

## Development and Corroboration of a Bioenergetics Model for Northern Pikeminnow Feeding on Juvenile Salmonids in the Columbia River

JAMES H. PETERSEN\*

U.S. Geological Survey, Biological Resources Division,  
Columbia River Research Laboratory, Cook, Washington 98605, USA

DAVID L. WARD

Oregon Department of Fish and Wildlife,  
Clackamas, Oregon 97015, USA

**Abstract.**—A bioenergetics model was developed and corroborated for northern pikeminnow *Ptychocheilus oregonensis*, an important predator on juvenile salmonids in the Pacific Northwest. Predictions of modeled predation rate on salmonids were compared with field data from three areas of John Day Reservoir (Columbia River). To make bioenergetics model estimates of predation rate, three methods were used to approximate the change in mass of average predators during 30-d growth periods: observed change in mass between the first and the second month, predicted change in mass calculated with seasonal growth rates, and predicted change in mass based on an annual growth model. For all reservoir areas combined, bioenergetics model predictions of predation on salmon were 19% lower than field estimates based on observed masses, 45% lower than estimates based on seasonal growth rates, and 15% lower than estimates based on the annual growth model. For each growth approach, the largest differences in field-versus-model predation occurred at the midreservoir area (–84% to –67% difference). Model predictions of the rate of predation on salmonids were examined for sensitivity to parameter variation, swimming speed, sampling bias caused by gear selectivity, and asymmetric size distributions of predators. The specific daily growth rate of northern pikeminnow predicted by the model was highest in July and October and decreased during August. The bioenergetics model for northern pikeminnow performed well compared with models for other fish species that have been tested with field data. This model should be a useful tool for evaluating management actions such as predator removal, examining the influence of temperature on predation rates, and exploring interactions between predators in the Columbia River basin.

Predation on juvenile salmonids *Oncorhynchus* spp. by northern pikeminnow *Ptychocheilus oregonensis* (formerly northern squawfish) occurs in lakes, free-flowing rivers, and reservoirs throughout the Columbia River basin (Jeppson and Platts 1959; Thompson and Tufts 1967; Buchanan et al. 1981; Tabor et al. 1993; Ward et al. 1995). Because of the economic and cultural importance of salmon in this region, numerous measures have been undertaken to reduce predation by northern pikeminnow on juvenile salmonids migrating through reservoirs on the Columbia River. Bypass systems at dams, originally constructed to route salmon around turbines, have been modified to minimize predator–prey encounters (Shively et al. 1996). Juvenile salmon are collected at several dams and transported in barges and trucks around lower Columbia River reservoirs to speed their passage and

reduce their exposure to predators (Solazzi et al. 1991). Also, a large-scale program was started in 1990 to remove a portion of the northern pikeminnow population so as to reduce predation mortality of salmon (Beamesderfer et al. 1996; Friesen and Ward 1999). The methods used to justify and evaluate these programs include monitoring the movements of radio-tagged predators and prey (Faler et al. 1988; Martinelli and Shively 1997), releasing freeze-branded or coded-wire-tagged juvenile salmon (Berggren and Filardo 1993; Giorgi et al. 1994), measuring growth and fecundity of predators (Parker et al. 1995; Beamesderfer et al. 1996), and modeling how juvenile salmonid mortality varies with predator density, river flow, and other variables (Beamesderfer et al. 1990; Lee 1991).

In John Day Reservoir, where several predation studies have been conducted, the annual loss of salmonids to northern pikeminnow has ranged from 1.4 to 8.1 million fish, the estimate depending on the modeling approach (Beamesderfer et al.

\* Corresponding author: jim.petersen@usgs.gov

Received January 7, 1998; accepted November 3, 1998

1990; Bledsoe 1990; Bledsoe et al. 1990; Rieman et al. 1991; Petersen 1994). The various models developed to estimate juvenile salmonid mortality due to predation depend on field measurement of the predation rate (salmon consumed  $\cdot$  predator<sup>-1</sup>  $\cdot$  day<sup>-1</sup>), which is expensive and difficult to measure in such a large system. In areas farther than 5 km from dams (midreservoir areas), where the largest proportion of the predator population resides, measured predation rates on juvenile salmon are often relatively low ( $<0.05$  salmon  $\cdot$  predator<sup>-1</sup>  $\cdot$  day<sup>-1</sup>) and the confidence intervals for these rates commonly include zero (Petersen et al. 1990; Petersen 1994; Ward et al. 1995). Modeling the response of northern pikeminnow to changes in salmonid density, the functional response, has also been problematic (Beamesderfer et al. 1990; Petersen and DeAngelis 1992) because direct estimates of salmonid densities are not available in most areas and predators often feed on alternative prey such as sculpins and crayfish. Finally, the mortality rate of prey in large systems, including rivers, may be influenced greatly by the movement and patchiness of prey and by the spatial scale of the model (De Roos et al. 1991; Pascual and Levin 1999; J. H. Petersen and D. L. DeAngelis, unpublished analyses).

In this paper we develop and corroborate an approach to estimating predation on juvenile salmonids that uses energetics relationships, temperature, and fish growth to indirectly estimate the consumption of salmon by northern pikeminnow. This approach avoids some of the problems associated with the methods mentioned above. After deriving the bioenergetics model and its parameters, we used data collected during 1983–1986 in John Day Reservoir of the Columbia River to examine how well the model predicted predation on salmon by northern pikeminnow. We compared three approaches for characterizing northern pikeminnow growth during spring through summer, when juvenile salmonids occur in the diet of northern pikeminnow. The sensitivity of modeled predation on salmon was examined with respect to parameter variation, sampling bias caused by gear selectivity, and skewed distributions of predator size.

A complete bioenergetics model for northern pikeminnow has not been developed, although Beauchamp et al. (1995) used a partially developed model to examine predation in Lake Ozette, Washington. Bioenergetics modeling has been used successfully with yellow perch *Perca flavescens*, largemouth bass *Micropterus salmoides*, walleye *Stizostedion vitreum vitreum*, northern pike *Esox*

*lucius*, adult salmonids, and several other species (e.g., Kitchell et al. 1977; Rice and Cochran 1984; Beauchamp et al. 1989; Wahl and Stein 1991). Bioenergetics has also been applied in large aquatic systems (Brandt and Kirsch 1993; Labar 1993; Lantry and Stewart 1993) and in the evaluation of predator–prey interactions (Lyons and Magnuson 1987; Stewart and Ibarra 1991; Labar 1993). A major advantage of the bioenergetics approach is that it does not require direct field estimates of predation rates (prey  $\cdot$  predator<sup>-1</sup>  $\cdot$  day<sup>-1</sup>), but instead uses fish growth as an integrator of fish energy budgets to estimate predation rate.

### Study Area

Predation rates, diets, and growth data were collected during 1983–1986 throughout the John Day Reservoir (Poe et al. 1991; Vigg et al. 1991), which is 123 km long, has an average width of 1.8 km, and has a surface area of 19,781 ha (Ward et al. 1995). John Day Reservoir extends upriver to the base of McNary Dam. Based on patterns of predator density and predation rates (Beamesderfer and Rieman 1991; Petersen 1994), we used data from three reservoir areas for our model analyses: the John Day Dam forebay (JDF; 4.7% of total surface area), the boat-restricted zone immediately below McNary Dam (MRZ; 0.3%), and a large midreservoir area (MID; 88.6%). A fourth area, downriver of MRZ (6.4%), was delineated in some earlier studies but this area was excluded from our analyses because relatively few predator samples were available from it and it is considered a transition zone between the MRZ and MID areas (Beamesderfer and Rieman 1991; Petersen 1994). Methods for collecting and processing northern pikeminnow have been described elsewhere (Poe et al. 1991; Vigg et al. 1991).

Water temperatures at McNary Dam and John Day Dam (U.S. Army Corps of Engineers, unpublished data) were used for simulations in the MRZ and JDF areas, respectively. Temperatures at dams may not be representative of temperatures in midreservoir areas because water may warm during passage through long reservoirs. During May through August 1994, average monthly temperatures at John Day Dam were 1.7–1.8°C higher than temperatures at a site 75 km upriver from the dam (M. Parsley, U.S. Geological Survey, unpublished data). For simulations at the MID location, we used the temperature differences observed in 1994 to correct John Day Dam temperatures observed during 1983–1986. Daily temperatures were inter-

polated between average monthly temperatures at each location.

### Model Development

#### Bioenergetics Equations and Parameters

The general balanced equation for energy is

$$\text{growth} = \text{consumption} - \text{respiration} \\ - (\text{egestion and excretion}).$$

We expanded components of this equation using the modeling approach and software of Hanson et al. (1997).

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

$$C = C_{\max} \cdot p \cdot F(T);$$

$C_{\max}$  = maximum specific consumption rate (g prey · g predator<sup>-1</sup> · d<sup>-1</sup>);

$p$  = proportion (0–1.0) of maximum consumption  $C_{\max}$ ;

$T$  = temperature (°C);

$F(T)$  = the temperature dependence function.

Maximum specific consumption was defined as an allometric function of predator mass:

$$C_{\max} = \alpha W^{\beta};$$

$W$  = fish mass (g);

$\alpha$  = intercept of the allometric function for consumption;

$\beta$  = slope of the allometric function for consumption.

To estimate the allometric parameters for  $C_{\max}$ , we used consumption and size data from Vigg and Burley (1991), who conducted laboratory feeding experiments with northern pikeminnow preying on juvenile chinook salmon. We used the maximum consumption for three size groups (501–1,100 g, 1,101–1,500 g, and 1,501–2,000 g) of northern pikeminnow preying on live salmonids at 21.5°C (Table 2 in Vigg and Burley 1991), which is near the optimum temperature for feeding and digestion for this species (Black 1953; Beyer et al. 1988; Vigg and Burley 1991). Allometric parameters were estimated by regressing the  $\log_e$ (average ration plus 1 SD) on the  $\log_e$ (midpoints of the mass range). Average mass for each size-group was not reported by Vigg and Burley (1991), so we used midpoints of 800, 1,300, and 1,750 g. We used ration + 1 SD for  $C_{\max}$  because only juvenile salmonid prey had been used in the experiments of Vigg and Burley (1991), whereas feed pellets or

relatively inactive prey are used in most  $C_{\max}$  experiments (e.g., Brett 1971; Stewart et al. 1983). Use of large, active prey like salmonids would likely yield underestimates of maximum ration, compared with pellets or inactive prey, because of higher rates of prey escape and occasional regurgitation (Gadomski and Hall-Griswold 1992; Petersen et al. 1994). The fitted allometric equation ( $r^2 = 0.96$ ;  $N = 3$ ) was

$$C_{\max} = 0.278W^{-0.197}.$$

Coefficients of the  $C_{\max}$  equation are similar to estimates for other large predators such as smallmouth bass ( $\alpha = 0.25$ ;  $\beta = -0.31$ ), walleye ( $\alpha = 0.25$ ;  $\beta = -0.27$ ), and northern pike ( $\alpha = 0.2045$ ;  $\beta = -0.18$ ) tabulated by Hewett and Johnson (1992) and Hanson et al. (1997). Using the average ration from Vigg and Burley (1991) and not adding 1 SD to the average produced a much poorer fit to mass ( $r^2 = 0.10$ ;  $N = 3$ ).

