Dynamics of a Northern Squawfish Population and the Potential to Reduce Predation on Juvenile Salmonids in a Columbia River Reservoir

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Abstract.—Northern squawfish *Ptychocheilus oregonensis* prey on salmonid smolts (*Oncorhynchus* spp.) in Columbia River reservoirs. We used simulation models to determine the potential influence of exploitation of northern squawfish on that predation. We also used correlation analysis to examine factors that may influence predation through predator recruitment. We based our simulations on estimates of mortality, relative year-class strength, and growth made from a 4-year study of resident fish predators in John Day Reservoir. Simulated predation declined with exploitation of fish longer than 275 mm (fork length) such that sustained exploitation of 10–20% annually reduced predation by 50% or more. The magnitude of change was related to the type of reproductive compensation. Recruitment was not obviously related to any environmental variable we examined, although year-class strength was negatively correlated with concurrent year-class strength of walleye *Stizostedion vitreum*. We believe that limited, but sustained, exploitation of northern squawfish provides an alternative to more radical control measures. We are uncertain about the potential recovery rate of exploited northern squawfish populations, however, and there is some risk that unsustained exploitation could aggravate predation. Any control program should evaluate density-dependent responses of predators.

Anadromous salmonids *Oncorhynchus* spp. represent an extremely valuable resource in the Columbia River basin, but abundance of these fish has declined in recent history. Major declines in survival of migrating juveniles have been attributed to the development of hydroelectric power (Ebel 1977; Raymond 1988). Most of the loss occurs within project reservoirs (Northwest Power Planning Council, Portland, Oregon, unpublished data), and predation by resident fishes is probably an important cause of mortality of juvenile salmonids in such reservoirs (Ebel 1977; Raymond 1979). Rieman et al. (1988) estimated that three predators, northern squawfish *Ptychocheilus oregonensis*, walleye *Stizostedion vitreum*, and smallmouth bass *Micropterus dolomieui*, consumed 9–19% of all juvenile salmonids that entered the John Day Reservoir each year. Northern squawfish accounted for about 80% of this predation, and large (>400 mm, fork length) northern squawfish were the most important predators.

Reduction in northern squawfish abundance could improve survival of Pacific salmon *Oncorhynchus* spp. and steelhead *O. mykiss*. A northern squawfish eradication program in Cultus Lake, British Columbia, produced a substantial increase in the production of sockeye salmon *O. nerka*

(Foerster and Ricker 1941). Since the work in Cultus Lake, eradication programs targeting squawfishes *Ptychocheilus* spp. have been widespread (Brown and Moyle 1981), and similar programs have been considered for reservoirs on the Columbia River.

Typical approaches to northern squawfish control included the use of toxicants, explosives, or intensive trapping and netting (e.g., Jeppson 1957; Jeppson and Platts 1959; MacPhee 1969; Hamilton et al. 1970; Rulifson 1984). None of these programs appears to have been continued as a part of routine management, and the reasons for discontinuing control programs are unclear.

Reproduction in fish may be stock dependent and resilient, and production might actually increase under exploitation (Ricker 1954; Goodyear 1980). One criticism of predator-control proposals has been that attempts to control a predator population might actually aggravate predation. If the population overcompensates, the result could be an increase in recruitment and numbers of young, rapidly growing and feeding predators.

Logistic, economic, and environmental constraints may also make predator-control efforts difficult or unappealing, especially in large reservoirs. The removal of the majority of northern squawfish from any single reservoir may prove difficult; their removal in several or all reservoirs in the Columbia River system might be a monumental task.

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The number of prey consumed depends on predator number and ultimately on the production and dynamics of the predator population. Large changes in abundance and production in fish stocks can result from minor changes in the processes of growth and mortality (Ricker 1963, 1975). Such changes are especially evident in the exploitation of long-lived, slow-growing stocks (Ricker 1963; Adams 1980; Francis 1986). Significant reductions in predation might result from restructuring the population through limited but sustained exploitation, even though a major part of a predator population cannot be removed.

Recruitment is often considered the single most important process influencing abundance in individual fish stocks (Le Cren 1960; Gulland 1978; Shepherd and Cushing 1980), and environmental variables have commonly been tied to reproductive success. Variation in flow or water level might have an important influence on recruitment in squawfishes (Moyle et al. 1983; Haynes et al. 1984; La Bolle 1984). Methods such as manipulation of water levels in reservoirs have been used to control undesirable fishes (Everhart et al. 1975). Manipulation of the northern squawfish's environment could provide another means of limiting recruitment and an alternative means of reducing predation.

The purpose of this paper is to examine alternative measures to control predation by northern squawfish in Columbia River reservoirs. We hypothesized that (1) limited exploitation of northern squawfish could produce important reductions in predation through changes in population structure and (2) environmental factors influencing year-class strength of northern squawfish could be manipulated to reduce recruitment and predation. Experimental control programs will be expensive and time consuming. We therefore used simulation modeling and correlation analysis, with existing data, to test our hypotheses.

Study Area

John Day Reservoir is one of four run-of-the-river impoundments operated for hydroelectric power generation and navigation on the lower Columbia River between Oregon and Washington. The reservoir is 123 km long with a surface area of about 21,000 hectares. Offshore depths range from 10 m in the upper reservoir to 50 m near John Day Dam. The reservoir grades from a riverine to a lentic character through its length, but current is measurable throughout. Hydraulic residence time ranges from 3 to about 12 d (La Bolle

1984), and daily flow pattern is regulated through McNary Dam at the head of the reservoir and John Day Dam. The shoreline is typically steep, parent material is basalt, and littoral habitat is limited. Precipitation is low and shoreline vegetation is limited. Surface temperatures range from 0 to 27°C with only weak stratification. Juvenile Pacific salmon and steelhead are present in the reservoir year-round, but most of the fish migrate through the system from April through August as smolts.

