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

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Abstract.—Adult northern squawfish *Ptychocheilus oregonensis,* walleyes *Stizostedion vitreum,* smallmouth bass *Micropterus dolomieu,* and channel catfish *Ictalurus punctatus* were sampled from four regions of John Day Reservoir from April to August 1983–1986 to quantify their consumption of 13 species of prey fish, particularly seaward-migrating juvenile Pacific salmon and steelhead (*Oncorhynchus* spp.). Consumption rates were estimated from field data on stomach contents and digestion rate relations determined in previous investigations. For each predator, consumption rates varied by reservoir area, month, time of day, and predator size or age. The greatest daily consumption of salmonids by northern squawfish and channel catfish (0.7 and 0.5 prey/predator) occurred in the upper end of the reservoir below McNary Dam. Greatest daily predation by walleyes (0.2 prey/predator) and smallmouth bass (0.04) occurred in the middle and lower reservoir. Consumption rates of all predators were highest in July, concurrent with maximum temperature and abundance of juvenile salmonids. Feeding by the predators tended to peak after dawn (0600–1200 hours) and near midnight (2000–2400). Northern squawfish below McNary Dam exhibited this pattern, but fed mainly in the morning hours down-reservoir. The daily ration of total prey fish was highest for northern squawfish over 451 mm fork length (>13.2 mg/g predator), for walleyes 201–250 mm (42.5 mg/g), for smallmouth bass 176–200 mm (30.4 mg/g), and for channel catfish 401–450 mm (17.1 mg/g). Averaged over all predator sizes and sampling months (April–August), the total daily ration (fish plus other prey) of smallmouth bass (28.7 mg/g) was about twice that of channel catfish (12.6), northern squawfish (14.1), and walleyes (14.2). However, northern squawfish was clearly the major predator on juvenile salmonids.

Knowledge of food consumption rates of piscivores leads to a better understanding of fish community dynamics. For example, consumption estimates are important for multispecies trophic dynamics models (Sainsbury 1986). During 1983–1986, adult northern squawfish, walleyes, smallmouth bass, and channel catfish were sampled from John Day Reservoir, Columbia River, to determine their consumption of 13 species of prey fish (common and scientific names are listed in Table 1). Because our particular interest was in predation on emigrating juvenile salmonids, we grouped the prey as salmonids and non-salmonids for analysis. To estimate daily consumption rates, we integrated data on stomach contents of fish collected in the reservoir with digestion rates determined from previous laboratory studies.

The estimation of fishes' food consumption in nature from the stomach contents was first proposed by Bajkov (1935) and has often been attempted since (see reviews by Jobling 1986 and Persson 1986). The method we used to estimate consumption rates was similar to that of Swenson (1972), who reconstructed average diel feeding patterns from pooled stomach contents of predators collected under natural conditions. This method is more refined than others, because it is not based solely on an extrapolation of laboratory data.

The importance of the salmonid fishery resource in the Columbia River and the rationale for studying the predation rates by resident fish populations on juvenile salmonid smolts was discussed by Poe et al. (1991, this issue). Prior to this study, northern squawfish were generally believed to be important predators on smolts in the Columbia River, especially at hatchery release sites and in tailraces of dams (Thompson 1959; Ebel 1977), but there were few data to support this

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TABLE 1.—Scientific and common names of predator and prey fish species studied for consumption rate estimates in John Day Reservoir, Columbia River, and of other fish species referenced in the text or tables.

Family	Species	Common name
Predators		
Cyprinidae	*Ptychocheilus oregonensis*	Northern squawfish[a]
Percidae	*Stizostedion vitreum*	Walleye
Centrarchidae	*Micropterus dolomieu*	Smallmouth bass[a]
Ictaluridae	*Ictalurus punctatus*	Channel catfish
Prey		
Salmonidae	*Oncorhynchus tshawytscha*	Chinook salmon
	O. kisutch	Coho salmon
	O. nerka	Sockeye salmon
	O. mykiss	Steelhead
Cyprinidae	*Acrocheilus alutaceus*	Chiselmouth
	Mylocheilus caurinus	Peamouth
Catostomidae	*Catostomus columbianus*	Bridgelip sucker
	C. macrocheilus	Largescale sucker
Percopsidae	*Percopsis transmontana*	Sand roller
Cottidae	*Cottus beldingi*	Prickly sculpin
Clupeidae	*Alosa sapidissima*	American shad
Other fishes referenced		
Cyprinidae	*Ptychocheilus grandis*	Sacramento squawfish
Percidae	*Perca flavescens*	Yellow perch
	Stizostedion canadense	Sauger
Centrarchidae	*Micropterus salmoides*	Largemouth bass
	Lepomis macrochirus	Bluegill
	L. gibbosus	Pumpkinseed
	Pomoxis nigromaculatus	Black crappie

[a] Juveniles of these species were also considered prey.

belief. Nor was much known about the effects on smolt mortality of three predators introduced into the Columbia River: walleye, smallmouth bass, and channel catfish. In this paper, we present consumption rate estimates for these four predators in John Day Reservoir during the season of principal juvenile salmonid emigrations (April–August). We consider these estimates in relation to salmonid versus total prey, diel cycles, months of the season, location in the reservoir, and size of the predators.