The temperature dependence function of consumption  $F(T)$  was modeled according to Thornton and Lessem's (1978) approach. This approach combines increasing and decreasing logistic equations to produce a dome-shaped function of consumption versus temperature. The Thornton and Lessem model has been used for species such as alewife *Alosa pseudoharengus*, coho salmon *Oncorhynchus kisutch*, chinook salmon *O. tshawytscha*, and steelhead *O. mykiss* (Stewart et al. 1981; Stewart and Binkowski 1986; Rand et al. 1993). Vigg and Burley (1991) derived parameters for the Thornton and Lessem model for northern pike-minnow except for the low optimum temperature (CTO) and the high optimum temperature (CTM; see Table 1), which we estimated using an iterative search method. We first calculated the maximum consumption rate at the optimum temperature (21.5°C) using the best-fit temperature-dependent equation of Vigg and Burley (their equation 5). Parameters CTO and CTM were found by iteratively searching for a higher temperature (CTO) and a lower temperature (CTM) that produced a consumption rate 2% above or below the computed maximum rate.

Activity-dependent respiration ( $R$ ), the amount of energy in mass equivalents of oxygen necessary to carry out standard and active metabolism, was modeled as

$$R = R_s \cdot \text{ACT};$$

$$R_s = \text{standard metabolism (g O}_2 \cdot \text{g}^{-1} \cdot \text{d}^{-1});$$

TABLE 1.—Parameter values used in the northern pikeminnow bioenergetics model. Parameters in capital letters (e.g., CA, CQ) refer to the formulation in the software of Hanson et al. (1997) for consumption (their equation 3), respiration (their equation 1), and egestion—excretion (their equation 1). Where available, lower and upper 95% confidence limits (95% CIs) are included for model parameters specific to northern pikeminnow. Sources: 1—computed from data in Vigg and Burley (1991); 2—Vigg and Burley (1991); 3—Cech et al. (1994); 4—Bevelheimer et al. (1985); 5—this paper; 6—Rice et al. (1983).

Parameter	Parameter description	Parameter value (95% CI)	Source
<b>Consumption (C)</b>			
$\alpha$ (CA)	Intercept: $C_{\max}$ versus predator mass	0.278 (0.264, 0.292)	1
$\beta$ (CB)	Slope: $C_{\max}$ versus predator mass	−0.197 (−0.281, −0.113)	1
CQ	Temperature for CK1 (°C)	0.0	2
CTO	Low optimum temperature (°C)	20.1	1
CTM	High optimum temperature (°C)	22.7	1
CTL	Temperature for CK4 (°C)	27.0	2
CK1	Proportion of $C_{\max}$ at CQ	0.001	2
CK2, CK3	Proportion of $C_{\max}$ at CTO, CTM	0.98	2
CK4	Proportion of $C_{\max}$ at CTL	0.01	2
<b>Respiration (R)</b>			
a (RA)	Intercept: R versus predator mass	0.00165 (0.00040, 0.00677)	3
b (RB)	Slope: R versus predator mass	−0.285 (−0.483, −0.087)	3
$\tau$ (RQ)	Coefficient: R versus temperature	0.105 (0.085, 0.125)	3
v (RTO)	Activity coefficient	0.1222	4
$\psi$ (RK1)	Swimming speed (cm · s <sup>−1</sup> )	9.2, 1.3, 5.0 <sup>a</sup>	5
SDA	Specific dynamic action	0.163	6
<b>Egestion and excretion</b>			
FA	Proportion of consumption egested	0.2	4
UA	Proportion of (consumption—egested)	0.07	4

<sup>a</sup> Swimming speeds in McNary Dam tailrace (MRZ), mid John Day Reservoir (MID), and John Day Dam forebay (JDF), respectively.

ACT = the multiplicative increment for active metabolism.

To estimate standard metabolism, we used the model

$$R_s = aW^b \cdot e^{\tau T};$$

W = fish mass (g);

a = intercept of the allometric function for respiration;

b = slope of the allometric function for respiration;

T = temperature (°C);

$\tau$  = the slope of the function for temperature effect on respiration rate.

This model has been used for a variety of large predators in coolwater systems (Rice et al. 1983; Stewart et al. 1983; Hewett and Johnson 1992). We used parameter values for a, b, and  $\tau$  from Cech et al. (1994), estimated for northern pikeminnow from the Columbia River (Table 1).

The increment for active metabolism in bioenergetics models has been the topic of considerable debate and disagreement (Hewett et al. 1991; Boisclair and Leggett 1991). To model the role of activity on respiration, we first assumed that northern

pikeminnow had different levels of activity depending on the type of prey in their diet (Boisclair and Leggett 1989). Northern pikeminnow in the Columbia River are omnivorous, feeding on molluscs, insects, plants, crustaceans, and fish (Poe et al. 1991; Ward et al. 1995). Northern pikeminnow eat both benthic and pelagic organisms (Poe et al. 1991; J. H. Petersen, unpublished analyses), and their activity probably varies with different foraging modes. During benthic foraging, northern pikeminnow search for crayfish, sculpins, bivalves, or other slow-moving prey, and activity would be relatively low. When northern pikeminnow forage on pelagic juvenile salmonids, their activity is likely higher with bursts of rapid swimming during attacks on mobile salmonids, movements into and out of salmonid patches, and occasional periods of inactivity for digestion.

Northern pikeminnow consumed mostly salmonids in the MRZ but primarily nonsalmonid benthic prey in the MID (Petersen 1994; Table 2). The average swimming speed for predators was estimated from radio-tagged fish in tailrace and non-tailrace areas of two lower Columbia River reservoirs (Martinelli and Shively 1997; T. Martinelli, U.S. Geological Survey, Cook, Washington, un-

TABLE 2.—Average diets of northern pikeminnow, by month and John Day Reservoir area. Data were collected in John Day Reservoir during 1983–1986. Sample size for diets ranged from 44 to 405 predators for each area–month stratum. Diet quality is also summarized.

Month or feature	Prey category			
	Salmonids	Nonsalmonid fishes	Crustaceans	Miscellaneous
<b>McNary Dam tailrace (MRZ): percent of prey</b>				
Apr	44	15	27	14
May	62	10	20	8
Jun	36	10	35	19
Jul	73	7	12	8
Aug	42	22	18	18
<b>Midreservoir (MID): percent of prey</b>				
Apr	6	38	36	20
May	9	18	54	19
Jun	4	17	48	31
Jul	1	16	56	27
Aug	3	13	43	41
<b>John Day Dam forebay (JDF): percent of prey</b>				
Apr	24	10	41	25
May	44	6	43	7
Jun	26	11	46	17
Jul	26	8	15	51
Aug	14	27	16	43
<b>Overall diet quality</b>				
Energy density (cal · g <sup>-1</sup> ) <sup>d</sup>	1,030 <sup>a</sup>	1,300 <sup>b</sup>	1,077 <sup>c</sup>	625 <sup>c</sup>
Proportion indigestible	0.033 <sup>e</sup>	0.033 <sup>e</sup>	0.1 <sup>e</sup>	0.4 <sup>e</sup>

<sup>a</sup> Rondorf et al. (1985) for juvenile spring chinook salmon (21–25 g) at McNary Dam.

<sup>b</sup> Brockson et al. (1968); Rotliers and Tucker (1982).

<sup>c</sup> Average of values from Cummins and Wuycheck (1971).

<sup>d</sup> 1,000 cal · g<sup>-1</sup> = 4,184 J · g<sup>-1</sup>.

<sup>e</sup> Stewart et al. (1983).

published data). Swimming speed was estimated as the straight-line distance between radio contacts divided by time; swimming speeds were uncorrected for local water velocity so estimated speeds were conservative. In dam tailraces, the average swimming speed was 9.2 cm · s<sup>-1</sup> for radio contacts less than 24 h apart. Outside of the dam tailraces, the average swimming speed was 1.3 cm · s<sup>-1</sup> exclusive of June and July, when predators may have been migrating to spawning sites (Martinelli and Shively 1997). Based on these average estimates of swimming speed, northern pikeminnow activity related to foraging may be several times greater in a dam tailrace than in a midreservoir area.

Activity ACT was modeled as

$$ACT = e^{v\psi};$$

$\psi$  = swimming speed (cm · s<sup>-1</sup>);

$v$  = coefficient for swimming speed.

For modeling, swimming speed was set at 1.3 cm · s<sup>-1</sup> in the MID and 9.2 cm · s<sup>-1</sup> in the MRZ. Activity of northern pikeminnow in a forebay was assumed to be lower than activity in the MRZ because water velocities and turbulence are greater in the tailrace environment. Activity in a forebay was assumed to be higher than in a midreservoir location because active juvenile salmon are a major prey item in forebays (Table 2). Thus, swimming speed was set to 5.0 cm · s<sup>-1</sup> in JDF, intermediate between activity in the MID and the MRZ.

Values for the activity coefficient  $v$  in Hanson et al. (1997) range from 0.0 for rainbow smelt *Osmerus mordax* to 0.901 for striped bass *Morone saxatilis*. As a working hypothesis, we used the activity coefficient from northern pike (0.122; Bevelheimer et al. 1985). This activity coefficient produced a multiplier of standard metabolism of 1.17 in the MID, where northern pikeminnow are assumed to be relatively inactive, and a multiplier of 3.07 for fish in the MRZ, where we assumed that predators were more active.

Lacking specific experimental data on the rates of egestion or excretion by northern pikeminnow, we used the simple proportional models of Kitchell et al. (1977):

$$\text{egestion} = FA \cdot \text{consumption};$$

$$\text{excretion} = UA \cdot (\text{consumption} - \text{egestion});$$

FA and UA are proportionality constants. We used parameters derived for esocids (Bevelheimer et al. 1985), which have a temperature range similar to that of northern pikeminnow. Consumption rates for most species are not especially sensitive to the formulation for egestion and excretion in bioenergetics models (Bartell et al. 1986).

