Temperature-Dependent Maximum Daily Consumption of Juvenile Salmonids by Northern Squawfish (*Ptychocheilus oregonensis*) from the Columbia River

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Maximum daily consumption rate (C_{max} as ration or number) of northern squawfish (*Ptychocheilus oregonensis*) from the Columbia River increased exponentially as a function of temperature. Predator weight did not explain a significant independent proportion of variation in C_{max}. The mean maximum daily ration, determined from replicate ad libitum feeding on juvenile Pacific salmon (*Oncorhynchus* spp.), was 0.47, 0.70, 3.39, and 4.50 $cg \cdot g^{-1}$ at 8.0, 12.5, 17.0, and 21.5°C, respectively. The corresponding mean daily number eaten was 0.50, 1.17, 4.25, and 7.01 prey per predator at the four increasing temperatures. To quantify the temperature-dependent consumption relation, replicate C_{max} data within the preferred temperature range were fitted to exponential and exponential sigmoid models. On the basis of a knowledge of thermal relations of northern squawfish, we combined hypothetical C_{max} data at temperature extremes with our mean experimental results to fit an algorithm suitable for use in simulation modeling. Both the generalized gamma and biological-rate (Thornton and Lessem. 1978. Trans. Am. Fish. Soc. 107: 284–287) algorithms were suitable to describe a hypothetical temperature–C_{max} model over the entire environmental temperature range of 0–27°C observed in the Columbia River.

Le taux de consommation quotidien maximal (C_{max} en termes de ration ou de nombre) de cyprinoïdes d'Orégon (*Ptychocheilus oregonensis*) du fleuve Columbia a augmenté exponentiellement en fonction de la température. Le poids des prédateurs n'a pas expliqué une proportion indépendante importante de variation de C_{max}. La ration quotidienne maximale moyenne, déterminée à partir d'une consommation à volonté répétée de jeune saumon du Pacifique (*Oncorhynchus*), a été de 0,47, 0,70, 3,39 et 4,50 $cg \cdot g^{-1}$ à 8,0, 12,5, 17,0 et 21,5°C respectivement. Le nombre quotidien moyen correspondant consommé a été de 0,50, 1,17, 4,25 et 7,01 proies par prédateur à ces mêmes températures croissantes. Pour quantifier la relation de la consommation en fonction de la température, des valeurs répétées de C_{max} dans la gamme optimale de température ont été appliquées à des modèles exponentiel et sigmoïde exponentiel. Connaissant les relations thermiques régissant le cyprinoïde du nord, nous avons appliqué des données, combinant des valeurs hypothétiques de C_{max} à des températures extrêmes et nos résultats expérimentaux moyens, à un algorithme utilisable en simulation sur modèle. Autant l'algorithme gamma généralisé que l'algorithme du taux biologique (Thornton et Lessem. 1978. Trans. Am. Fish. Soc. 107 : 284–287) convenaient bien à un modèle hypothétique température–C_{max} sur toute la plage des températures du milieu de 0 à 27°C, observée dans le fleuve Columbia.

The northern squawfish (*Ptychocheilus oregonensis*) is native to the Columbia River and is a major predator of seaward migrating juvenile salmonids. Such predation is especially high where salmonids are abundant and concentrated (Brown and Moyle 1981), e.g. during hatchery releases (Thompson 1959) and below dams during smolt migration periods (Ebel 1977). In John Day Reservoir, the northern squawfish had the highest rates of salmonid consumption of four major fish predators (Vigg et al. 1991). Northern squawfish was the most abundant piscivore (Beamesderfer and Rieman 1991). The total loss of salmonid juveniles to predation in John Day Reservoir was nearly 3 million fish annually or about

14% of seaward migrants, and northern squawfish accounted for about 78% of the fish predation mortality (Rieman et al. 1991). In comparison, about 2% of the juvenile salmonid population was lost to bird predation at a mid-Columbia dam (Ruggerone 1986). Little is known of the in-river losses of juvenile salmonids due to other mortality agents such as disease, parasitism, and starvation.

The relation between maximum consumption and temperature is fundamental for understanding the predation dynamics of northern squawfish. It is well known that the evacuation rate of northern squawfish increases greatly with increasing temperature (Falter 1969; Steigenberger and Larkin 1974; Beyer et al. 1988). Predator size is another factor that generally affects consumption rates (Brett 1971), and northern squawfish have a piscivorous size threshold. Poe et al. (1991) found that northern squawfish began feeding on salmonids at a length of about 250 mm (about 190 g) and that fish became a major constituent

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of the diet at a length of about 350 mm (about 560 g). However, there are no published studies on the maximum number and ration of salmonids that northern squawfish can consume at various temperatures or predator sizes.

Daily ration is defined as the weight of the daily meal expressed as a percentage of predator body weight, i.e. centigrams per gram per day (Ricker 1946). Maximum consumption (C_{max}) is the physiological maximum daily ration that determines the ultimate upper bound on the growth potential of a fish (Stewart and Binkowski 1986). Quantification of maximum consumption as a function of temperature is prerequisite to modeling predator–prey dynamics when one uses either the bioenergetics approach (Kitchell 1983; Rice et al. 1982) or the empirical approach based on the functional response of predation rate to prey density (Vigg 1988; Beamesderfer et al. 1990).