Methods

Effects of Exploitation

We used a population model to determine whether changes in exploitation of northern squawfish would affect predation. We based simulations on 4 years of data from a study of resident fish predators in John Day Reservoir (Beamesderfer et al. 1987). Altogether, 10,993 squawfish were sampled throughout the reservoir with a variety of gear. Detailed descriptions of the sampling program are in Nigro et al. (1985) and Beamesderfer et al. (1987). The length-frequency (fork length) and scale data from these samples provided the basis for estimates of mortality and growth used in our population analysis.

Population model.—We used a generalized population model designed for simulation of age-structured populations (Beamesderfer 1988). The model was an adaptation of those presented by Taylor (1981) and Walters (1969), and used inputs of growth (von Bertalanffy coefficients; Ricker 1975), age-specific natural mortality, and exploitation rates. Recruitment was described by a Beverton–Holt or Ricker stock–recruitment function (Ricker 1975). Output of the model included annual summaries of numbers, gross production (total tissue elaboration in the population), and recruitment (Table 1). Simulations could be run for up to 250 years.

We estimated the model parameters from our growth and mortality data and the best available data for other functions. We observed no age-specific trend in natural mortality and assumed it to be constant with age after age 1. We assumed that natural mortality operated concurrently with any mortality imposed through exploitation.

We did not incorporate any density-dependent variation in growth or mortality after the first age-class in the model. Although compensation of that sort is known in fish (Goodyear 1980), compensation in the form of stock-dependent recruitment is probably more important (Gulland 1978; Shep-

TABLE 1.—Equations[a] and definitions of variables and parameters used in a model of the population dynamics of northern squawfish.

Variable or parameter	Definition	Equation number
$N_{x,t}$	Age-specific number of fish in the population in any year	
	$= (N_{x-1,t-1})(S_{x-1})$	1
x	Age	
t	Year	
S_x	Age-specific annual rate of survival	
	$= 1 - [m_x + n_x - (m_x)(n_x)]$	2
m_x	Exploitation rate (harvest mortality rate)	
n_x	Conditional natural mortality rate	
L_x	von Bertalanffy equation for length at age	
	$= L_\infty\{1 - \exp[-k(x - t_0)]\}$	3
L_∞	Asymptotic length (i.e., at infinity) from the von Bertalanffy equation	
k	von Bertalanffy equation parameter	
t_0	von Bertalanffy equation parameter	
W_x	Weight at age	
	$= (a_w)(L_x)^{b_w}$	4
a_w	Length–weight equation coefficient	
b_w	Length–weight equation exponent	
$B_{x,t}$	Annual production of any age-class	
	$= \{[(N_{x-1,t-1})(W_{x-1}) + (N_{x,t})(W_x)]/2\}$	
	$\cdot [\log_{10}(W_{x-1}) - \log_{10}(W_x)]$	5
E_x	Weighted predation effect of any age-class	
	$= (B_x)(WF_x)$	6
WF_x	Age-specific weighting factor	
$P_{x,t}$	Potential recruitment contributed by each age-class at or above the age of female maturity	
	$= (N_{x,t})(pf)(ps)(F_x)$	7
pf	Proportion of the population that is female	
ps	Proportion of the population of females that spawns in any year	
F_x	Age-specific fecundity of females	
	$= (a_f)(L_x)^{b_f}$	8
a_f	Length–fecundity equation coefficient	
b_f	Length–fecundity equation exponent	
P_t	Net potential recruitment contributed by all ages in any given year	
	$= \Sigma P_{x,t}$	9
R_t	Number of age-1 recruits to the population (corresponds to $N_{1,t}$)	
	$= (P_t)\exp\{a_r[1 - (P_t/P_r)]\}$	
	(Ricker equation)	10
	$= (P_t)/\{1 - (A_b)[1 - (P_t/P_r)]\}$	
	(Beverton–Holt equation)	11
a_r	Ricker recruitment equation parameter describing shape of curve	
P_r	Replacement reproductive potential at equilibrium	
A_b	Beverton–Holt recruitment equation parameter describing shape of curve	

[a] The von Bertalanffy growth equation and the Ricker and Beverton–Holt recruitment equations are as described by Ricker (1975).

herd and Cushing 1980). Our data showed no obvious compensation in growth based on correlations of growth and year-class size. We chose then to represent density-dependent compensation through several recruitment models. Because little information is available describing recruitment in squawfishes, we used three models to represent a range of possible responses (Figure 1) and bound our results. We used Beverton–Holt functions with $A = 0.5$ and $A = 0.98$ (Ricker 1975; A_b in Table 1) as representations of a population with low productivity and another population for which recruitment is nearly independent of stock, respectively. We used a domed Ricker function with $a = 1.7$ (Ricker 1975; a_r in Table 1) to represent a population capable of overcompensation.

In simulations based on the assumption of stock-dependent recruitment, we considered adult stock to be a function of adult female numbers and sizes. We calculated potential reproduction from the relative fecundity of each female (Table 1, equation 7). We assumed that fecundity was directly proportional to weight. Realized reproduction was a function of potential reproduction and a density-dependent component expressed by the recruitment models (Table 1, equations 10 and 11). In all simulations, survival from realized reproduction (age 0) to age 1 was calculated to produce a stable population at an arbitrarily selected equilibrium stock size (10,000 age-1 fish) when the population was not exploited.