#### *Diet of Northern Pikeminnow and Energy Density*

Juvenile salmonids, other fish, and crayfish commonly account for the largest proportion of the diet of northern pikeminnow (Poe et al. 1991; Vigg et al. 1991; Table 2). In John Day Reservoir, juvenile salmon composed from 1% (MID, July) to 73% (MRZ, July) of the diet of northern pikeminnow (Table 2).

The bioenergetics model converts the masses of predators and prey to an energy density (energy per gram) for computations. Northern pikeminnow energy density (ED; joules per gram wet mass) was estimated with an equation for Cyprinidae (Hartman and Brandt 1995)

$$ED = -981 + 251.1 \cdot W_{\text{dry}};$$



$W_{\text{dry}}$  is percent dry weight. The dry weight of northern pikeminnow is 30.6% of their wet mass (Vigg and Burley 1991;  $r^2 = 0.99$ ;  $N = 12$ ), so the predicted energy density of northern pikeminnow was  $1,602 \text{ cal} \cdot \text{g}^{-1}$  ( $6,703 \text{ J} \cdot \text{g}^{-1}$ ). The energy density of spring chinook salmon varied little from  $1,030 \text{ cal} \cdot \text{g}^{-1}$  ( $4,310 \text{ J} \cdot \text{g}^{-1}$ ) during their out-migration through the lower Columbia River (Rondorf et al. 1985). Nonsalmonid fishes in northern pikeminnow diets were primarily prickly sculpins *Cottus asper* (unpublished analyses; Poe et al. 1991). The energy density of cottids ranges from  $1,245 \text{ cal} \cdot \text{g}^{-1}$  ( $5,209 \text{ J} \cdot \text{g}^{-1}$ ; *C. perplexus*; Brocksen et al. 1968) to  $1,371 \text{ cal} \cdot \text{g}^{-1}$  ( $5,736 \text{ J} \cdot \text{g}^{-1}$ ; slimy sculpin *C. cognatus*; Rottiers and Tucker 1982), so we used  $1,300 \text{ cal} \cdot \text{g}^{-1}$  ( $5,439 \text{ J} \cdot \text{g}^{-1}$ ) for the nonsalmonid fish category. Crustaceans in the diet of northern pikeminnow are usually crayfish *Pacifastacus leniusculus* (Poe et al. 1991), which have an average energy density of  $1,077 \text{ cal} \cdot \text{g}^{-1}$  ( $4,506 \text{ J} \cdot \text{g}^{-1}$ ; Cummins and Wuycheck 1971). The miscellaneous food category was largely indigestible material derived from molluscs, insects, plants, and other organic material. We estimated an energy density of  $625 \text{ cal} \cdot \text{g}^{-1}$  ( $2,615 \text{ J} \cdot \text{g}^{-1}$ ) for this category using values from Cummins and Wuycheck (1971). Energy density was assumed to be constant throughout the year for northern pikeminnows and all food categories.

### Spawning

The time of spawning and the mass lost during spawning must be subtracted from observed growth changes in the bioenergetics model. Larvae (1–2 weeks old) of northern pikeminnow have been collected from mid-June to early August in John Day and The Dalles reservoirs; peak abundance of larvae occurs in July (Gadomski and Barfoot 1998). Gonad mass and the reproductive condition of northern pikeminnow in four lower Columbia River reservoirs (Bonneville, The Dalles, John Day, and McNary; 1993–1995) were used to characterize spawning. The gonadosomatic index ( $100 \times \text{gonad mass/body mass}$ ) for fully ripe fish tended to be highest in June (12% for females; 6% for males) and then declined gradually through July and early August. Spent females were not observed until early July; males followed a similar pattern, based on fewer data. Spawning loss was estimated as

$$\text{spawning loss (\%)} = \text{GSI}_r - \text{GSI}_s;$$

$\text{GSI}_r$  is the gonadosomatic index of ripe fish and

$\text{GSI}_s$  is the gonadosomatic index of spent fish. Spawning loss was estimated for all 2-weeks periods in June through mid-August whenever at least 10 individuals were available to compute both  $\text{GSI}_r$  and  $\text{GSI}_s$  (D. L. Ward, Oregon Department of Fish and Wildlife, unpublished data). For all years and reservoirs combined, females lost an average 6.3% body mass ( $\text{SE} = 0.3$ ;  $N = 16$  2-weeks periods) and males lost an average 1.9% body mass ( $\text{SE} = 0.4$ ;  $N = 8$  2-weeks periods). For modeling purposes, we assumed a 1:1 female : male ratio of northern pikeminnow, that all fish spawned on June 15, and the typical individual had a spawning loss of 4.1% of body mass on June 15 (average of male and female loss).

### Size and Growth

During all years and months, the largest northern pikeminnow were found in the MRZ, and predators at MID and JDF were often 100–300 g smaller (Figure 1). In the MRZ, mean size declined until August, when it increased slightly. In the JDF, mean size increased between April and May, then decreased during June through August in these areas. In the MID, mean size decreased each month until August, when it increased from 664 g (July) to 707 g (August).

To corroborate the bioenergetics model, we compared estimates of predation by northern pikeminnow on salmon made with a modification of the Swenson and Smith method (Vigg et al. 1991; called “field” predation below) to estimates of predation made with the bioenergetics model (called “model” predation below; see “Predation on Juvenile Salmon” below). We did not have cohort-specific growth of northern pikeminnow and corresponding predation rates on salmon to corroborate the bioenergetics model (e.g., Rice and Cochran 1984), but instead had predation rates from field samples that included fish of a broad range of sizes and ages (Vigg et al. 1991). Having samples of fish from various age-groups made it more difficult to measure the growth of the “average” fish because individuals of different sizes obviously grow at different rates.

Lacking cohort-specific growth, we used three approaches to characterize the growth of the average fish and compared our corroboration results among these approaches. The approaches (referred to as “observed,” “seasonal,” and “annual” below) differed in how we estimated the size of the average fish at the end of each sample period. The size of fish at the start of a period was the observed average mass of predators collected during a

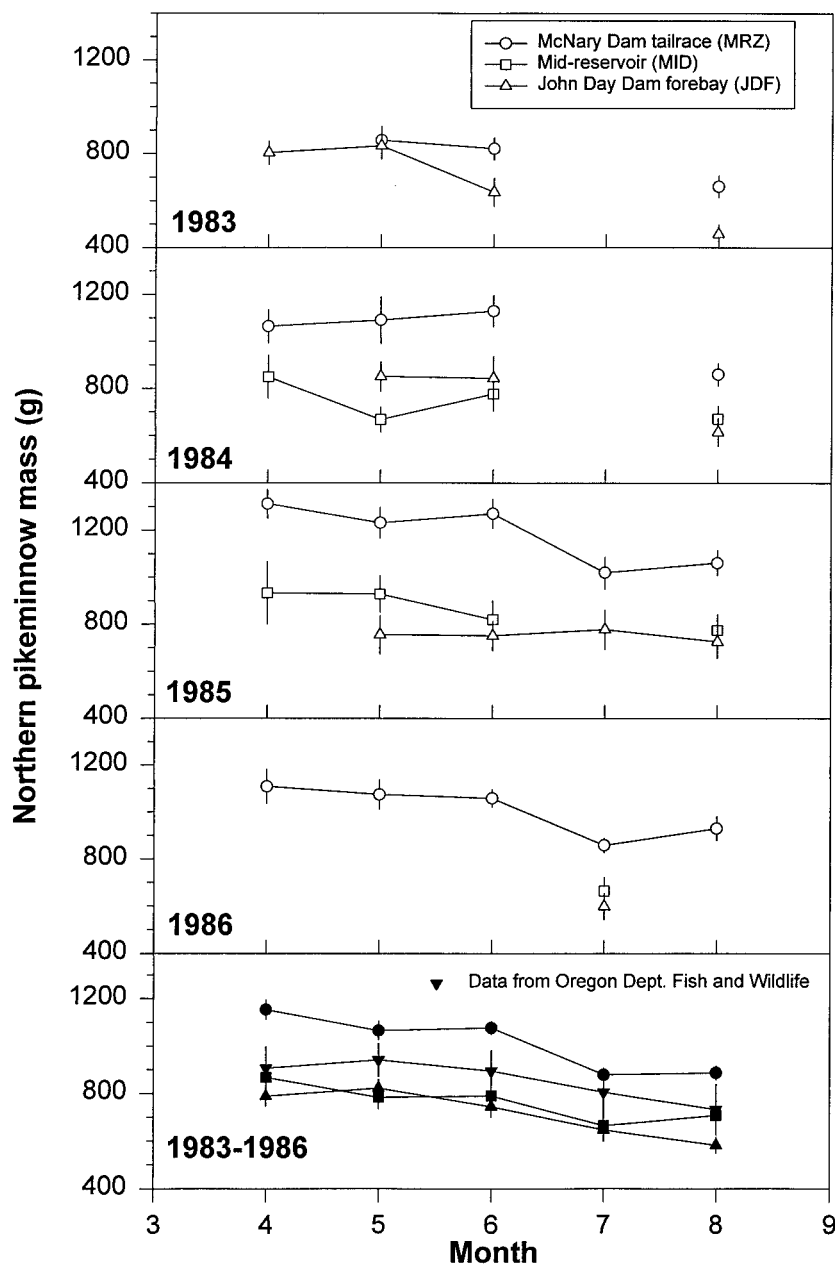


FIGURE 1.—Average mass ( $\pm 2$  SE) of northern pikeminnow collected during 1983 through 1986 in three areas of John Day Reservoir. Data are combined across years in the bottom panel. Northern pikeminnow collected and marked throughout the John Day Reservoir by the Oregon Department of Fish and Wildlife during 1983–1986 are also shown in the bottom panel. Sample sizes ranged from 26 to 512 during individual years (top four panels) and from 26 to 614 for the combined data (bottom panel). Months with data extend from April (4) to August (8).

month. The first method for estimating growth simply used the observed mass of the fish collected during the second month as the final size of the average fish (Figure 1). For the other two methods,

a daily growth rate was estimated and was used to predict the change in size over a 30-d period.

In the seasonal approach, we used tag-recapture data from 1983 to 1986 to estimate rates of daily

TABLE 3.—Specific seasonal growth rates of northern pikeminnow in John Day Reservoir (1983–1986), based on mark–recapture data.