Our objectives in the present work were to quantify the maximum daily consumption of northern squawfish with respect to temperature and predator size using an empirical model and to develop a hypothetical model of maximum consumption for the entire environmental temperature range of northern squawfish habitats. We fitted our data to various mathematical equations, i.e. exponential, exponential sigmoid, generalized gamma, Thornton and Lessem (1978), and polynomial. We tested a variety of algorithms in order to make comparisons with previous maximum consumption rate studies on other predatory fish species and to evaluate which model would be most suitable for use in northern squawfish dynamic ecosystem models. Maximum consumption of juvenile salmonids was evaluated in terms of number and ration consumed per day by northern squawfish fed to satiation (i.e. the physiological maximum). Comparative data on in situ stomach contents and thermal preference and lethal relations of this predator at the lower and upper extremes were used to hypothesize the probable temperature–consumption relation outside the range of our experimental data.

Materials and Methods

Northern squawfish were collected during April–October 1987 and July–September 1988 from the John Day Reservoir, Columbia River (Fig. 1). The primary collection method was electroshocking from a 6.4-m boat. Northern squawfish were also collected by hook and line from the tailrace of McNary Dam, John Day Reservoir. The thermal history of the habitat sampled was obtained from the records of the U.S. Army Corps of Engineers (B. Eby, U.S. Army Corps of Engineers, Walla Walla District, WA, pers. comm.). Northern squawfish were transported to and maintained at the U.S. Fish and Wildlife Service (USFWS), Columbia River Field Station, Cook, WA. They were fed a maintenance diet of juvenile chinook salmon (*Oncorhynchus tshawytscha*) and coho salmon (*O. kisutch*) reared at the USFWS Little White Salmon - Willard National Fish Hatchery.

Laboratory Facilities

Tests were conducted with 12 circular fiberglass tanks (1365 L) in a recirculating system consisting of a biofilter, sand filter, ultraviolet lights, and thermostatically controlled heaters. General operational procedures were documented by Lucchetti and Gray (1988). The system was contained in a laboratory having air temperature and photoperiod regulation. The annual

variation in the temperature of the well-water supply was about 6°C (4–10°C), pH was about 7.0, and total hardness was 20 mg·L^{-1}. The proportion of water reused could be varied from 0 to 100% but was below about 10% during our study.

The protocol of the experiments was similar to that summarized by Stewart and Binkowski (1986). Predator weight and temperature were treatments of the experiment that were systematically varied. Characteristics held constant were duration of the feeding experiment (48 h), prey species composition and size range, photoperiod (12:12 h, light–dark), and light intensity (1.5 lx). Both number (six) and individual weight (about 5% coefficient of variation) of northern squawfish per tank were also held constant to standardize feeding behavior.

Tests were designed to encompass the preferred thermal range of northern squawfish that we postulated (10–21°C) and be within the range of temperatures observed in the Columbia River (0–27°C) (USFWS, Columbia River Field Station, unpubl. data). Tests were scheduled for four target temperatures: 8.0, 12.5, 17.0, and 21.5°C (Fig. 2). For this paper, we define "acclimization period" as the 60-d interval in the natural environment preceding the acclimation period and "acclimation period" as the approximately 30-d interval in the laboratory tanks before the test (2-d duration). Actual test temperatures were within 0.4°C of the target temperatures.

To obtain size-specific C_{max} relations, we tested a size range of northern squawfish (Fig. 3A), stratified by weight group. The size of northern squawfish we tested (>500 g) was based on the predator size (350 mm) at which prey fish became predominant in the diet. When possible, four replicates (groups of six fish) of the three following weight ranges were tested at each temperature: 501–1100, 1101–1500, and 1501–2000 g. For each replicate, the total grams of prey consumed per total grams of predator made one observation; thus, each observation represented a mean value for the six fish. Each test group was as uniform in weight as practicable, i.e. the mean coefficient of variation in weight for the 58 test groups was 4.3%.

Because of problems in collecting sufficient numbers of large predators during late summer, we were unable to obtain a balanced experimental design. The number of replicates for each test temperature was stratified by predator size (Table 1). The 17.0°C treatment was repeated in 1988 (experiment 5) because no large fish (>1500 g) were tested in experiment 3. During 1988, we were again unable to collect enough large northern squawfish for a balanced design. However, we used the combined results from both tests at 17.0°C (experiments 3 and 5). Overall, we made five tests at four different temperatures including a total of 58 replicate tests with six predators each.

Test Procedure

Northern squawfish were sorted by weight, and groups of six fish were randomly placed in the 12 tanks and allowed to acclimate to the test temperature for at least 1 mo before the tests. Only healthy, actively feeding fish were used. They were deprived of food for sufficient time to empty the gut, as calculated from a temperature-dependent evacuation rate equation developed by Beyer et al. (1988). During the tests, northern squawfish with initially empty stomachs were fed juvenile coho and chinook salmon of a selected size range (Fig. 3B) at the start, every 4 h during, and near the end of a 48-h period (i.e. 14 feedings). The final feeding was 47.5 h from the start. Prey fish were weighed when they were introduced into the tanks. Those not eaten were weighed at the end of the test (±0.1 g).