We simulated potential predation as gross production weighted by a consumption-to-growth conversion efficiency (Table 1, equations 5 and 6). We reasoned that simulations of gross predator production could be used to represent expected trends in prey consumption, given the appropriate conversion for each predator age-class. A relative conversion factor was calculated as smolts consumed/growth; both numerator and denominator were expressed in terms of mg/g of predator per day. We weighted annual gross production in each age-class by the predicted conversion factor and summed over all ages to predict total prey consumption (potential predation) in each year of simulation. We standardized potential predation in each simulated year- or age-class as a proportion of total predation in an unexploited population at equilibrium.

Parameter estimates. — We used two methods to estimate total mortality based on age composition and two methods to estimate natural mortality based on empirical models. To estimate age composition, we used the length frequency of the total
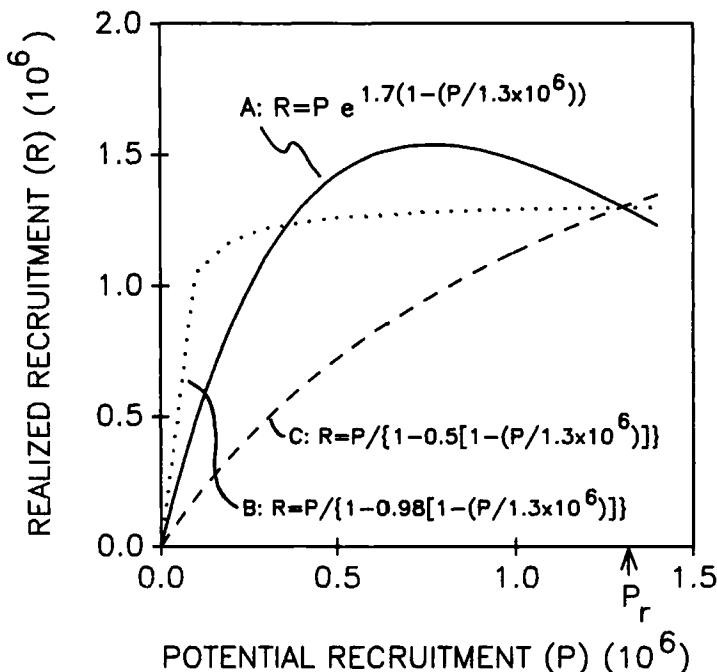
FIGURE 1.—Reproduction models used in simulations of predation by northern squawfish in John Day Reservoir. (A) Ricker function for $a = 1.7$; (B) and (C) Beverton–Holt functions for $A = 0.98$ and $A = 0.50$, respectively; a and A are defined as a_r and A_b in Table 1; the curves are as described by Ricker (1975). The arrow at P_r represents the equilibrium for all curves at a realized recruitment of 1.3×10^6.

sample and an age–length key developed for each year. Aging methods were outlined by Jearld (1983). We corrected the length frequencies for size-related vulnerability, as described by Beamesderfer and Rieman (1988b). We pooled age frequencies for each year to generate a single catch curve and estimated total mortality by regression (Ricker 1975). We also used relative catch (corrected for sampling effort) of individual year-classes in each sampling year to produce cohort-specific catch curves. We estimated total mortality over all ages by a separate regression for each year-class.

We used an empirical model (Pauly 1980) to predict natural mortality from our own observations of growth (von Bertalanffy coefficients described below) and available data on reservoir temperature (records of the U.S. Army Corps of Engineers, Portland, Oregon). We used a second model to predict natural mortality from the gonad-osomatic index (GSI; gonad weight as a percentage of body weight) of ripe females (Gunderson and Dygert 1988). We calculated a weighted mean GSI (Gunderson and Dygert 1988) from an unpublished relationship of ripe gonad weight and female body weight in John Day Reservoir (S. Vigg, U.S. Fish and Wildlife Service, National Fishery Re-

search Center, personal communication). The weighted mean GSI was 7%.

Northern squawfish are not considered a game fish in John Day Reservoir, and annual exploitation by anglers appears to be less than 2% (Beamesderfer et al. 1987). For that reason, we assumed no fishing mortality, and estimates of natural mortality should, therefore, be equivalent to estimates of total mortality.

We described growth from analysis of 893 scales, as in the work on age composition. Fork length at annulus formation was back-calculated, as described by Bagenal and Tesch (1978). To describe growth for the purposes of our simulations, we fit the estimated mean length at age with the von Bertalanffy model (Ricker 1975). Weight at age was estimated with the coefficients from a regression of weight on length (Ricker 1975).

To estimate relative conversion efficiency, we used empirical estimates of salmonid consumption over 4 years (Vigg et al. 1988) and our estimates of annual growth. We assumed that all growth occurred from April to August and averaged consumption estimates for the same period. Because growth may actually occur outside this period and because northern squawfish consume

prey other than salmon smolts, our estimates do
not represent gross conversion efficiency for all
food. Rather, the estimates represent only a rela-
tive conversion for salmonid consumption by
predators of different sizes. We related estimates
of conversion efficiency to predator sizes equiva-
lent to each age-class and used a regression to pre-
dict conversion efficiency for the simulations (Fig-
ure 2).

Simulations.—In our simulations of exploita-
tion, we used model populations with the stock-
dependent recruitment functions. We varied ex-
ploitation from 0.05 to 0.80 (annual rates). We
exploited only fish longer than 275 mm, a size
approximating that at recruitment to most gears
(Beamesderfer and Rieman 1988b) and first ma-
turity (Beamesderfer 1983). We sustained exploi-
tation in each run for 20 years. For runs in which
the populations did not reach equilibrium within
20 years, we present results in that last year.

We also simulated changes in predation follow-
ing short-term removals. Model populations were
exploited at a rate high enough to reduce predation
by 50% in 5 years. We then terminated exploita-
tion and allowed populations to grow to equilib-
rium, and we recorded time for recovery to 90%
of the unexploited level.