Period	Growth rate (SE) (% · d <sup>-1</sup> )	N	Probability that growth rate = 0
Apr–May	−0.14 (0.12)	27	0.25
Jun–Jul	−0.77 (0.19)	20	<0.001
Aug	−0.49 (0.12)	29	<0.001

growth. Northern pikeminnow were captured by electrofishing in John Day Reservoir, measured (mass, nearest g; fork length, nearest mm), marked with Floy tags, and released at the same location. Recaptured fish were measured and changes in size were computed. Marked predators had an average initial mass of 883 g (range = 180–1,828 g;  $N = 251$ ;) and an average fork length of 395 mm (range = 253–523 mm;  $N = 313$ ). Daily growth rate GS ( $\text{g} \cdot \text{d}^{-1}$ ) was estimated from tagged fish by (Ricker 1979) as

$$\text{GS} = (\log_e W_2 - \log_e W_1) / (t_2 - t_1);$$

$W_1$  (g) = fish mass on day  $t_1$ ;

$W_2$  (g) = fish mass on day  $t_2$ .

A separate daily growth rate was estimated for prespawning (April–May), spawning (June–July), and postspawning (August–September) periods. Only individuals that were tagged and recaptured within the same period were used in the following analysis; individuals tagged in one period and recaptured in a later period were not included because growth might have been confounded with weight loss due to spawning. To determine the average size of fish at the end of a sample interval with this approach, we assumed fish grew for 30 d at the rates in Table 3 and added the computed growth mass to the initial observed mass.

The daily growth rate estimated from tagged individuals was negative but not significantly different from zero during the prespawning period (Table 3). During the spawning months of June–July and the postspawning month of August, the daily specific growth rate was significantly less than zero, suggesting weight loss or size-specific emigration of northern pikeminnow during these periods (Table 3). Handling and tagging may have caused some bias in the growth rate of tagged fish compared with untagged fish. For those predators recaptured within 5 d after the initial marking, fish lost at average of 1.5% of their mass, although this loss was not significantly different from zero (average = 1.5%; SE = 1.0;  $N = 29$ ;  $P > 0.05$ ;  $t$ -test on arcsine-transformed percentages).

In the annual approach, we used an annual growth model for northern pikeminnow to derive a daily growth rate, which was used to predict final size. Daily growth rate, GA ( $\text{g} \cdot \text{d}^{-1}$ ) was estimated as

$$\text{GA} = \Delta W / \Delta t;$$

$\Delta W$  (g) = expected change in mass during 1 year;

$\Delta t$  = number of days within the year when northern pikeminnow might have positive growth.

The expected change in mass  $\Delta W$  was determined by regression for fish aged 5–15 years ( $r^2 = 0.97$ ;  $N = 11$ ) as

$$\Delta W = e^{4.343 - 0.00169 W_0};$$

$W_0$  is the size (g) of the fish at the start of the 1-year period. Data to fit the equation for  $\Delta W$  were calculated from the growth model of Rieman and Beamesderfer (1990). We assumed that all positive growth occurred between April 1, which corresponds roughly to the seasonal beginning of a rise in temperature and the start of the juvenile salmonid outmigration period, and October 31, when water temperature typically begins a rapid decline ( $\Delta t = 214$  d). If the sample was for the June–July period, we subtracted a spawning loss from the predicted final mass (4.1% = average for males and females; see “Spawning” above).

To demonstrate patterns of specific rates during a year, we simulated growth of an 8–9-year-old northern pikeminnow (669–813 g) in the MRZ during 1986 (Figure 2). Maximum water temperature during 1986 was 20.8°C, close to the average for 1983–1986 (21.0°C). Specific consumption, excretion, and egestion rates were very low during winter months when temperature was below 4°C (Figure 2A). The respiration rate was closely correlated with temperature, but other physiological rates showed some declines during mid to late summer. The specific growth rate for northern pikeminnow was positive from April 22 to October 29 with peaks in early July and in early October (Figure 2B). Relatively high temperatures in July, August, and early September caused specific egestion, excretion, and consumption rates to decline, the net result being decreases in specific growth rate during those months.

#### Predation on Juvenile Salmon

Field and model estimates of predation on salmon were made from data collected in the three areas



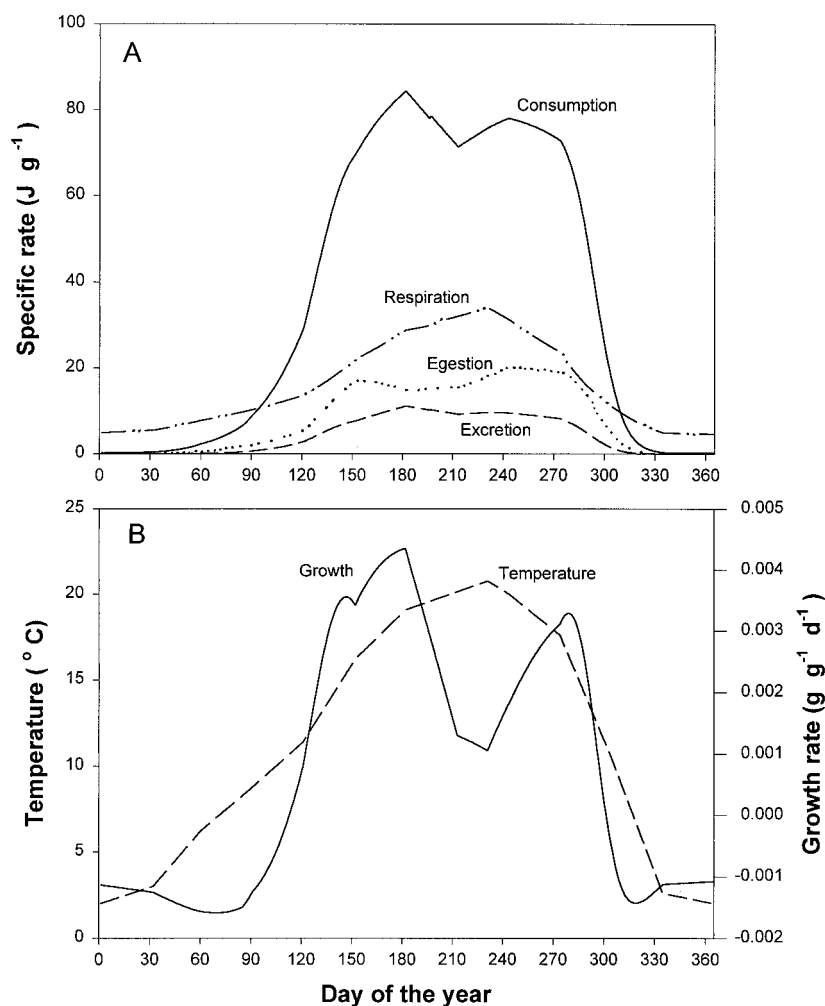


FIGURE 2.—Simulated seasonal changes in (A) specific bioenergetics rates and (B) growth rate of age-8 northern pikeminnow, as well as in temperature (B) in the McNary Dam tailrace, John Day Reservoir zone MRZ, 1986. Northern pikeminnow diets for January–March and September–December were arbitrarily set to 33% nonsalmonid fish, 34% crustaceans, and 33% miscellaneous, because diet data were not available for those periods.

(MRZ, MID, and JDF) of John Day Reservoir (1983–1986; Poe et al. 1991; Vigg et al. 1991). From this data set, we selected 2-month periods for which at least 15 predators per month were available for making field estimates of predation rates (Petersen et al. 1990) and at least 25 predators per month were available for determining the average mass of northern pikeminnow. For all model estimates of the predation rate on salmon, we used field data on the diet of predators and water temperature for that area and period. Simulated fish grew from the 15th day of the first month to the 15th day of the second month, and reported model estimates of the rate of predation are the average of the 30 daily values.

The absolute difference between model and field predation rates on salmon (model – field) and the ratio of model and field predation estimates (model : field) were significantly correlated for each growth method (Pearson correlation coefficients  $> 0.52$ ;  $P < 0.04$ ) so we discuss only the ratio of estimates below. Ratios were  $\log_e$ -transformed to improve normality for statistical tests. The model : field ratio of predation on salmon was not affected by year or month nested within year (nested analysis of variance, ANOVA;  $P > 0.45$ ). Time-by-location effects could not be explicitly tested because of the small sample size and the lack of a midreservoir sample for summer months (Table 4). For further analyses, data were pooled across months and years.

TABLE 4.—Field and bioenergetic model estimates of the predation rate on salmon by northern pikeminnow (NPM) in three areas within the John Day Reservoir (1983–1986). Field estimates of predation rate were made by the modified Swenson and Smith (1973) method (Vigg 1991). Bioenergetic model predictions of predation rate were made by three methods to determine the growth of predators in a 2-month period.

Predation rate (mg salmon · g NPM <sup>-1</sup> · d <sup>-1</sup> )					
			Model prediction, per growth method		
Year	Period (months)	Field (2 SE)	Observed final mass	Seasonal growth method	Annual growth method
McNary Dam tailrace (MRZ)					
1983	May–Jun	11.0 (4.2)	7.5	6.2	9.9
1984	Apr–May	6.2 (2.8)	5.6	4.6	5.4
1984	May–Jun	6.1 (3.4)	5.5	2.8	5.1
1985	Apr–May	13.0 (3.8)	5.2	8.4	9.8
1985	May–Jun	13.4 (4.4)	15.2	9.0	14.2
1985	Jun–Jul	21.8 (7.8)	13.9	19.2	26.5
1985	Jul–Aug	24.2 (12.4)	14.4	10.2	13.8
1986	Apr–May	6.7 (2.8)	6.4	5.6	7.6
1986	May–Jun	5.4 (3.0)	9.3	6.7	10.6
1986	Jun–Jul	15.5 (7.8)	9.6	13.2	19.5
1986	Jul–Aug	21.9 (9.4)	20.5	13.0	18.3
Midreservoir (MID)					
1984	Apr–May	2.2 (2.4)	a	0.6	0.9
1984	May–Jun	2.0 (2.0)	0.5	a	0.3
1985	Apr–May	2.1 (3.6)	0.3	0.3	0.5
1985	May–Jun	1.9 (4.0)	a	0.1	1.0
John Day Dam forebay (JDF)					
1983	Apr–May	12.3 (5.4)	6.4	4.5	6.0
1983	May–Jun	17.1 (9.6)	a	1.5	3.7
1984	May–Jun	7.8 (4.2)	3.4	1.4	4.4
1985	May–Jun	5.5 (4.0)	4.2	2.3	5.1
1985	Jun–Jul	6.9 (4.6)	16.7	8.4	14.7
1985	Jul–Aug	8.4 (5.2)	4.3	3.8	5.9

<sup>a</sup> No estimate was possible from the observed or predicted change between initial and final mass (proportion of maximum consumption [ $p$ ] was less than 0.0 or more than 1.0).