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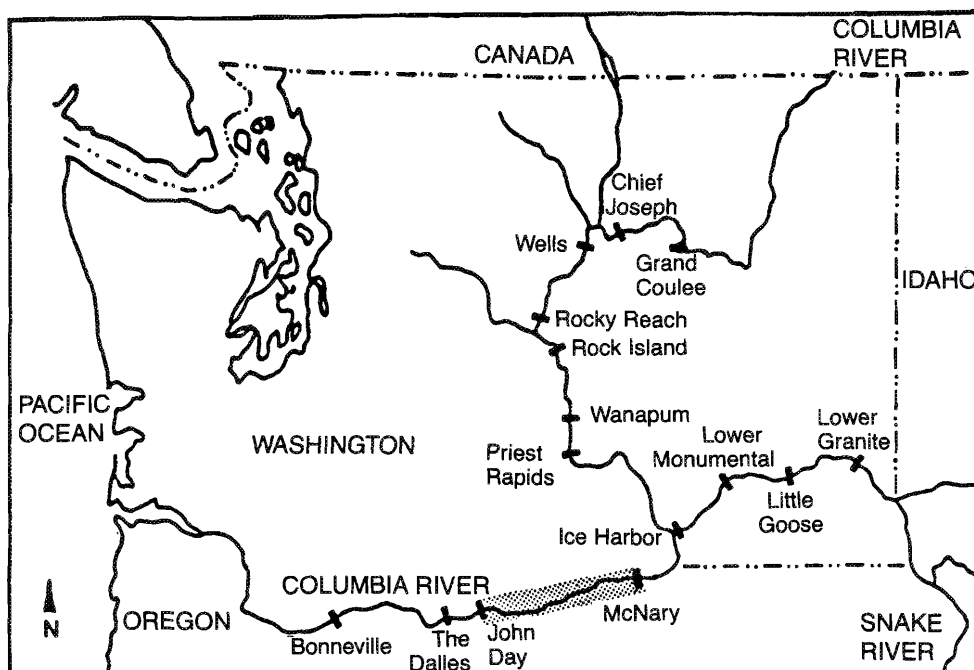*Can. J. Fish. Aquat. Sci., Vol. 48, 1991*

FIG. 1. Location of John Day Reservoir (shaded) in the Columbia River Basin (bars represent dams on the rivers).

Individual northern squawfish weights, minus the weight of stomach contents, were measured (± 1 g) at the end of the experiment. Maximum daily ration of the sample was calculated as total weight of prey fish consumed (centigrams) per total predator weight (grams) per 24 h, i.e. centigrams per gram per day.

Water temperature was continuously monitored in each test tank with calibrated recording meters. Dissolved oxygen (milligrams per litre) was measured daily with a calibrated meter. Gross mineral, nutrient, and trace metal analyses were conducted once on the water source before the study, on 9 March 1987.

Empirical Model of C_{max}: Temperature Range 8–21.5°C

The maximum consumption data, within the 8.0–21.5°C range of our experiments, were fitted using regression techniques to two nonlinear functions of temperature. First, an exponential model:

(1) $\quad C_{max} = ae^{bT}$

where C_{max} is maximum consumption rate as either daily ration (centigrams per gram) or number consumed (smolts per predator), T is temperature (degrees Celsius), and a and b are empirical constants. Thus, the daily C_{max} is represented as a proportion of predator weight or number consumed per predator, and an exponential function of temperature (Brett 1971; Kerr 1971; Elliot 1976). We used least-squares linear regression with natural log transformations to estimate the coefficients from the data:

(2) $\quad \ln C_{max} = \ln a + (bT)$.

Second, an exponential sigmoid model was fitted to the data by least-squares nonlinear regression:

(3) $\quad C_{max} = a/\{1 + be^{(cT)}\}$

where T is environmental temperature, a is the asymptotic consumption rate, and b and c are empirical constants.

Theoretical Model of C_{max}: Temperature Range 0–27°C

Three different algorithms were used to model C_{max} over the entire temperature range that exists in northern squawfish habitats, i.e. 0–27°C. To model the relations beyond the range of our experimental data, we used the mean values from our experiments at the range of 8–21.5°C and temperature relations (preferred and lethal) observed by other workers and made assumptions about decreasing consumption rates as temperature approached the lower and upper incipient lethal levels, i.e. no consumption at 0–1°C nor at 27–30°C. We also assumed that 21.5°C approximates the optimum temperature for peak consumption. First, we fitted the mean experimental and hypothetical data to the generalized gamma function (L. J. Bledsoe, Center for Quantitative Science, University of Washington, Seattle, WA, pers. comm.):

(4) $\quad C_{max} = \{(T/T_0)^a\} \{e^{((a/b)\ (c - ((T/T_0)^a b)))}\}$

where C_{max} is maximum consumption rate as either daily ration (centigrams per gram) or number consumed (smolts per predator) normalized to 1, T is environmental temperature (degrees Celsius), T_0 is the assumed temperature for peak consumption (21.5°C), and a, b, and c are empirical constants.