To examine the uncertainty in our predictions,
we tested the sensitivity of our model population
to key parameters. We used a Beverton–Holt stock–
recruitment model with $A = 0.98$ for each simu-
lation. We independently varied growth (L_∞ in the
von Bertalanffy model; Ricker 1975), mortality
rate, and conversion efficiency (the slope in the
conversion–length regression) over the range of
estimates for mortality or by ±25% of the param-
eter estimate for growth and conversion. We used
the level of exploitation necessary to reduce po-
tential predation to 50% of the unexploited level
as the output for comparison.

Year-Class Strength

We used two approaches to index relative year-
class strength for cohorts produced between 1971
and 1984. The first method was described by El-
Zarka (1959). In the second, we used a regression
approach to estimate relative year-class strength
from annual catch curves. We assumed that mor-
tality was constant, and equal for ages five and
older, and that those ages were fully recruited to
the samples. We assumed that mortality was equal
to our "best" estimate and calculated the residuals
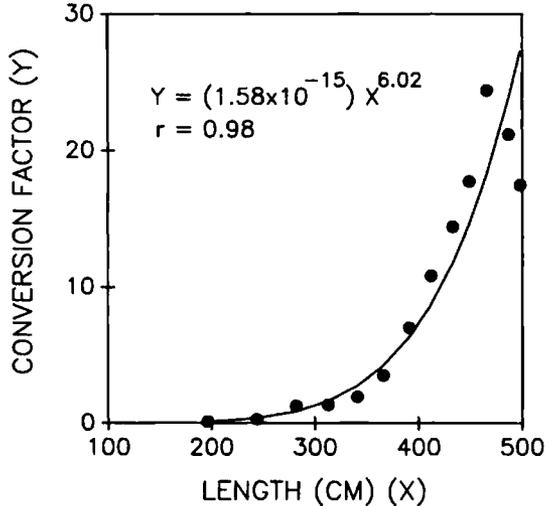from a simple linear regression ($\log_e$[cohort catch]

FIGURE 2.—Relationship of prey consumption-to-
growth conversions and predator length used in simu-
lations of predation by northern squawfish in John Day
Reservoir.

against age) with negative slope equal to our mor-
tality estimate. We standardized the residuals to
a mean of 0 and calculated an index of year-class
strength as the mean residual for all sampled years.

We examined correlations between physical and
biological variables and year-class strength to
identify potential methods of manipulating re-
cruitment. Physical variables included seasonal
data on flow, reservoir water levels, and temper-
ature, and represented conditions during the entire
year (prespawning period, incubation period, rear-
ing period, and first winter) for the year of year-
class formation (Table 2). The biological variables
included estimates of growth within a year-class
and concurrent and previous year-class strengths
of smallmouth bass and walleye (Table 2). We
related both indexes of northern squawfish year-
class strength to each variable with the nonpara-
metric Spearman rank correlation procedure (Zar
1974).

Because we used a large number of correlations
in an exploratory fashion, we did not calculate
probabilities or identify statistical significance for
individual correlations. We considered correlation
coefficients of consistent sign (positive or negative)
larger than 0.60 for both indexes of year-class
strength as evidence of a relationship between year-
class strength and the variable in question. Data
on flow and temperature were obtained from rec-
ords of the U.S. Army Corps of Engineers, Port-

TABLE 2.—Variables used in correlations with two indexes of northern squawfish year-class strength.

Variable	Period represented[a]
Walleye year-class strength	Previous year
	Concurrent year
Smallmouth bass year-class strength	Previous year
	Concurrent year
Length at age (growth)	Age 1
	Age 3
Mean daily flow	May
	Jun
	Jul
	Aug
	Mar–May inclusive
	Jun–Aug inclusive
	Jan–Dec inclusive
Degree-days[b]	Nov–Mar inclusive (following spawning)
Mean daily distribution	May
	Jun
	Jul
	Aug
	Mar–May inclusive
	May–Jun inclusive
	Jun–Aug inclusive
Rate of temperature increase (°C/d)[c]	May
	Jun
	Jul
	Aug
Mean daily water level in reservoir	May
	Jun
	Jul
Standard deviation of water level in reservoir	May
	Jun
	Jul
	Aug

[a] Periods were selected to represent prespawning, spawning, incubation, or rearing. Spawning is in June.
[b] A degree-day is a unit representing a one-degree increase in mean daily temperature above 0°C.
[c] Rate of increase was estimated by regression.

land, Oregon. Growth was represented as back-calculated length-at-age. Year-class strengths of walleye and smallmouth bass were based on data from Connolly and Rieman (1988) and were calculated by the method of El-Zarka (1959).

Results

Effects of Exploitation

Parameter estimates.—Our interpretation of the catch curve generated from pooled age-composition data was uncertain. The right limb of the curve was not linear or smooth. Regressions fit to the data resulted in estimates of total instantaneous mortality ranging from 0.14 to 0.44, depending on the portion of the curve we used (Figure 3). Mortality that we estimated with cohort analysis was also variable and ranged from 0.13
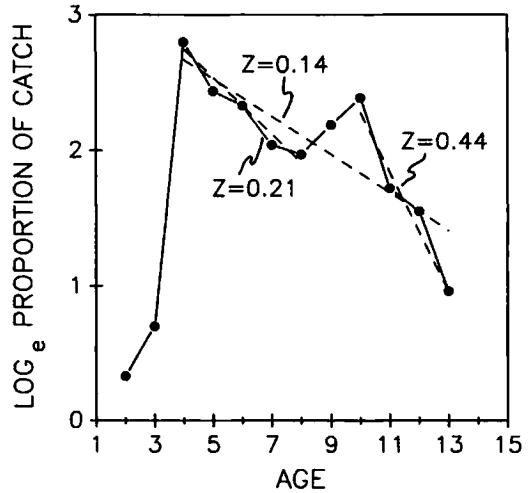

FIGURE 3.—Catch curve for northern squawfish sampled in John Day Reservoir, 1983–1986. Total instantaneous mortalities (Z) estimated by regression are shown for segments of the curve indicated by the dashed lines.

to 0.57 for year-classes 1972–1978 (Table 3). The mortality estimates did not show any age-specific trend. Mortality estimated with data on growth and temperature was 0.24. Mortality estimated from reproductive effort was 0.15.