Using the observed average mass measured during the second month as the final mass, we obtained model estimates of the predation rate on salmon for 18 of 21 periods (Table 4). The bioenergetics model estimates of predation were 19% less than the field estimates (Table 5), and the average model : field ratio was different from 1.0 ( $P = 0.02$ ; Table 5). The mean ratio varied among the three reservoir areas (ANOVA;  $P < 0.01$ ), being significantly less in the MID area than in both the MRZ and the JDF areas. The mean model : field ratio of predation rates was not significantly different from 1.0 in the JDF, MID, or MRZ areas ( $P > 0.09$ ; Table 5). For three periods, April–May 1984 in the MID, May–June 1985 in the MID, and May–June 1983 in the JDF

(Table 4), the bioenergetics model could not produce a growth scenario that would match the large observed changes in mass between the first and second months (–181 g, –110 g, and –195 g, respectively) even if the proportion of maximum consumption ( $p$ ) was set to 0.0.

By the seasonal growth method, the average model prediction of predation rate on salmon for all areas was 45% less than the average field estimate (Table 5), the largest difference among the three types of growth methods. As with the other growth methods, the largest average difference occurred in the MID area (–84%; Table 5).

With the annual growth model to estimate growth increment, model estimates of predation were 15% less than the field estimates for all areas combined. Model estimates of predation for the MID area were 67% less than field estimates, whereas MRZ and JDF differences were considerably less (+4% and –16%, respectively; Table 5). The log<sub>e</sub>-transformed ratio of model : field predation rates was significantly different from zero for all rates pooled (Table 5), largely because of the poor fit in MID area.

The proportion of maximum consumption ( $p$ ) in the bioenergetics model was slightly higher in the MRZ than in the JDF or the MID for two out of three growth analyses (Table 5). The range of model : field ratios was quite large for all growth methods (Table 5). The model : field ratios of predation rates were highly correlated among all three methods used to determine the final average mass of northern pikeminnow (Pearson correlation coefficients  $> 0.79$ ,  $P < 0.001$ ).

### Sensitivity Analyses

#### *Sensitivity to Model Parameters*

Sensitivity studies were conducted on predator energy density and parameters for maximum consumption, respiration, and activity. Individual parameters were systematically varied  $\pm 10\%$  from their nominal value and the cumulative consumption of salmonids was compared with a baseline simulation for northern pikeminnow (Lantry and Stewart 1993). The baseline simulation was for a predator in the MRZ that grew from 1,000 to 1,050 g between May 1 and July 31. Model sensitivity to parameter variation was similar in all reservoir areas so results are not shown for MID and JDF. We used the average temperature and diet at the MRZ during 1983–1986 in these simulations.

Cumulative consumption of salmon was least

TABLE 5.—Ratio of bioenergetics model estimates to field estimates of the rate of predation on salmon by northern pikeminnow in three areas of John Day Reservoir (1983–1986). The predation rate from the bioenergetics model was estimated by three methods for determining the final mass of predators during a 2-month period; *P* is the probability that the average log<sub>e</sub>-transformed ratio was different from zero (*t*-test).

Growth method and reservoir zone	Ratio of model to field rate of predation on juvenile salmon			Range (minimum–maximum)	Proportion of maximum consumption (p); average (SE)
	Average ratio	<i>P</i>	<i>N</i>		
Observed mass					
McNary Dam tailrace (MRZ)	0.86	0.09	11	0.40–1.72	0.44 (0.06)
Midreservoir (MID)	0.2	0.11	2	0.14–0.25	0.49 (0.20)
John Day Dam forebay (JDF)	0.93	0.38	5	0.44–2.42	0.35 (0.06)
All areas	0.81	0.02	18	0.14–2.42	0.42 (0.04)
Seasonal growth					
McNary Dam tailrace (MRZ)	0.72	<0.01	11	0.42–1.24	0.36 (0.04)
Midreservoir (MID)	0.16	0.05	3	0.05–0.27	0.25 (0.13)
John Day Dam forebay (JDF)	0.45	0.03	6	0.09–1.22	0.19 (0.04)
All areas	0.55	<0.01	20	0.05–1.24	0.30 (0.03)
Annual growth					
McNary Dam tailrace (MRZ)	1.04	0.88	11	0.57–1.96	0.50 (0.04)
Midreservoir (MID)	0.33	0.02	4	0.15–0.53	0.46 (0.13)
John Day Dam forebay (JDF)	0.84	0.24	6	0.28–3.04	0.37 (0.03)
All areas	0.85	0.02	21	0.15–2.13	0.46 (0.03)

sensitive (–1 to +1%) to changes in the parameters for maximum consumption ( $\alpha$  and  $\beta$ ) and predator energy density, and was moderately sensitive (–16 to +20%) to changes in respiration parameters ( $a$ ,  $b$ ,  $\tau$ , and  $v$ ; Table 6). For the most sensitive parameter, a 10% increase in the coefficient for metabolism dependence on mass ( $b$ ) caused cumulative consumption to increase 20%. The intercept ( $a$ ) and coefficient ( $b$ ) for metabolism versus mass had the highest variation about their parameter estimates (uncertainty; Table 6), 38 and 35%, respectively. The high sensitivity of model output to respiration parameters is consistent with analyses of bioenergetics models for oth-

er fish species (Kitchell et al. 1977; Bartell et al. 1986; Hartman and Brandt 1993).

#### *Sensitivity to Swimming Speed*

Model predictions may be sensitive to swimming speed, which is difficult to measure for active predators. For sensitivity analysis of swimming speeds, we selected three sets of data that yielded large differences between model and field estimates of predation rate on salmon. Swimming speed was varied incrementally until the model predation rate was similar to the field predation rate. This allowed us to determine whether small changes in swimming speed could explain large differences in model and field rates of predation.

For the MID area during May–June 1984, swimming speed would have had to increase from 1 cm · s<sup>–1</sup> to about 20 cm · s<sup>–1</sup> before model and field predation rates corresponded (Figure 3). Swimming speed had to be varied by more than 10 cm · s<sup>–1</sup> in the forebay example and more than 5 cm · s<sup>–1</sup> in the tailrace example to match the predation rate estimates from the field (Figure 3).

#### *Sampling Bias in Size Distributions*

Bioenergetics modeling is based on the assumption that an “average” individual can be used to represent the response of a cohort or a population. If the size distribution of individuals in the cohort or population is strongly skewed toward large or small individuals, use of an average size to represent the group may produce biased results.

TABLE 6.—Sensitivity of the bioenergetics model to parameter change and to the uncertainty of parameter estimates. Sensitivity is the percentage difference between a nominal simulation and one in which the parameter was varied  $\pm 10\%$ . Uncertainty is 100 · SE/parameter estimate. Parameter symbols are defined in Table 1.

Parameter	Sensitivity by varying parameter:		Uncertainty
	+10%	–10%	
$\alpha$ (CA)	–1	+1	2.5
$\beta$ (CB)	–1	+1	21.3
$a$ (RA)	+9	–9	37.8
$b$ (RB)	+20	–16	34.7
$\tau$ (RQ)	+19	–15	9.5
$v$ (RTO)	+11	–9	<sup>a</sup>
Predator energy density	+1	–1	<sup>a</sup>

<sup>a</sup> Uncertainty was not applicable because these parameters were derived from other species.

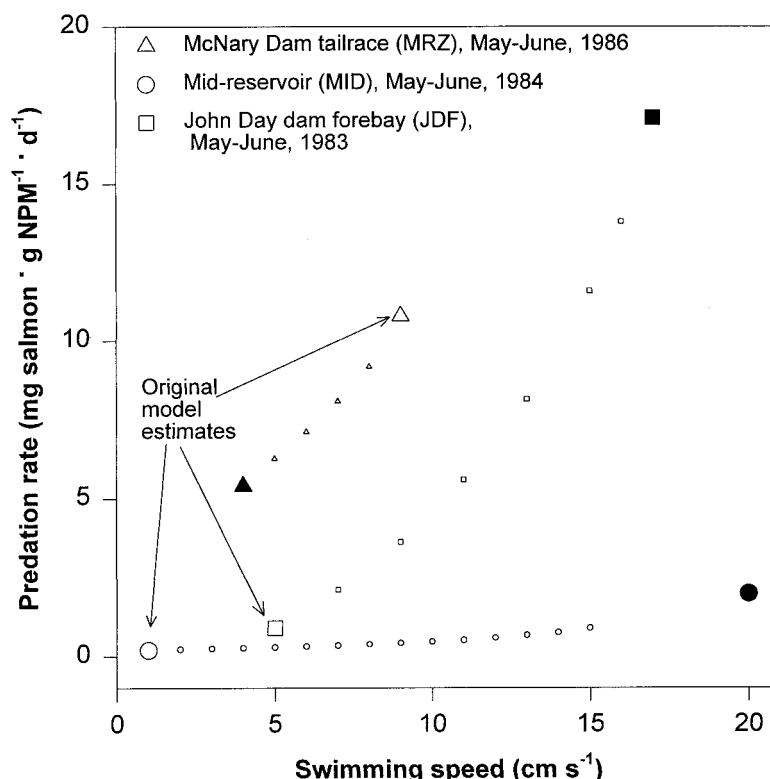


FIGURE 3.—Effects of northern pikeminnow (NPM) swimming speed on the rate of predation on salmon by northern pikeminnow in three areas of John Day Reservoir. Large open symbols are predation rates predicted by the bioenergetics model for nominal predator swimming speeds in each area. Large closed symbols denote field predation rate estimates and the corresponding swimming speeds necessary to achieve them according to the bioenergetics model. Small symbols are interpolations.

Such bias might be introduced by gear selectivity or nonrandom sampling. We examined how gear selectivity and skewed weight distributions of northern pikeminnow might influence bioenergetics predictions of the rate of predation on salmon.