Second, we used the biological-rate temperature algorithm of Thornton and Lessem (1978):

(5) $\quad C_{max} = K_A(T) \cdot K_B(T)$

$$K_A(T) = \frac{K_1 e^{v_1(T - T_1)}}{1 + K_1 \{e^{v_1(T - T_1)} - 1\}}$$

$$K_B(T) = \frac{K_2 e^{v_2(T - T_2)}}{1 + K_2 \{e^{v_2(T - T_2)} - 1\}}$$
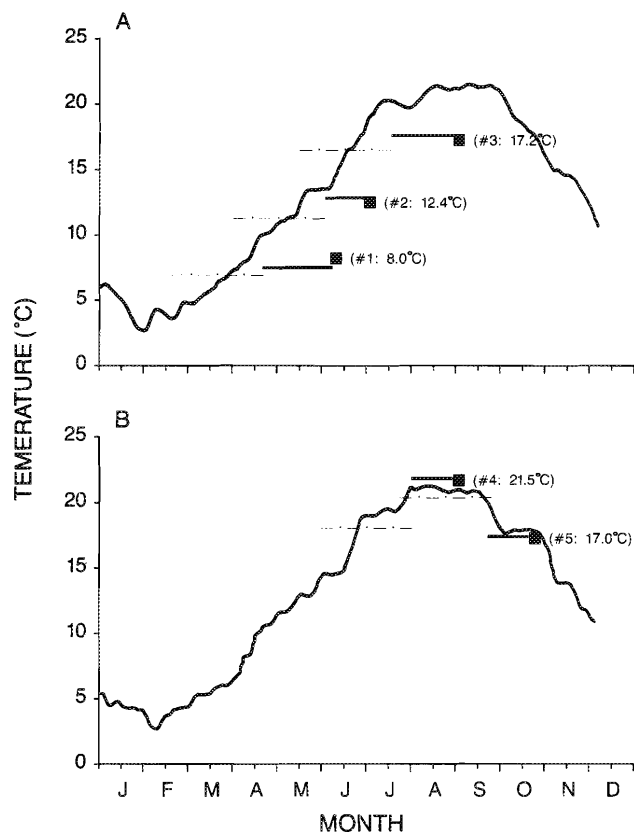
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FIG. 2. Experimental temperatures during (A) 1987 and (B) 1988: river water (long solid line), acclimization (dashed-dotted lines), acclimation (short solid lines), and test (solid squares). Mean test temperature values are in parentheses.

where C_{max} is maximum consumption rate normalized to 1, T is environmental temperature (degrees Celsius), T_1 is the temperature at the lower consumption threshold, T_2 is the temperature at the upper consumption threshold, K_1 is the rate multiplier near the lower threshold temperature, K_2 is the rate multiplier near the upper threshold temperature, v_1 is the empirical lower specific rate coefficient, and v_2 is the empirical upper specific rate coefficient (see Thornton and Lessem (1978) for a detailed derivation of coefficients).

Third, we used a polynomial model:

(6) $\quad C_{max} = a(T)^2 + b(T)^3 + c(T)^4 + d(T)^5 + e(T)^6$

where T is environmental temperature (degrees Celsius), the y-intercept is zero, and a, b, c, d, and e are empirical constants.

Wet–Dry Weight Relations

Juvenile coho or chinook salmon were randomly collected from each of three size groups (mean weight in parentheses): five small coho salmon (4.3 g), 25 medium chinook salmon (13.3 g), and 30 large coho salmon (26.9 g). Each fish was killed, blotted dry, and weighed to the nearest 0.001 g with an electronic balance. At the end of each test, one northern squawfish from each of the three size groups (i.e. 500–1100, 1101–1500, and >1500 g) was weighed to the nearest gram, labeled, and frozen for later dry weight determination.

The fresh juvenile salmon and the thawed northern squawfish were cut into sections and blended separately to a homogeneous
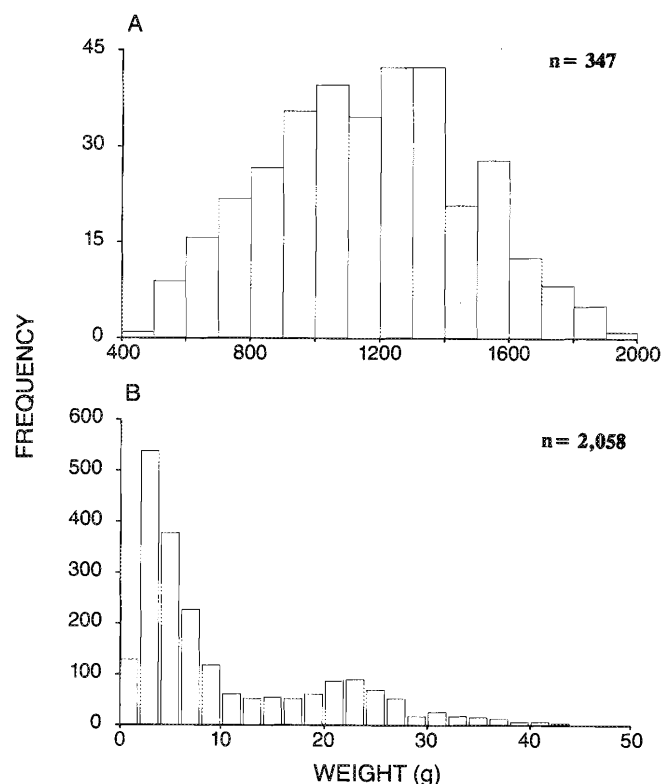

FIG. 3. Size frequency distributions of (A) northern squawfish and (B) juvenile salmon.