Our attempts to estimate mortality empirically (catch curve, cohort analysis) produced highly variable and uncertain results. The direct methods are both subject to sampling error or other bias. Variation in year-class strength makes the catch curve speculative (Ricker 1975). Both methods could incorporate error from aging based on scale analysis. The variation among cohort estimates and a lack of any trend with increasing age also result in uncertainty.

The indirect estimates of mortality based on growth and temperature (0.24) and independently on reproductive effort (0.15) were relatively low. Although the empirical models used for the estimates were not developed for cyprinids, they should not be discounted. These models do seem to provide good predictions of mortality across broad taxonomic boundaries (Pauly 1980; Gunderson and Dygert 1988). Our estimate based on growth was similar to mortality estimated for northern squawfish (0.27) in Lake Washington (Bartoo 1977) and the mean of our cohort estimates (0.30). For these reasons and because of the uncertainty in our direct estimates, we chose 0.25 as a best approximation of average mortality for use in the simulations and analyses of year-class

TABLE 3.—Age-specific catch (number of fish, corrected for effort) and total instantaneous mortality for year-classes of northern squawfish in John Day Reservoir.

| Year-class | Catch at age | | | | | | | | | | Total instantaneous mortality |
	5	6	7	8	9	10	11	12	13	14	
1978	103	74	96	14							0.57
1977		146	127	173	69						0.19
1976			178	126	192	91					0.16
1975				130	145	188	54				0.23
1974					129	215	105	105			0.13
1973						159	82	30	34		0.56
1972							23	53	44	10	0.27

strength. For lack of better information, we made the simplest assumption that mortality was constant with age after age 1. We recognized the uncertainty in the mortality estimates and used the range of estimates for all methods (0.14–0.44) in our sensitivity analysis.

We aged northern squawfish in our samples to 16 years. The length at age we estimated for all northern squawfish in John Day Reservoir was asymptotic. We found that a von Bertalanffy model described the data well (Figure 4).

The growth of northern squawfish in John Day Reservoir was at the upper range of that summarized for other populations. Growth was similar to that of the Lake Washington population but higher than that reported for other populations in Idaho, British Columbia, and Montana (Beamesderfer 1983). We found no correlation between growth of individual age-classes and associated year-class strength. We found no evidence that growth was affected by abundance over the range of year-class sizes that we measured.

Simulations.—Simulated exploitation of northern squawfish longer than 275 mm had an important influence on predation. Predation declined in exponential fashion with increasing exploitation in each simulation, although results were dependent on the recruitment function we used. Sustained exploitation of about 9 and 13% was nec-
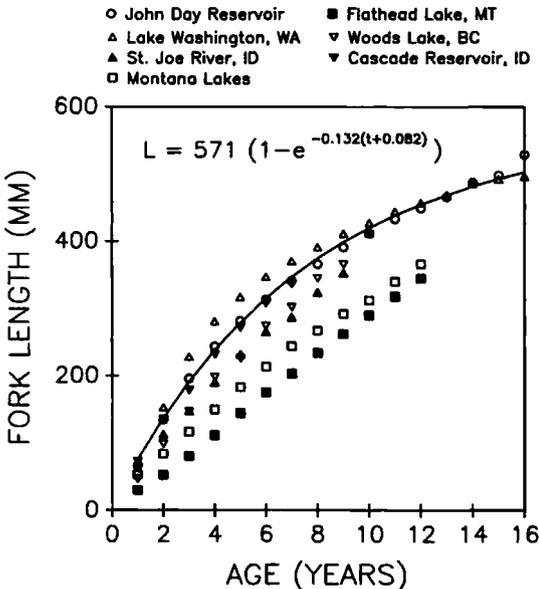

FIGURE 4.—Back-calculated fork lengths at age for northern squawfish in John Day Reservoir. The solid line represents the von Bertalanffy model (Ricker 1975) fit to the means. The data for other populations were summarized by Beamesderfer (1983). L = fork length; t = age.
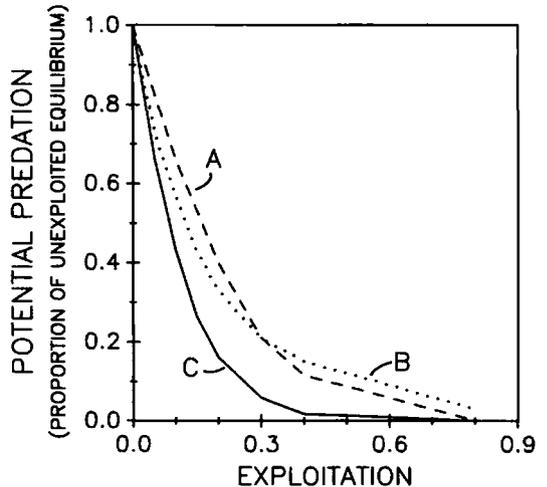