Frequency distributions of the mass of northern pikeminnow captured during monthly periods (1983–1986) were examined for normality and skewness for arbitrarily minimum samples of 25 predators per month. Forty-five percent of all samples were nonnormally distributed (17 of 38; Shapiro–Wilks  $W$ ,  $P < 0.05$ ;  $N = 26$ –512). The JDF had the highest percentage of nonnormal distributions (75%, 9 of 12) and the MID location had the lowest percentage (22%, 2 of 9). Of those sample distributions that were significantly different from normal, 76% had a positive skewness statistic (13 of 17; mean skewness = 0.986) and the rest were negatively skewed (mean skewness =  $-0.385$ ).

The effect of gear selectivity on size distribution

of northern pikeminnow in John Day Reservoir was described by Beamesderfer and Rieman (1988). Small northern pikeminnow are less likely to be captured by electrofishing than large predators. Electrofishing vulnerability was used to compute an adjusted average size for each field sample. Modeled predation rates on salmonids based on adjusted and unadjusted average sizes were compared. We used an equation of Beamesderfer and Rieman (1988) relating vulnerability or recapture rate ( $V$ ) to fork length (FL, mm) ( $r^2 = 0.98$ ;  $N = 5$ ),

$$V = -(408.1 - \text{FL})^2 / 12,261.8,$$

and a fork-length–mass (FL– $W$ ) relationship ( $r^2 = 0.98$ ;  $N = 5,458$ ),

$$\log_{10}\text{FL} = (\log_{10}W + 5.116) / 3.085,$$

to compute vulnerability in relation to fish mass.

Adjustments for gear selectivity caused rela-

TABLE 7.—Salmonids consumed by theoretical populations of northern pikeminnow ( $N = 1,000$ ) with normal and skewed weight distributions. The mean size of northern pikeminnow (NPM) was 1,000 g for all distributions. Cumulative consumption was the sum of consumption by 50 individuals at the 5th and 95th percentiles, 200 individuals at the 25th and 75th percentiles and 500 individuals at the median size. Each individual was assumed to gain 10% of its original body mass during April 1–August 31 based on average diets and conditions from the McNary Dam tailrace.

Distribution type	Skewness coefficient	Starting mass of predators (g) (5, 25, 50, 75, and 95th percentiles)	Salmon consumed (kg per 1,000 NPM)
Normal	0.0	500, 700, 1,000, 1,300, 1,500	2,039
Positively skewed	+1.16	650, 750, 900, 1,400, 1,750	2,036
Negatively skewed	-0.97	400, 600, 1,100, 1,200, 1,400	2,035

tively small changes in average predator body sizes for start and final times. The percent change in average body mass (final – start times) ranged from –23 to +16% for unadjusted size and from –21 to +17% for adjusted size. In almost all periods (17 of 19; 2 samples were unchanged), the growth increment shifted in the same direction with either unadjusted or adjusted sizes. Use of adjusted sizes raised predation rates an average of 8.5% over use of unadjusted rates ( $N = 21$ ;  $SE = 5.4$ ), which was not significantly different from zero ( $P > 0.05$ ;  $t$ -test on arcsine-transformed percentages).

The effect of skewed weight distributions of northern pikeminnow on predation efficacy was trivial (<1%) for our theoretical populations (Table 7). The degree of skewness for these theoretical populations was approximately the same as observed in samples from John Day Reservoir.

### Discussion

Bioenergetics modeling is an alternative method for estimating the rate of predation on juvenile salmonids by northern pikeminnow in the Columbia River and in other rivers, streams, or lakes. Because northern pikeminnow are important predators on salmonids in many systems (Ricker 1941; Jeppson and Platts 1959; Buchanan et al. 1981; Rieman et al. 1991; Ward et al. 1995), modeling tools are needed for quantifying the overall salmonid loss and for evaluating management techniques that aim to limit predation-related mortality. The bioenergetics model developed here provides researchers and managers with a new tool for estimating salmonid mortality and exploring the influence of temperature or diet variation.

With the observed size of northern pikeminnow to determine the growth increment, the bioenergetics model underpredicted the predation rate on salmon by 19%. Apart from the three midreservoir comparisons for which proportional differences were consistently high (Table 5), the average modeled rate of predation was only 12% less than the

field rate of predation. When tagged individuals were used to estimate seasonal growth, the model underpredicted predation rate by 45% on average. The closest agreement between model and field estimates of predation rate (a –15% average) was achieved by using a growth rate derived from an annual growth model.

Ney (1993) summarized field tests of bioenergetics models and tabulated the percent difference between model and field predictions. The best agreement between a “Wisconsin-type” model (Hewett and Johnson 1992) and field predation estimates occurred with age-3 largemouth bass (+8% for the model; Rice and Cochran 1984); the poorest agreement was for age-0 *Esox* spp. (–39 to –52%; Wahl and Stein 1991). Age-3 northern pike differences ranged from –86 to +59% (Diana 1983), the broadest documented range. We had a broad range of individual differences between model and field predation rate, but our average log-transformed difference was not different from zero (arithmetic ratios were not different from 1.0) in five of six area comparisons for observed final weight or annual growth methods. Our difference of –15% between model and field predation rates for the annual growth method compares quite well to other field evaluations of bioenergetics models.

The differences observed between the estimates for field and model predation rates, especially in the midreservoir area, could have been caused by inadequacies in the data used to make the estimates, biases in the method used to compute the field predation rates, or problems with the bioenergetics model. Some of the largest discrepancies in model-versus-field estimates of predation rate can be traced to an unlikely change in the average size of northern pikeminnow during the sample period. For example, predation rate could not be estimated for the April–May 1984 period in the MID area, where average mass dropped from 849 g ( $N = 26$ ) to 668 g ( $N = 102$ ). Also, model-



predicted predation rate was 95% less than field-predicted predation rate for the May–June 1983 period in the JDF area, where average predator mass declined from 832 g ( $N = 129$ ) to 637 g ( $N = 53$ ). Such large declines in predator mass during 2-month periods are unlikely given the data summarized above on growth of tagged individuals. Increasing the sample size of predators would not necessarily improve model predictions. The absolute value of the proportional difference between field and model predictions (its magnitude) was not correlated with initial, final, or total numbers of northern pikeminnow collected in a 2-month period (Pearson correlation coefficients; all  $P > 0.90$ ).

Movement of large or small northern pikeminnow from one area of the reservoir to another could explain some of the differences in the field–model comparisons. Martinelli and Shively (1997) radio-tagged northern pikeminnow (320–550 mm FL) in Columbia River reservoirs and observed upriver movements during June of fish released at mid-reservoir locations, although many of these fish later returned to the midreservoirs in August and September. Fish released near dams tended to move less than fish released in midreservoir areas. Earlier studies suggested that many northern pikeminnow remain in local areas or perhaps return to an area after a spawning migration. Northern pikeminnow tagged and recaptured in the same reservoir area during March–September were: forebay = 89% ( $N = 27$  total recaptures in this area), mid-reservoir = 67% ( $N = 48$ ), and tailrace = 87% ( $N = 67$ ) (Nigro et al. 1985; Beamesderfer et al. 1987). Forty percent of fish were recaptured at the same specific station where they were originally released.

Other differences between model and field predation rates might have been caused by a poor characterization of the “average” diet for a particular 2-month period. Petersen and DeAngelis (1992) showed that northern pikeminnow in the McNary Dam tailrace captured juvenile salmonids during discrete feeding bouts rather than randomly through time. Capture rate varied from 0.4 to 4.2 salmon per d over a 4-d period in one example. Predation on salmonids in areas distant from Columbia River dams also occurred during brief feeding bouts (J. H. Petersen, unpublished analyses). The infrequent capture of salmonids by northern pikeminnow makes it more difficult to characterize the typical diet of the predator without frequent sampling over a long period. In the data set we used to corroborate the bioenergetics model, north-

ern pikeminnow were generally sampled over two 2–4 d periods in each 2-month test interval (Poe et al. 1991; Vigg et al. 1991). Because juvenile salmonid densities vary greatly in space and time (Mains and Smith 1964; Healy 1991; McCann et al. 1994), this sampling schedule may have been inadequate for describing the average proportion of the diet that was salmonids. Rice and Cochran (1984), for example, had good success modeling largemouth bass rations but they used 2-week measurement intervals of bass ration and growth in their bioenergetics model. More frequent measurements of northern pikeminnow diet and size may have improved our comparison between field and model results. Future studies should consider how sampling design and the frequency of occasional feeding events interact in determining the average diet of an omnivorous fish.

Additional data on swimming speeds are unlikely to improve the correlation between field and model estimates of predation rate for some areas. In the JDF and MRZ areas, increasing the swimming speed by  $1\text{--}2\text{ cm}\cdot\text{s}^{-1}$  would increase the rate of predation on salmon roughly 10% (Figure 3) in the bioenergetics model. The average difference between model and field estimates of predation for these areas was only 10%, based on the observed final mass (Table 5). Changes of  $1\text{--}2\text{ cm}\cdot\text{s}^{-1}$  in average swimming speed are certainly possible given the observed variation in displacements of radiotagged fish (Martinelli and Shively 1997). In the midreservoir area, however, northern pikeminnow swimming speed would have to be increased by more than  $15\text{ cm}\cdot\text{s}^{-1}$  to produce a modeled predation rate equivalent to the field predation rate. Swimming speeds of  $15\text{ cm}\cdot\text{s}^{-1}$  or more were observed in fewer than 17% of the long-term movements ( $>24\text{ h}$  recontacts) of radiotagged northern pikeminnow moving into or through midreservoir areas (Martinelli and Shively 1997). Some of the higher rates of swimming among long-term movements were likely associated with spawning migrations rather than with foraging.

We were unable to make model and field comparisons of predation on salmonids for the mid-reservoir area during summer because data that met our selection criteria were not available. We can, however, make some approximate calculations of model and field predation rates to compare for this period. A bioenergetics model estimate for predation rate during July through August is 18 g of salmon consumed by an 800-g predator, given mean temperatures and diets from 1983–1986 and no net mass gain during July–August. Based on

field estimates of predation in Petersen (1994), the total consumption of salmonids by an 800-g predator from the midreservoir for this period would have been about 45 g of salmon. The difference in these field-versus-model estimates is 27 g (45–18 g), giving a field estimate 60% higher than the corresponding model estimate. Thus our estimate of a higher predation rate from field methods in spring than from the bioenergetics model is supported for the summer period as well.

Differences between the model and field estimates of predation rate do not necessarily mean that the bioenergetics model is a biased predictor, because field estimates also require assumptions that may be controversial and untested (Eggers 1977, 1979; Elliott and Persson 1978; Boisclair and Leggett 1988). Our method used to compute field rates of predation required assumptions about temporal and spatial applicability of the data, use of laboratory derived digestion rates, and validity of pooling stomach contents across individuals to estimate consumption per average predator (Swenson and Smith 1973; Vigg et al. 1991).