TABLE 1. Number of replicates (six fish per replicate) for each treatment of the maximum consumption experiment.

Predator size group		Test number and temperature (°C)					
Weight (g)	Length (mm)	1 8.0	2 12.5	3 17.0	4 21.5	5 17.0	Sum
501–1100	358–432	4	4	4	6	7	25
1101–1500	433–477	4	4	6	4	5	23
1501–2000	478–522	4	4	0	2	0	10
Total		12	12	10	12	12	58

mixture in a commercial blender. The mixture was then reweighed to the nearest 0.001 g before drying. Each blended fish was assigned a separate ceramic crucible and dried at 60°C for at least 6 d or until the weight was constant for three consecutive weighings, whereupon the final dry weight measurement was made. Equations for converting wet to dry weight were calculated by using least-squares linear regressions with y-intercept of zero.

Results

In all experiments combined, 341 northern squawfish averaging 1148 g consumed 2363 juvenile salmonids averaging 8.0 g; this translates to a maximum daily consumption rate of 2.4 cg·g^{-1} or 3.5 salmonids·predator^{-1}. However, maximum consumption rate was significantly related to temperature and varied somewhat with predator size. The mean maximum daily

TABLE 2. Maximum consumption rates of salmonid prey (mean percent daily ration and number per predator) by northern squawfish predators at different water temperatures. Standard deviations of consumption estimates are in parentheses.

Predator weight (g)	Temperature (°C)	Mean ration (cg·g^{-1})	Number per predator	Number of replicate tests
501–1100	8.0	0.75 (0.67)	0.52 (0.40)	4
	12.5	0.91 (0.39)	1.25 (0.36)	4
	17.0[a]	3.52 (2.14)	4.06 (2.22)	11
	21.5	4.23 (3.24)	6.03 (4.42)	6
1101–1500	8.0	0.27 (0.28)	0.40 (0.40)	4
	12.5	0.70 (0.61)	1.27 (0.99)	4
	17.0[a]	3.25 (1.27)	4.41 (2.30)	11
	21.5	5.42 (1.19)	8.50 (2.43)	4
1501–2000	8.0	0.28 (0.21)	0.46 (0.32)	4
	12.5	0.48 (0.42)	1.00 (0.58)	4
	17.0[a]	—	—	0
	21.5	3.48 (2.95)	7.00 (5.89)	2
Mean of replicate tests[b]	8.0	0.47 (0.46)	0.50 (0.33)	11
	12.5	.70 (0.47)	1.17 (0.64)	12
	17.0	3.39 (1.72)	4.25 (2.19)	22
	21.5	4.50 (2.55)	7.01 (3.87)	12

[a]Mean of two experiments, tests 3 and 5.
[b]Mean of all individual replicate tests per temperature.

ration (centigrams per gram) increased as a function of temperature from about 0.5 at 8.0°C to 4.5 at 21.5°C (Table 2; Fig. 4A). Likewise, the mean number consumed increased from 0.5 at 8.0°C to 7.0 salmonids·predator^{-1} at 21.5°C (Fig. 4B).

Empirical Model of Maximum Daily Ration

The maximum daily ration data versus temperature were fitted to an exponential equation (equation 1):

$$C_{max} = 0.0544 \ e^{(0.2095T)}$$

where C_{max} is the maximum daily ration and T is temperature (degrees Celsius). To better describe the known leveling off of maximum daily ration at an optimum temperature, we fitted an exponential sigmoid function to the data (equation 3):

$$C_{max} = 4.7377/\{8.776e^{(-0.5069T)}\}.$$

Coefficients for the temperature models in terms of number of salmonids per predator are given in Table 3.

No significant bivariate relation was observed between northern squawfish weight and replicate C_{max} measurements ($p > 0.05$); however, mean C_{max} generally decreased with
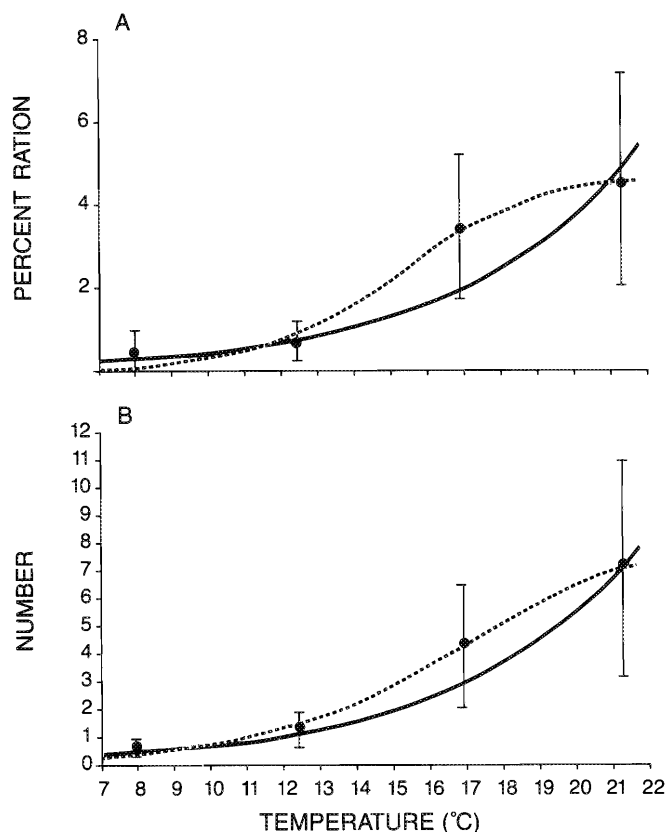