FIGURE 5.—Simulations of potential predation by northern squawfish in John Day Reservoir with varied levels of sustained exploitation. Curve A represents simulations with the Ricker (1975) recruitment model; curves B and C represent simulations with Beverton–Holt models (Ricker 1975) for $A = 0.98$ and $A = 0.50$, respectively; $A = A_b$ defined in Table 1. Simulations were run for 20 years and results represent predation at the new equilibrium or in year 20.
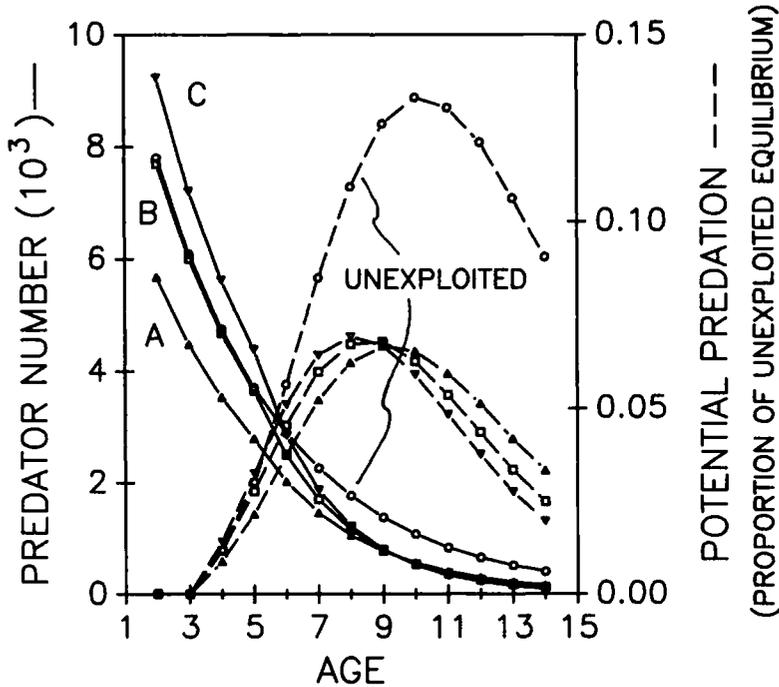
FIGURE 6.—Simulations of potential predation and predator number by age-classes of northern squawfish in John Day Reservoir with no exploitation and with exploitation resulting in 50% reduction of total predation. (A) Simulations with the Ricker (1975) recruitment model; (B) and (C) simulations with Beverton–Holt models (Ricker 1975) for $A = 0.98$ and $A = 0.50$, respectively; $A = A_b$ defined in Table 1. The predation observations represent the proportion of total consumption in the unexploited population attributed to the individual age-classes.

essary to reduce predation to 50% of the unexploited level with the two Beverton–Holt functions (Figure 5). Exploitation of 17% was necessary to achieve the same result with the domed function.

Middle and older age-classes contributed most heavily to the simulated predation in unexploited populations (Figure 6). With exploitation, predation declined in older fish, and the relative prey consumption by age shifted toward younger fish (Figure 6).

The time necessary to reduce predation to 50% of the unexploited level declined rapidly with increasing exploitation in all simulations. We found that predation could be halved in 10 years with exploitation between 15 and 25%, depending on the recruitment function. Predation was reduced by 50% within 3 years with exploitation exceeding 30% and any recruitment function.

The response of the population to a stop in exploitation was substantially different for the three simulations (Figure 7). With the least productive recruitment function, it took nearly 30 years for potential predation to reach 90% of the unexploited level (C in Figure 7). With the other models,
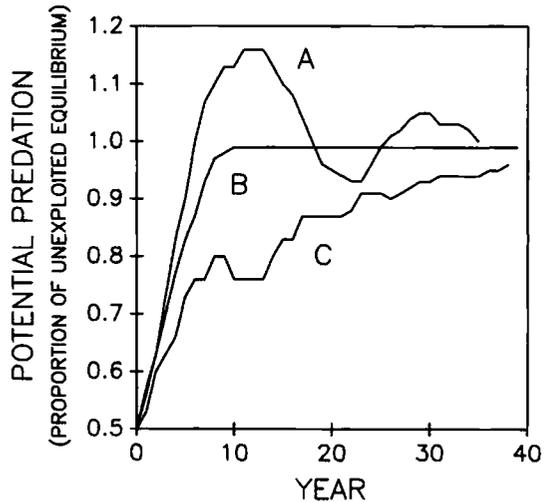

FIGURE 7.—Simulations of potential predation following termination of exploitation of northern squawfish in John Day Reservoir. (A) Simulations with the Ricker (1975) recruitment model; (B) and (C) simulations with Beverton–Holt models (Ricker 1975) for $A = 0.98$ and $A = 0.50$, respectively; $A = A_b$ defined in Table 1. Model populations were exploited until predation was 50% of the unexploited equilibrium and then allowed to grow.

TABLE 4.—Sensitivity of model output to changes[a] in parameter estimates.

Parameter estimated	Parameter estimate	Exploitation for 50% predation[b]
Growth (k)		
Best estimate	57.1	0.13
Upper bound	71.3	0.12
Lower bound	42.8	0.26
Conversion efficiency		
Best estimate	6.0	0.13
Upper bound	4.5	0.12
Lower bound	7.5	0.14
Mortality		
Best estimate	0.25	0.13
Upper bound	0.44	0.20
Lower bound	0.14	0.10

[a] Growth and conversion efficiency were changed ±25% of the estimate; mortality was changed by the ranges of estimates.

[b] Exploitation resulting in a 50% reduction of simulated predation.

predation recovered to 90% within 6 years. In the simulation with the domed reproduction model, predation exceeded (114%) the unexploited level before oscillating toward equilibrium (A in Figure 7).