Cochran and Knutsen (1988) showed that the use of mean body size in bioenergetics modeling does not necessarily produce biased estimates of consumption; however, size-selective sampling or mortality will bias the size distribution and thus the consumption estimates. In our simulations, the rate of predation on salmon was predicted well from the average size of northern pikeminnow because sampling bias and the asymmetry of most size distributions were both relatively weak. Analyses based on size change for each age, rather than average size, might improve the estimate of cumulative consumption of salmon by a northern pikeminnow population, but using the average or median (Rice and Cochran 1984) size in an area may be adequate for most purposes.

The bioenergetics model developed for northern pikeminnow should be helpful in evaluating management actions and exploring how other species affect northern pikeminnow predation on juvenile salmonids. Energetic modeling could be used to estimate changes in salmonid mortality as the result of a large predator removal program in the Columbia and Snake rivers (Beamesderfer et al. 1996). Diet shifts or changes in growth rate as a result of changes in predator density following removals could be modeled. Impoundment of the Columbia River has caused water to warm earlier in the spring, reach a higher temperature during summer, and remain warm later into the fall (Quinn and Adams 1996). Preliminary analyses with the

bioenergetics model for northern pikeminnow showed that such warmer temperatures increase the potential for predation on juvenile salmonids by as much as 45–60% (J. F. Kitchell and J. H. Petersen, unpublished analyses). Finally, several introduced piscivores occur in the Columbia River (Poe et al. 1994) and interactions between these species and northern pikeminnow could be examined through energetics modeling (e.g., Kitchell and Crowder 1986; Jones et al. 1993; Labar 1993).

### Acknowledgments

Constructive comments by D. Beauchamp, P. Connolly, J. Kitchell, D. Schindler, and an anonymous reviewer greatly improved the manuscript. D. Gadowski, T. Martinelli, and M. Parsley provided unpublished data and analyses. This research was funded by the Bonneville Power Administration, through contracts administered by W. Maslen, which we appreciate.

### References

- Bartell, S. M., J. E. Breck, R. H. Gardner, and A. L. Brenkert. 1986. Individual parameter perturbation and error analysis of fish bioenergetics models. *Canadian Journal of Fisheries and Aquatic Sciences* 43:160–168.
- Beamesderfer, R. C., and B. E. Rieman. 1988. Size selectivity and bias in estimates of population statistics of smallmouth bass, walleye, and northern squawfish in a Columbia River reservoir. *North American Journal of Fisheries Management* 8:505–510.
- Beamesderfer, R. C., and B. E. Rieman. 1991. Abundance and distribution of northern squawfish, walleyes, and smallmouth bass in John Day Reservoir, Columbia River. *Transactions of the American Fisheries Society* 120:439–447.
- Beamesderfer, R. C., B. E. Rieman, L. J. Bledsoe, and S. Vigg. 1990. Management implications of a model of predation by resident fish on juvenile salmonids migrating through a Columbia River reservoir. *North American Journal of Fisheries Management* 10:290–304.
- Beamesderfer, R. C., B. 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. Bonneville Power Administration, Portland, Oregon.
- Beamesderfer, R. C., D. L. Ward, and A. A. Nigro. 1996. Evaluation of the biological basis for a predator control program on northern squawfish (*Ptychocheilus oregonensis*) in the Columbia and Snake rivers. *Canadian Journal of Fisheries and Aquatic Sciences* 53:2898–2908.
- Beauchamp, D. W., M. G. LaRiviere, and G. L. Thomas. 1995. Evaluation of competition and predation as limits to juvenile kokanee and sockeye salmon pro-

- duction in Lake Ozette, Washington. *North American Journal of Fisheries Management* 15:193–207.
- Beauchamp, D. A., D. J. Stewart, and G. L. Thomas. 1989. Corroboration of a bioenergetics model for sockeye salmon. *Transactions of the American Fisheries Society* 118:597–607.
- Berggren, T. J., and M. J. Filardo. 1993. An analysis of variables influencing the migration of juvenile salmonids in the Columbia River basin. *North American Journal of Fisheries Management* 13:48–63.
- Bevelhimer, M. S., R. A. Stein, and R. F. Carline. 1985. Assessing significance of physiological differences among three esocids with a bioenergetics model. *Canadian Journal of Fisheries and Aquatic Sciences* 42:57–69.
- Beyer, J. M., G. Lucchetti, and G. Gray. 1988. Digestive tract evacuation in northern squawfish (*Ptychocheilus oregonensis*). *Canadian Journal of Fisheries and Aquatic Sciences* 45:548–553.
- Black, E. C. 1953. Upper lethal temperatures of some British Columbia freshwater fishes. *Journal of the Fisheries Research Board of Canada* 10:196–210.
- Bledsoe, L. J. 1990. Columbia River ecosystem model (CREM)—modeling approach for evaluation of control of northern squawfish populations using fisheries exploitation. Pages 206–238 in A. A. Nigro, editor. *Developing a predation index and evaluating ways to reduce juvenile salmonid losses to predation in the Columbia River basin*. Bonneville Power Administration, Portland, Oregon.
- Bledsoe, L. J., S. Vigg, and J. H. Petersen. 1990. Pages 221–338 in A. A. Nigro, editor. *Simulation estimates of salmonid predation loss to northern squawfish in a Columbia River reservoir. Developing a predation index and evaluating ways to reduce juvenile salmonid losses to predation in the Columbia River basin*. Bonneville Power Administration, Portland, Oregon.
- 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. *Canadian Journal of Fisheries and Aquatic Sciences* 45:138–145.
- Boisclair, D., and W. C. Leggett. 1989. Among-population variability of fish growth: II. Influence of prey type. *Canadian Journal of Fisheries and Aquatic Sciences* 46:468–482.
- Boisclair, D., and W. C. Leggett. 1991. If computers could swim or fish could be programmed: a response to comments by Hewett et al. (1991). *Canadian Journal of Fisheries and Aquatic Sciences* 48:1337–1344.
- Brandt, S. B., and J. Kirsch. 1993. Spatially explicit models of striped bass growth potential in Chesapeake Bay. *Transactions of the American Fisheries Society* 122:845–869.
- Brett, J. R. 1971. Satiation time, appetite, and maximum food intake of sockeye salmon (*Oncorhynchus nerka*). *Journal of the Fisheries Research Board of Canada* 28:409–415.
- Brocksen, R. W., G. E. Davis, and C. E. Warren. 1968. Competition, food consumption, and production of sculpins and trout in laboratory stream communities. *Journal of Wildlife Management* 32:51–75.
- Buchanan, D. V., R. M. Hooten, and J. R. Moring. 1981. Northern squawfish (*Ptychocheilus oregonensis*) predation on juvenile salmonids in sections of the Willamette River basin, Oregon. *Canadian Journal of Fisheries and Aquatic Sciences* 38:360–364.
- Cech, J. J., Jr., D. T. Castleberry, T. E. Hopkins, and J. H. Petersen. 1994. Northern squawfish, *Ptychocheilus oregonensis*, O<sub>2</sub> consumption rate and respiration model: effects of temperature and body size. *Canadian Journal of Fisheries and Aquatic Sciences* 51:8–12.
- Cochran, P. A., and K. J. Knutsen. 1988. Error in estimation of feeding rates from changes in mean body mass. *Canadian Journal of Fisheries and Aquatic Sciences* 45:1494–1498.
- Cummins, K. W., and J. C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. *Mitteilungen Internationale Vereinigung für theoretische und angewandte Limnologie* 18:1–158.
- De Roos, A. M., E. McCauley, and W. G. Wilson. 1991. Mobility versus density-limited predator-prey dynamics on different spatial scales. *Proceedings of the Royal Society of London, Series B* 246:117–122.
- Diana, J. S. 1983. An energy budget for northern pike (*Esox lucius*). *Canadian Journal of Zoology* 61:1968–1975.
- Eggers, D. M. 1977. Factors in interpreting data obtained by diel sampling of fish stomachs. *Journal of the Fisheries Research Board of Canada* 34:290–294.
- Eggers, D. M. 1979. Comments on some recent methods for estimating food consumption in fish. *Journal of the Fisheries Research Board of Canada* 36:1018–1019.
- Elliott, J. M., and L. Persson. 1978. The estimation of daily rates of food consumption for fish. *Journal of Animal Ecology* 47:977–990.
- Faler, M. P., L. M. Miller, and K. I. Welke. 1988. Effects of variation in flow on distribution of northern squawfish in the Columbia River below McNary Dam. *North American Journal of Fisheries Management* 8:30–35.
- Friesen, T. A., and D. L. Ward. 1999. Management of northern pikeminnow and implications for juvenile salmonid survival in the lower Columbia and Snake rivers. *Transactions of the American Fisheries Society* 128:406–435.
- Gadomski, D. M., and C. A. Barfoot. 1998. Diel and distributional abundance patterns of fish embryos and larvae in the lower Columbia and Deschutes rivers. *Environmental Biology of Fishes* 51:353–368.
- Gadomski, D. M., and J. A. Hall-Griswold. 1992. Predation by northern squawfish on live and dead juvenile chinook salmon. *Transactions of the American Fisheries Society* 121:680–685.
- Giorgi, A. E., D. R. Miller, and B. P. Sanford. 1994. Migratory characteristics of juvenile ocean-type