FIG. 4. Maximum consumption of juvenile salmonids by northern squawfish as a function of temperature, fitted to exponential (equation 1, solid line) and exponential sigmoid (equation 3, dotted line) models for (A) daily percent ration and (B) number consumed. Mean values of maximum consumption (solid circles; $n = 11$–22) are bounded by 1 standard deviation (bars).

increasing predator weight (Fig. 5A). To test the efficacy of a multiple regression approach (e.g. Wootton et al. 1980), we regressed the C_{max} residuals (ration and numbers) from both temperature models (equations 1 and 3) on northern squawfish weights. The inclusion of weight as an additional independent variable did not explain a significant proportion of variability ($R^2 = 0.0003$–0.025).

Theoretical Model of Maximum Daily Ration

Models of generalized gamma (equation 4), the Thornton and Lessem (1978) biological-rate algorithm (equation 5), and the polynomial (equation 6) were fitted to mean maximum consumption rates over the entire environmental temperature range, i.e. 0–27°C (Table 3). These relations were derived from our maximum consumption experiments, a knowledge of in situ consumption rates, the upper thermal relations of northern squawfish, and assumptions of the cessation of feeding at low and high thermal extremes (Fig. 6).

Wet–Dry Weight Relations

The linear regression equations for the combined coho salmon and chinook salmon (equation 7) and the northern squawfish (equation 8) were as follows:

(7) $D_c = 0.218(W_c)$ $\qquad (n = 60, R^2 = 0.99)$

(8) $D_s = 0.306(W_s)$ $\qquad (n = 12, R^2 = 0.99)$

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TABLE 3. Coefficients for five models of maximum consumption rate (ration and number) as a function of temperature.

Model	Equation from text[a]	Coefficients (statistics)	Maximum consumption measure	
			Ration	Number
8–21.5°C				
Exponential	1	a	0.0544	0.0818
		b	0.2095	0.2066
		(n)	57	57
		(R^2)	0.520	0.593
Sigmoid	3	a	4.7377	8.4897
		b	7.7760	6.0781
		c	−0.5069	−0.3545
		(n)	57	57
		(R^2)	0.512	0.535
0–27°C				
Generalized	4	T_0	21.5	21.5
Gamma		a	2.8227	3.3627
		b	13.7319	13.7628
		(n)	6	6
		(R^2)	0.979	0.997
Thornton	5	T_1	0	0
and Lessem		T_2	27	27
1978		K_1	0.001	0.001
		K_2	0.01	0.01
		v_1	0.4944	0.4521
		v_2	1.8380	1.8381
		(n)	6	6
		(R^2)	0.965	0.983
Polynomial	6	a	0.05904	0.11405
		b	−0.01735	−0.03209
		c	0.00181	0.00318
		d	−0.00007	−0.00001
		e	9.9×10^{-7}	1.7×10^{-6}
		(n)	6	6
		(R^2)	0.959	0.953

[a]Equations:

Exponential:
$$C_{max} = ae^{bT}$$

Sigmoid:
$$C_{max} = 21.5/\{(1 + b)e^{(cT)}\}$$

Generalized Gamma:
$$C_{max} = \{(T/T_0)^a\} \{e^{((a/b)(1 - ((T/T_0)^b)))}\}$$

Thornton and Lessem (1978):
$$C_{max} = K_A(T) \cdot K_B(T)$$
$$K_A(T) = \frac{K_1 e^{v_1(T - T_1)}}{1 + K_1 \{e^{v_1(T - T_1)} - 1\}}$$
$$K_B(T) = \frac{K_2 e^{v_2(T - T_2)}}{1 + K_2 \{e^{v_2(T - T_2)} - 1\}}$$