The range of the mortality estimates resulted in outputs ranging from 54% to −23% (Table 4). The model output was not sensitive to a 25% increase for L_∞ in the growth equation (Table 4). The output was sensitive to a reduction in growth such that the changes produced a 108% increase in exploitation necessary to reduce predation by 50%. The model was not sensitive to ±25% changes in the slope of the conversion efficiency relation (Table 4).

Year-Class Strength

The two indexes of year-class strength for northern squawfish varied in similar fashion ($r = 0.85$) with year (Figure 8). Data converted from the catch-curve index varied approximately sevenfold. Both indexes suggested that an especially weak year-class occurred in 1979. The pattern of variation did not appear to be strictly random, and we did not find any strong ($r > 0.60$) or biologically meaningful correlations between either index of year-class size and any of the variables representing the physical environment, fish growth, or interaction with smallmouth bass. The index of concurrent year-class size for walleye was negatively correlated with both northern squawfish indexes ($r = -0.86$ and -0.67). A very strong 1979 year-class of walleye coincided with the weak 1979 year-class of northern squawfish (Figure 8).
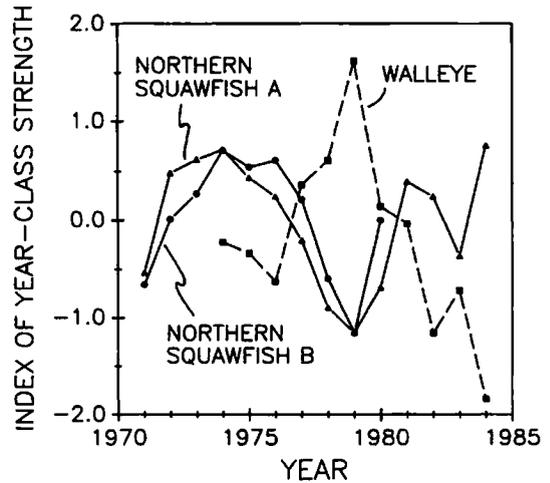

FIGURE 8.—Indexes of relative year-class strength for northern squawfish and walleye in John Day Reservoir. (A) Data for northern squawfish by the method of El-Zarka (1959); (B) data for northern squawfish by the regression method. Data for walleye are from Connolly and Rieman (1988).

Discussion

Effects of Exploitation

Increasing mortality of northern squawfish through exploitation could substantially influence predation on juvenile salmonids. Heavy exploitation (30% or more) can reduce predation quickly and dramatically. Our modeling results are consistent with the evidence from actual eradication efforts (Foerster and Ricker 1941; Pintler and Johnson 1958; Jeppson and Platts 1959). Other work indicates, however, that removal of squawfishes has not always benefited salmonids (Hamilton et al. 1970; Pollard 1972; Moyle et al. 1983). Whether predation was actually an important cause of salmonid mortality or whether removals were really intensive in these latter studies is not clear.

We also show that substantial reductions in predation are possible with limited (<20%) but sustained exploitation of northern squawfish. The disproportionate effect is a result of mortality compounded through multiple age-classes and a pronounced reduction in prey consumption by older fish.

We found that potential predation declined with sustained exploitation in all simulations. The relative benefit realized from exploitation, however, was dependent on the reproduction model. Exploitation necessary for a 50% reduction in predation ranged about twofold (9–17%) between

simulations with the least productive Beverton–Holt model ($A = 0.50$) and the Ricker model. Even with that range, however, we consider the exploitation necessary for a significant reduction in predation to be low.

The rate of increase in predation following a stop in exploitation cannot be predicted with certainty. We show that the benefit from exploitation can be long term (40-year recovery) if the population is unproductive (Beverton–Holt, $A = 0.50$). On the other hand, predation could rebound quickly (within 5 years) if the predator population has a stronger recruitment response. In simulations with the Ricker model, a drop in exploitation actually resulted in overcompensation such that predation exceeded the equilibrium level. The rapid response was caused by replacement of juveniles through strong recruitment and by a shift in the age structure of the population with exploitation. Because size at first prey consumption and size at which fish were first exploited were similar, and because recruitment was nearly stable or enhanced through exploitation, potential predators were "stockpiled" in age-classes below those being exploited. When removals stopped, those fish quickly became effective predators.

The result suggests some risk in a control program that is not sustained. Obviously, the response is dependent on reproduction and recruitment in an exploited population. We selected a domed function only to illustrate possible trends. The reproductive response in northern squawfish could be more resilient than that in our simulations. In that case the increase in predation would be greater than that shown here.

Little information is available on the reproductive response of northern squawfish. None of the large removal experiments suggest, that northern squawfish populations showed any density-dependent response (Foerster and Ricker 1941; Jeppson and Platts 1959; Hamilton et al. 1970; Pollard 1972), but apparently none of the studies was maintained for more than 5 or 6 years, and the dynamics of the populations were not monitored. Moyle et al. (1983) do suggest that a population of Sacramento squawfish *Ptychocheilus grandis* recovered within 10 years following removals in a California river. The authors felt these fish were adapted to repopulation following catastrophic events. Removal experiments with another cypriniform, the white sucker *Catostomus commersoni*, produced some compensation in growth (Parker 1958) and recruitment (Johnson 1977). In

most eradication programs, however, no reproductive compensation was found (Trippel and Harvey 1987).