- chinook salmon, *Oncorhynchus tshawytscha*, in John Day Reservoir on the Columbia River. Fishery Bulletin 92:872–879.
- Hanson, P. C., T. B. Johnson, D. E. Schindler, and J. F. Kitchell. 1997. Bioenergetics model 3.0 for Windows. University of Wisconsin, Sea Grant Institute, Technical Report WISCU-T-97-001, Madison.
- Hartman, K. J., and S. B. Brandt. 1993. Systematic sources of bias in a bioenergetics model: examples for age-0 striped bass. Transactions of the American Fisheries Society 122:912–926.
- Hartman, K. J., and S. B. Brandt. 1995. Estimating energy density of fish. Transactions of the American Fisheries Society 124:347–355.
- Healy, M. C. 1991. Pages 313–393 in C. Groot and L. Margolis, editors. Life history of chinook salmon (*Oncorhynchus tshawytscha*). Pacific salmon life histories. University of British Columbia Press, Vancouver.
- Hewett, S. W., and B. L. Johnson. 1992. Fish bioenergetics model 2. A generalized bioenergetics model of fish growth for microcomputers. University of Wisconsin, Sea Grant Institute, Technical Report WIS-SG-92-250, Madison.
- Hewett, S. W., C. E. Kraft, and B. L. Johnson. 1991. Consumption, growth, and allometry: a comment on Boisclair and Leggett (1989a, 1989b, 1989c, 1989d). Canadian Journal of Fisheries and Aquatic Sciences 48:1334–1337.
- Jeppson, P., and W. S. Platts. 1959. Ecology and control of the Columbia River squawfish in northern Idaho lakes. Transactions of the American Fisheries Society 88:197–202.
- Jones, M. L., J. F. Koonce, and R. O'Gorman. 1993. Sustainability of hatchery-dependent fisheries in Lake Ontario: the conflict between predator demand and prey supply. Transactions of the American Fisheries Society 122:1002–1018.
- Kitchell, J. F., and L. B. Crowder. 1986. Predator–prey interactions in Lake Michigan: model predictions and recent dynamics. Environmental Biology of Fishes 16:205–211.
- 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*). Journal of the Fisheries Research Board of Canada 34:1922–1935.
- Labar, G. W. 1993. Use of bioenergetics models to predict the effect of increased lake trout predation on rainbow smelt following sea lamprey control. Transactions of the American Fisheries Society 122:942–950.
- Lantry, B. F., and D. J. Stewart. 1993. Ecological energetics of rainbow smelt in the Laurentian Great Lakes: an interlake comparison. Transactions of the American Fisheries Society 122:951–976.
- Lee, D. C. 1991. A stochastic, compartmental model of the migration of juvenile anadromous salmonids in the Columbia River basin. Ecological Modelling 54:227–245.
- Lyons, J., and J. J. Magnuson. 1987. Effects of walleye predation on the population dynamics of small littoral-zone fishes in a northern Wisconsin lake. Transactions of the American Fisheries Society 116:29–39.
- Mains, E. M., and J. M. Smith. 1964. The distribution, size, time, and current preferences of seaward migrant chinook salmon in the Columbia and Snake rivers. Washington Department of Fisheries Fisheries Research Papers 2:5–43.
- Martinelli, T. L., and R. S. Shively. 1997. Seasonal distribution, movements and habitat associations of northern squawfish in two lower Columbia River reservoirs. Regulated Rivers: Research and Management 13:543–556.
- McCann, J. A., E. E. Kofoot, C. R. Sprague, J. A. Jackson, and D. H. Feil. 1994. Pages 151–170 in D. W. Rondorf and W. H. Miller, editors. Distribution of juvenile chinook salmon and American shad in McNary and John Day reservoirs. Identification of the spawning, rearing and migratory requirements of fall chinook salmon in the Columbia River basin. Bonneville Power Administration, Portland, Oregon.
- Ney, J. J. 1993. Bioenergetics modeling today: growing pains on the cutting edge. Transactions of the American Fisheries Society 122:736–748.
- Nigro, A. A., R. C. Beamesderfer, J. C. Elliott, M. P. Faler, L. M. Miller, B. L. Uremovich, and D. L. Ward. 1985. Abundance and distribution of walleye, northern squawfish, and smallmouth bass in John Day Reservoir, 1985. Bonneville Power Administration, Portland, Oregon.
- Parker, R. M., M. P. Zimmerman, and D. L. Ward. 1995. Variability in biological characteristics of northern squawfish in the lower Columbia and Snake rivers. Transactions of the American Fisheries Society 124:335–346.
- Pascual, M., and S. A. Levin. 1999. From individuals to population densities: searching for the intermediate scale of nontrivial determinism. Ecology 80:2225–2236.
- Petersen, J. H. 1994. Importance of spatial pattern in estimating predation on juvenile salmonids in the Columbia River. Transactions of the American Fisheries Society 123:924–930.
- Petersen, J. H., and D. L. DeAngelis. 1992. Functional response and capture timing in an individual-based model: predation by northern squawfish (*Ptychocheilus oregonensis*) on juvenile salmonids in the Columbia River. Canadian Journal of Fisheries and Aquatic Sciences 49:2551–2565.
- Petersen, J. H., D. M. Gadomski, and T. P. Poe. 1994. Differential predation by northern squawfish (*Ptychocheilus oregonensis*) on live and dead juvenile salmonids in the Bonneville Dam tailrace (Columbia River). Canadian Journal of Fisheries and Aquatic Sciences 51:1197–1204.
- Petersen, J. H., M. G. Mesa, J. Hall-Griswold, W. C. Schrader, G. W. Short, and T. P. Poe. 1990. Magnitude and dynamics of predation on juvenile salmonids in Columbia and Snake River reservoirs. Bonneville Power Administration, Portland, Oregon.
- Poe, T. P., H. C. Hansel, S. Vigg, D. E. Palmer, and L.



- A. Prendergast. 1991. Feeding of predaceous fishes on out-migrating juvenile salmonids in John Day Reservoir, Columbia River. *Transactions of the American Fisheries Society* 120:405–420.
- Poe, T. P., R. S. Shively, and R. A. Tabor. 1994. Ecological consequences of introduced piscivorous fishes in the lower Columbia and Snake rivers. Pages 347–360 in D. J. Stouder, K. L. Fresh, and R. J. Feller, editors. *Theory and application in fish feeding ecology*. University of South Carolina Press, Columbia.
- Quinn, T. P., and D. J. Adams. 1996. Environmental changes affecting the migratory timing of American shad and sockeye salmon. *Ecology* 77:1151–1162.
- Rand, P. S., D. J. Stewart, P. W. Seelback, M. L. Jones, and L. R. Wedge. 1993. Modeling steelhead population energetics in Lakes Michigan and Ontario. *Transactions of the American Fisheries Society* 122: 977–1001.
- 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. *Environmental Biology of Fishes* 9:263–275.
- Rice, J. A., and P. A. Cochran. 1984. Independent evaluation of a bioenergetics model for largemouth bass. *Ecology* 65:732–739.
- Ricker, W. E. 1941. The consumption of young sockeye salmon by predaceous fish. *Journal of the Fisheries Research Board of Canada* 5:293–313.
- Ricker, W. E. 1979. Growth rates and models. Pages 677–743 in W. S. Hoar, D. J. Randall, and J. R. Brett, editors. *Fish physiology*, volume 8. Academic Press, New York.
- Rieman, B. E., and R. C. Beamesderfer. 1990. Dynamics of a northern squawfish population and the potential to reduce predation on juvenile salmonids in a Columbia River reservoir. *North American Journal of Fisheries Management* 10:228–241.
- Rieman, B. E., R. C. Beamesderfer, S. Vigg, and T. P. Poe. 1991. Estimated loss of juvenile salmonids to predation by northern squawfish, walleyes and smallmouth bass in John Day Reservoir, Columbia River. *Transactions of the American Fisheries Society* 120:448–458.
- Rondorf, D. W., M. S. Dutchuk, A. S. Kolok, and M. L. Gross. 1985. Bioenergetics of juvenile salmon during the spring outmigration. Bonneville Power Administration, Portland, Oregon.
- Rottiers, D. V., and R. M. Tucker. 1982. Proximate composition and caloric content of eight Lake Michigan fishes. U.S. Fish and Wildlife Service Technical Papers 108:1–8.
- Shively, R. S., T. P. Poe, M. B. Sheer, and R. Peters. 1996. Criteria for reducing predation by northern squawfish near juvenile salmonid bypass outfalls at Columbia River dams. *Regulated Rivers: Research and Management* 12:493–500.
- Solazzi, M. F., T. E. Nickelson, and S. L. Johnson. 1991. Survival, contribution, and return of hatchery coho salmon (*Oncorhynchus kisutch*) released into freshwater, estuarine, and marine environments. *Canadian Journal of Fisheries and Aquatic Sciences* 48: 248–253.
- Stewart, D. J., and F. P. Binkowski. 1986. Dynamics of consumption and food conversion by Lake Michigan alewives: an energetics–modeling synthesis. *Transactions of the American Fisheries Society* 115: 643–661.
- Stewart, D. J., and M. Ibarra. 1991. Predation and production by salmonine fishes in Lake Michigan, 1978–88. *Canadian Journal of Fisheries and Aquatic Sciences* 48:909–922.
- Stewart, D. J., J. F. Kitchell, and L. B. Crowder. 1981. Forage fishes and their salmonid predators in Lake Michigan. *Transactions of the American Fisheries Society* 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. *Canadian Journal of Fisheries and Aquatic Sciences* 40:681–698.
- Swenson, W. A., and L. L. Smith. 1973. Gastric digestion, food consumption, feeding periodicity, and food conversion efficiency in walleye (*Stizostedion vitreum vitreum*). *Journal of the Fisheries Research Board of Canada* 30:1327–1336.
- Tabor, R. A., R. S. Shively, and T. P. Poe. 1993. Predation on juvenile salmonids by smallmouth bass and northern squawfish in the Columbia River near Richland, Washington. *North American Journal of Fisheries Management* 13:831–838.
- Thompson, R. B., and D. F. Tufts. 1967. Predation by Dolly Varden and northern squawfish on hatchery-reared sockeye salmon in Lake Wenatchee, Washington. *Transactions of the American Fisheries Society* 96:424–427.
- Thornton, K. W., and A. S. Lessem. 1978. A temperature algorithm for modifying biological rates. *Transactions of the American Fisheries Society* 107:284–287.
- Vigg, S., and C. C. Burley. 1991. Temperature-dependent maximum daily consumption of juvenile salmonids by northern squawfish (*Ptychocheilus oregonensis*) from the Columbia River. *Canadian Journal of Fisheries and Aquatic Sciences* 48:2491–2498.
- Vigg, S., T. P. Poe, L. A. Prendergast, and H. C. Hansel. 1991. Rates of consumption of juvenile salmonids and alternative prey fish by northern squawfish, walleyes, smallmouth bass, and channel catfish in John Day Reservoir, Columbia River. *Transactions of the American Fisheries Society* 120:421–438.
- Wahl, D. H., and R. A. Stein. 1991. Food consumption and growth of three esocids: field tests of a bioenergetics model. *Transactions of the American Fisheries Society* 120:230–246.
- Ward, D. L., J. H. Petersen, and J. J. Loch. 1995. Index of predation on juvenile salmonids by northern squawfish in the lower and middle Columbia River and in the lower Snake River. *Transactions of the American Fisheries Society* 124:321–334.