Polynomial:
$$C_{max} = a(T)^2 + b(T)^3 + c(T)^4 + d(T)^5 + e(T)^6.$$

where D_c is the dry weight of the combined salmon, W_c is the wet weight of the combined salmon, D_s is the dry weight of the northern squawfish, and W_s is the wet weight of the northern squawfish.
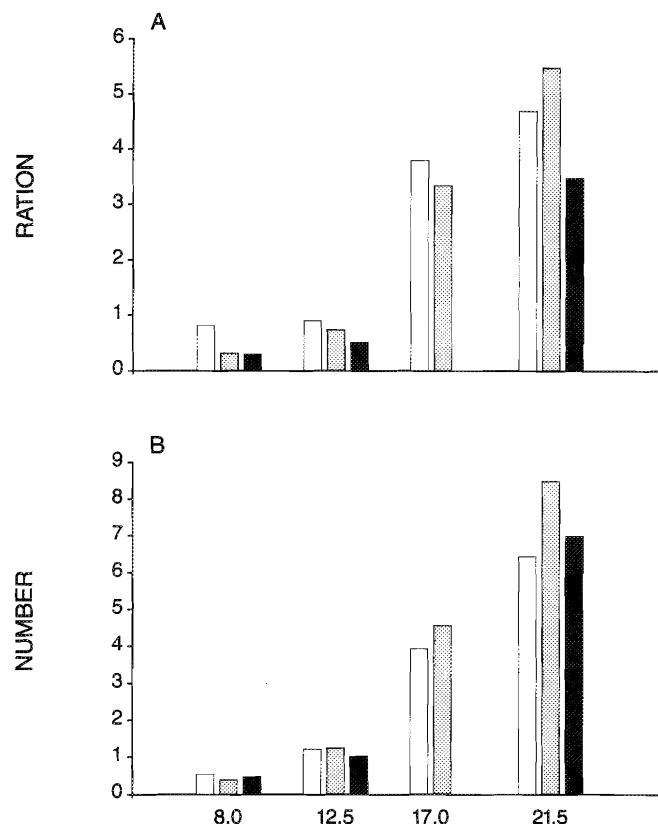

FIG. 5. Maximum consumption of juvenile salmonids by northern squawfish stratified by temperature and predator size group (small, clear; medium, shaded; and large, black) for (A) daily percent ration and (B) number consumed.

Discussion

Empirical Model of Maximum Daily Ration

We found that temperature was the overriding variable affecting the maximum consumption rate of northern squawfish. The exponential sigmoid (equation 3) was the most realistic model of temperature dependency of consumption rate within the tested temperature range because it incorporates the asymptotic C_{max} at high temperatures, i.e. it does not increase without bounds at temperatures above the test range. Based on available temperature relations for northern squawfish (e.g. Black 1953; Dimick and Merryfield 1945; Steigenberger and Larkin 1974), we assumed that the optimum temperature for peak consumption is near the highest temperature we tested (21.5°C), but further work will be required to refine optimum temperatures for consumption and growth.

Insignificant additional variability in C_{max} was explained by including predator weight as a predictor variable. The lack of a significant relation between predator weight and C_{max} may be due to the variability of consumption rate among weight replicates and interactions between temperature and weight effects. Inspection of the graphed data, however, indicates that mean ration generally had the expected decreasing trend with increasing predator weight (Fig. 5A). This size relation, however, was not consistent at all temperatures, i.e. the medium-sized group at 21.5°C was anomalous. Another factor affecting the weight relation in our experiments was the exclusion of small northern squawfish (<500 g); these mostly
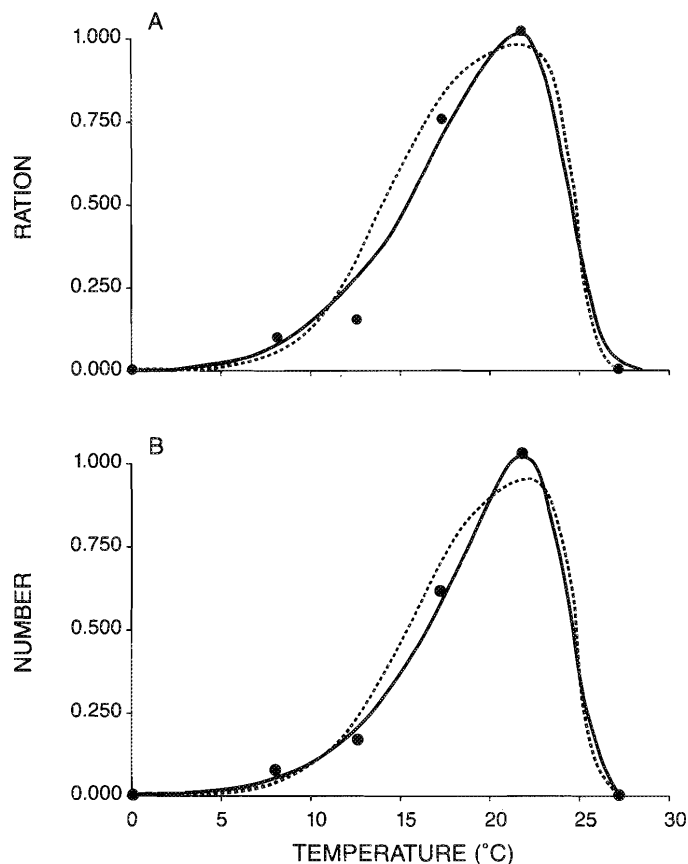

FIG. 6. Generalized gamma (solid line) and Thornton and Lessem (1978) (dotted line) models for maximum consumption in terms of (A) daily ration (cg·g^{-1}) and (B) number per predator, normalized to 1.

nonpiscivorous fish may have higher metabolic requirements and thus consume larger daily rations.

Decreasing consumption rate with increasing predator weight is consistent with general theory, but is inconsistent with mean consumption rates observed in John Day Reservoir (Vigg et al. 1991). In that study, observed mean daily ration of northern squawfish increased with predator size. This apparent discrepancy may be explained by the fact that the mean daily ration in John Day Reservoir (<1.5 cg·g^{-1}) was considerably below the physiological rations determined here, and other factors (e.g. food availability and behavioral dominance relations) probably constrain consumption in nature.