We can hypothesize the reproductive response for northern squawfish from other information. Resilient populations of fish (i.e., with domed recruitment functions) are associated with high fecundities (Cushing 1971; Cushing and Harris 1973; Colby and Nepzy 1981); strong density-dependent responses in growth and mortality (Harris 1975), and fast-growing, relatively short-lived species. Fecundity for northern squawfish, ranging from 6,000 to 70,000 eggs per female (Cartwright 1956; Olney 1975), is one to two orders of magnitude less than fecundities for stocks that Cushing (1971) considered resilient. Growth of northern squawfish in John Day Reservoir was high relative to that of other northern squawfish stocks. Growth also was not correlated with year-class strength. Density-dependent growth was not obvious, and even better growth with a population reduction should not be expected. Northern squawfish also grow slowly and exhibit relatively low mortality compared with that of other species. We conclude that we should not expect strong compensation in recruitment of exploited northern squawfish stocks. We believe, then, that the range of reproduction functions used in our simulations bound the trends expected in northern squawfish predation. Some risk exists that compensation could aggravate predation, but we think our simulation with overcompensation represents a worst case.

We believe limited but sustained exploitation represents a better alternative for northern squawfish control than intensive removals or eradication. Radical removals are probably socially or environmentally unacceptable, or just too difficult. Large-scale eradications in other areas have been attempted with toxicants and explosives (Jeppson 1957; Jeppson and Platts 1959; MacPhee 1969; Moyle et al. 1983), and similar approaches have been considered for the Columbia River (Rulifson 1984). The Columbia River is a multistate and multicommunity water source, however, and environmental concerns surround the use of toxicants (F. R. Young, Oregon Department of Fish and Wildlife, personal communication). Effects on other valuable fishes are also possible with any nonselective approach. Intensive removals with nets and traps have been successful in small systems (Foerster and Ricker 1941; Hamilton et al. 1970). Removal of large numbers of northern squawfish spread over reservoirs as large as John

Day (21,000 hectares) or the entire Columbia River Basin, however, could be a monumental task.

Selective fisheries are possible on a limited scale. Trapping and angling techniques are effective on northern squawfish. A selective fishery could probably produce exploitation on the order of 20% if management could develop the necessary effort in an economical way. An approach might be to develop a subsidized or self-sustaining commercial fishery. A market, the interest, and the economics of a potential fishery are yet to be analyzed. The approach is appealing, however, because at least some of the cost of a long-term control program could be recovered in yield.

Important uncertainties exist in our analysis. Even though predation by northern squawfish may be reduced with exploitation, the potential for rapid recovery in the population represents a risk in short-term control programs. In addition to our reproduction functions, we relied on several other simplifying assumptions. We assumed no compensation in growth or mortality of exploited northern squawfish. Our estimates of growth were high, and we also believe from other work (Beamesderfer and Rieman 1988a) that population densities are relatively low. Strong compensation in either process seems unlikely. Cushing and Harris (1973) and Gulland (1978) emphasized that compensation in reproduction and yearling recruitment is more important to production in exploited populations than compensation in growth or mortality of postjuvenile fish. The recruitment function we used should outweigh any compensation in growth and mortality, but the magnitude of change could be different. Although we believe strong compensation is unlikely, benefits from a control program could be less than anticipated.

The uncertainty of the model response to a reduction in growth shows that an overestimate of growth could also lead to an overestimate of the benefit from control. Scale analysis has a subjective component and error is possible. However, if our mortality estimates are realistic, growth must approach our estimate for fish to reach the sizes we observed. Our results do suggest that benefits from exploitation may not be the same among all predator populations.

The model was sensitive to uncertainty in our mortality estimates. The uncertainty was not enough to alter our conclusion regarding the effects of exploitation, however. Results were within those bounded by our uncertainty in the reproduction response.

Our analysis was limited to a single predator and did not consider the potential for any response in the remaining fish community. To reason that a reduction in predation by northern squawfish would result in a reduction of total predation, we must assume that no other predators compensate for the loss of northern squawfish. In natural and complex communities, that type of compensation may be expected (Campbell 1979; Larkin 1979). In the Columbia River reservoirs, northern squawfish represent the only important salmonid predator native to the system. Other predators, including walleye, smallmouth bass, and channel catfish *Ictalurus punctatus*, have been introduced. Interactions among members of the native and introduced community are not predictable.

Year-Class Strength

Factors that influence recruitment of northern squawfish will influence predation. We did not find any correlation, however, between year-class size and physical variables of temperature, reservoir water levels, or flow. A potential to manage predation through direct manipulation of the reservoir environment was not obvious.

We did find a negative correlation between concurrent year-classes of walleye and northern squawfish. Walleye might influence northern squawfish through predation. Walleyes are capable of important predation on other larval and juvenile cyprinids (Lyons 1987) and probably influence year-class size of littoral-zone species (Lyons 1987; Lyons and Magnuson 1987) similar to northern squawfish.

If walleyes are important in limiting recruitment of northern squawfish, management of walleye could influence predation on salmonids. Walleyes are a predator on salmonids, but much less important than are northern squawfish (Rieman et al. 1988). Management favoring walleye might provide a net benefit in salmonid survival. Although physical variables are known to influence walleye year-class formation in other systems (Busch et al. 1975; Koonce et al. 1977; Serns 1982), similar relations have not been demonstrated for Columbia River stocks (Connolly and Rieman 1988). Further work to define factors controlling year-class strength of walleye and the interaction between walleyes and northern squawfish in the Columbia River could be useful.

Summary

Our objective in this analysis was to examine management alternatives and illustrate possible responses in predation given some basic infor-

mation about the dominant predator population in a system. Our results suggest that important changes in predation could be made by sustained exploitation of the northern squawfish population and perhaps by manipulating walleye in John Day Reservoir. Our simulation approach had important limitations, and some risk is present. Further research can address some of these limitations. However, because of the economic and social importance of Columbia River salmonids and their apparent limitation by predation, control programs may be undertaken in the near future. Any such effort should include research to document compensation in predator populations and the fish community. Any evaluation of a control program must also be designed to isolate the effects of an experiment from inherent variation in the system.

Acknowledgments

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