvenile salmon during the spring outmigration. Annual Report 1983, (Contract DE-AI79-82BP35346), Bonneville Power Administration, Portland, OR.
- Rondorf, D.W., J.W. Beeman, J.C. Faler, M.B. Free, E.J. Wagner. 1989. Assessment of smolt condition for travel time analysis. Annual report to Bonneville Power Administration, Portland, Oregon (Contract number DE-AI79-87BP35245).
- Schreck, C.B. 1981. Stress and compensation in teleostean fishes: response to social and physical factors. Pages 295-321 in A.D. Pickering, editor. Stress and fish. Academic Press, London.
- Sigismondi, L.A. and L.J. Weber. 1988. Changes in avoidance response time of juvenile chinook salmon exposed to multiple acute handling stresses. Trans. Am. Fish. Soc. 117:196-201.
- Snedecor, G. W. and W. G. Cochran. 1980. Statistical Methods, Seventh Edition. The Iowa State University Press, Ames Iowa.
- Sokal, R.R., and F.J. Rohlf. 1981. Biometry, 2nd edition. Freeman Press, San Francisco.
- Stein, R.A. 1977. Selective predation, optimal foraging, and the predator-prey interaction between fish and crayfish. Ecology 58:1237-1253.
- Stewart, D. J. and F. P. Binkowski. 1986. Dynamics of consumption and food conversion by Lake Michigan alewives: An energetics-modeling synthesis. Tran. Am. Fish. Soc. 115:643-661.
- Stewart, D. J., J. F. Kitchell and L. B. Crowder. 1981. Forage fishes and their salmonid predators in Lake Michigan. Trans. Am. Fish. Soc. 110:751-763.

- Stewart, D. J., D. Weininger, D. V. Rottiers, and T. A. Edsall. 1983. An energetics model for lake trout, Salvelinus namaycush: application to the Lake Michigan population. Can. J. Fish. Aquat. Sci. 40:681-698.
- Swenson, W. A. and L. L. Smith Jr. 1973. Gastric digestion, food consumption, feeding periodicity, and food conversion efficiency in walleye (Stizostedion vitreum vitreum). J. Fish. Res. Bd. Canada 30:1327-1336.
- Temple, S.A. 1987. Do predators always capture substandard individuals disproportionately from prey populations? Ecology, 68:669-674.
- Thornton, K. W. and A. S. Lessem. 1978. A temperature algorithm for modifying biological rates. Trans. Am. Fish. Soc. 107:284-287.
- Van Oosten, J. 1957. The skin and scales, p. 207-244. In: M. E. Brown (ed.) The physiology of fishes. Vol. 1. Academic Press, New York, NY.
- Vigg, S. 1988. Functional response of northern squawfish predation to salmonid prey density in McNary Tailrace, Columbia River. In: Poe, T. P. and B. E. Rieman (eds.), 1988. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-86. Final Report, (Contracts DE-A179-82BP34796 and DE-A179-82BP35097) Bonneville Power Administration, Portland, OR.
- Vigg, S. and C. C. Burley (Manuscript in Review). Temperature dependent maximum daily consumption of juvenile salmonids by northern squawfish (Ptychocheilus oregonensis) from the Columbia River.
- Vigg, S., T. P. Poe, L. A. Prendergast, and H. C. Hansel, 1988. Predation by resident fish on juvenile salmonids in a mainstem Columbia River Reservoir: Part II. Consumption rates of northern squawfish, walleye, smallmouth bass, and channel catfish. In: Poe, T. P. and B. E. Rieman (eds.), 1988. Predation by resident fish on juvenile salmonids in John Day Reservoir, 1983-86. Final Report, (Contracts DE-A179-82BP34796 and DE-A179-82BP35097) Bonneville Power Administration, Portland, OR.
- Vigg, S. and L. A. Prendergast (Manuscript in preparation). Gonad development and spawning of northern squawfish in a mainstem Columbia River reservoir.
- Wahl, D.H. and R.A. Stein. 1988. Selective predation by three esocids: The role of prey behavior and morphology. Trans. Am. Fish. Soc. 117:142-151.

- Webb, P.W. 1976. The effect of size on the fast-start performance of rainbow trout Salmo salar and a consideration of piscivorous predator-prey interactions. J. Exp. Biol. 65:157-177.
- Webb, P.W. 1984a. Body and fin form and strike tactics of four teleost predators attacking fathead minnow (Pimephales promelas) prey. Can. J. Fish. Aquat. Sci. 41:157-165.
- Webb, P.W. 1984b. Chase response latencies of some teleostean piscivores. Comp. Biochem. Physiol. 79A:45-48.
- Werner, E.E. and D.J. Hall. 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (Lepomis macrochirus). Ecology 55:1042-1052.
- Winberg, G. G. 1956. Rate of metabolism and food requirements of fishes. Belorussian Univ., Minsk. 253 p. (Transl. by Fish. Res. Bd. Can. Transl. Ser. No. 164, 1960).
- Wright, L.D. 1970. Forage size preference of the largemouth bass. Prog. Fish Cult. 32:39-42.
- Zar, J.H. 1984. Biostatistical analysis. Prentice-Hall, Inc. Englewood Cliffs, N.J.

## APPENDIX A

Copies of this draft manuscript are available upon request from the Columbia River Field Station.

Vigg, S. and C-C. Burley. 1990. Temperature dependent maximum daily consumption of juvenile salmonids by northern squawfish (*Ptychocheilus oregonensis*) from the Columbia River. Can. J. Fish. Aquat. Sci. 47: 1233-1241.

### Abstract

Maximum daily consumption rate ( $C_{\max}$  as ration or number) of northern squawfish (*Ptychocheilus oregonensis*) from the Columbia River, increased exponentially as a function of temperature. Predator weight did not explain a significant independent proportion of variation in  $C_{\max}$ . The mean maximum daily ration, determined from replicate *ad libitum* feeding on juvenile Pacific salmon (*Oncorhynchus spp.*), was 0.45, 0.67, 3.51, and 4.51  $cg \cdot g^{-1}$  at 8.0, 12.5, 17.0, and 21.5°C, respectively. To quantify the temperature dependent consumption relation for use in simulation modeling, replicate  $C_{\max}$  data within the preferred temperature range were fit to exponential and exponential sigmoid models. Based on a knowledge of thermal relations of northern squawfish, hypothetical  $C_{\max}$  data at temperature extremes were combined with our results: this enabled us to fit gamma and Thornton and Lessem (1978) models over the entire environmental temperature range (0-27°C) observed in the Columbia River.