Brett (1979) summarized the factors that affect maximum consumption: (1) duration of a given feeding (satiation time), (2) individual meal size (stomach capacity), (3) time between meals (feeding interval), and (4) interaction among the factors. Temperature and consumer size are usually the most important abiotic and biotic determinants of these factors; C_{max} increases with temperature within the range a species normally inhabits and decreases with fish size (Brett 1979). Wootton et al. (1980) presented various models for predicting maximum daily consumption rates of fishes: four models with predator body weight as the independent variable, five models with temperature, and two multivariate (weight and temperature) models. They concluded that a bivariate power model for weight and a multiple regression power model incorporating weight and temperature had the best empirical fits for two species,

Gasterosteus aculeatus and *Phoxinus phoxinus*. Similarly, Elliott (1975) found that a multivariate (weight and temperature) power relation was an appropriate model for brown trout (*Salmo trutta*). Thus, the conclusions of previous studies on other predaceous fish species are not in agreement with our results which indicated that an exponential sigmoid model (temperature–C_{max}) was most appropriate for northern squawfish within the preferred temperature range.

Theoretical Model of Maximum Daily Ration

Both the biological-rate algorithm (Thornton and Lessem 1978) and the generalized gamma models are suitable to describe maximum consumption rate of northern squawfish as a function of temperature, over the environmental temperature range observed in the Columbia River (0–27°C). The Thornton and Lessem (1978) model has been used for a variety of species, including two species that are predators in John Day Reservoir, i.e. smallmouth bass (*Micropterus dolomieui*) and channel catfish (*Ictalurus punctatus*); therefore, interspecific comparisons in the coefficients and the shape of the curves can be made. The generalized gamma model is a simpler mathematical algorithm, has a slightly better fit to the data, and passes through the data point at peak consumption. Both models provide a reasonable fit to the mean temperature–consumption data ($R^2 > 0.96$) and have coefficients that can be interpreted in terms of biological processes.

Maximum daily ration for many fishes increases with increasing temperature to a maximum near the preferred temperature of the species and declines to near zero just below the maximum lethal temperature (Elliott 1976; Kitchell et al. 1977; Brett 1983; Bevelhimer et al. 1985; Stewart and Binkowski 1986). The survival of northern squawfish (percent) was 100 at 26.4°C, 50 at 29.3°C, and 0 at 32.0°C for fish acclimated at 18.9–22.2°C (Black 1953). Thus the incipient upper lethal temperature is about 29°C (Brown and Moyle 1981). Based on field observations, northern squawfish prefer temperatures of about 16–22°C (Dimick and Merryfield 1945). Northern squawfish digested fish at rates of 5, 14, and 40–50%·h^{-1} at temperatures of 4–6, 10–12, and 24°C, respectively (Steigenberger and Larkin 1974). Falter (1969) and Beyer et al. (1988) also observed acceleration in digestion rate with temperature. From these data, we predict that temperature-specific C_{max} will be near zero at 0°C, very low at 4°C, will peak at 20–24°C and will be near zero at 27°C. Temperature of McNary Dam discharge ranges from about 0.5 to 23.5°C; subsurface temperatures measurements in the reservoir were significantly higher, especially in backwater areas (about 27°C).

The polynomial equation (6) had the lowest fit (R^2), over the entire environmental temperature range, of the three models of northern squawfish maximum consumption rate. Diana (1987) used a multivariate model for maximum consumption rate of northern pike (*Esox lucius*) that incorporated a power function of predator weight and a polynomial function of temperature. We do not consider the polynomial model valid because it has the undesirable characteristics of being purely empirical with no underlying theoretical basis, of having coefficients with no biological meaning, and of exhibiting unrealistic cyclic behavior at the lower and upper extremes.

We analyzed the relation between temperature and C_{max} both in terms of daily ration and number of salmon consumed per northern squawfish. In applying our results to predation models, we believe that the use of ration as the measure of C_{max} is usu-

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ally more appropriate because it standardizes the weight of salmonid prey consumed per unit weight of predator. In nature, where both the size of predator and prey vary substantially on a seasonal or spatial basis, erroneous predictions of C_{max} could be derived if number were used as the criterion variable (unless the mean weights of the northern squawfish and salmonid prey were very similar to those of our test fish). For example, extremely high numbers of salmon fry ($>200 \cdot predator^{-1}$) have been observed in the stomachs of northern squawfish in a backwater below Little White Salmon Hatchery near Cook, WA (USFWS, unpubl. memorandum, 1951). Our results are presented in wet weight; however, for greater utility, we present conversion factors of wet to dry weight for both adult northern squawfish and juvenile salmon.

Both the functional response relation (Vigg 1988) and maximum consumption rate relation are central to prototype predation simulation models for the John Day Reservoir (Beamesderfer et al. 1990) and the Columbia River System (L. J. Bledsoe, Center for Quantitative Science, University of Washington, Seattle, WA, pers. comm.). Modeling predator–prey dynamics may be the only practical way to quantify the system-wide losses to predators and for understanding the factors affecting predation in a river as large and perturbed as the Columbia.

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