Methods

Study design.—John Day Dam impounds the Columbia River for 123 km upstream to McNary Dam. A detailed description of the study site and characteristics of the juvenile salmonid seaward migration were given by Poe et al. (1991, this issue), who also described predator collections, stomach contents analyses, and overall sampling design. Predators were sampled on a diel schedule (four 6-h periods per day) for at least three con-secutive days during each month of the smolt out-migration (April–August) in 1983–1986 (except in July 1983 and July 1984). We sampled four general reservoir regions each year: McNary Dam tailrace (5 km downstream from McNary Dam); Irrigon (20 km); Arlington (75 km); and John Day Dam forebay (118 km). McNary Dam tailrace and John Day Dam forebay each were subdivided into the area within 1 km of the dams (referred to here as "restricted zones" because boats are prohibited from them) and the remainder, giving a total of six reservoir areas. Arlington was not sampled in 1983, and the McNary Dam tailrace restricted zone was the only area sampled each month in 1986. For estimates of prey consumption rate and subsequent analyses of juvenile salmonid mortality (Rieman et al. 1991, this issue), however, we stratified the reservoir into only two reservoir areas: the restricted zone of the McNary Dam tailrace and the remainder of the John Day Reservoir. This allowed us to test the hypothesis, developed by previous workers (e.g., Ebel 1977), that pre-

TABLE 2.—Linear regression model $(Y = a + bX)$ statistics for fork length (Y) regressed on other length measurements (X), solved by least squares, for 11 species of prey fish in John Day Reservoir. All lengths are in millimeters; r^2 values are 0.99–1.00 except as footnoted.

Prey species	N	Nape to base of tail		Standard length		Total length	
		a	b	a	b	a	b
American shad	44	4.20	1.269	1.45	1.060	−0.15	0.890
Chinook salmon	53	7.40	1.194	2.22	1.049	−2.16	0.941
Steelhead	46	7.01	1.233	5.34	1.042	−1.57	0.958
Bridgelip sucker	52	13.45	1.216	6.08	1.069	−3.94	0.961
Largescale sucker	58	5.43	1.268	3.40	1.091	−1.64	0.936
Chiselmouth	52	8.40	1.217	4.01	1.077	−2.52	0.906
Peamouth	40	−1.02	1.337	−1.80	1.144	−2.01	0.923
Northern squawfish	50	5.60	1.299	1.81	1.083	−0.19	0.899
Sand roller[a]	46	2.45	1.373	2.16	1.094	0.90	1.890
Smallmouth bass	36	7.61	1.172	1.85	1.101	0.01	0.956
Prickly sculpin	49	2.18	1.458	3.44	1.151	0.00	1.000

[a] $r^2 = 0.94$ for nape to base of tail and 0.96 for standard and total lengths.

dation rates are higher immediately below Columbia River dams than in other parts of the reservoir.

For most consumption estimates, we pooled the data over the 4 years of study (1983–1986). This gave us larger sample sizes and overcame problems of unbalanced sampling during some years. We believe that pooling of annual data cost us little information because there were only small year-to-year differences in predator diets, passages of juvenile salmonids at McNary Dam, predator population sizes, and environmental conditions such as water temperature and flow (Fish Passage Center 1988; Beamesderfer and Rieman 1991, this issue; Poe et al. 1991; Rieman et al. 1991; U.S. Army Corps of Engineers, unpublished data).

Consumption estimates.—We estimated daily consumption of two prey groups—four salmonids and nine non-salmonids (Table 1)—by four predators. We estimated daily consumption rates of predators following the method developed by Swenson (1972) and described in detail by Swenson and Smith (1973) and Wahl and Nielsen (1985). Our calculation involved eight steps (Figure 1). (1) Stomach contents of predators were evaluated on a diel schedule throughout the period of juvenile salmonid migration. (2) Original prey weight was back-calculated from preestablished regressions of weight against body length and bone measurements. (3) Percent digestion or mass evacuated was taken as the difference between sample and calculated original prey weights. (4) Regression equations from the literature were used to predict evacuation rates as a function of time, temperature, fish size, and meal size for each pred-

ator (northern squawfish: Beyer et al. 1988; smallmouth bass: Beyer and Burley, unpublished data; walleyes: Swenson and Smith 1973 and Wahl and Nielsen 1985; channel catfish: Shrable et al. 1969). (5) Duration of the digestion period and time of ingestion of each prey fish item were calculated from data derived from steps (3) and (4). (6) The mass of prey consumed per diel time period per prey size category per day was calculated. (7) The data from (6) were divided by the number of potential predators in the sample for each diel time–prey size stratum to estimate average mass consumed per average predator. (8) Daily ration (mg prey/g predator) and number of prey consumed (prey/predator) were derived from mean predator and prey weights for the sample. Thus, this technique reconstructs an average diel feeding pattern from pooled stomach contents of a sample of predators collected from natural environment. The consumption calculation can be summarized by the equation

$$C = \sum_{i-1}^{t} \sum_{j-1}^{s} \frac{\sum_{k-1}^{p} W_{ij}}{F_{ij}}; \quad (1)$$

C is the daily consumption (g) by an average predator; W_{ij} is the undigested weight of prey fish of a given size category (j) during a given diel time interval (i), and F_{ij} is the number of potential predators from the sample that could have contained prey fish of size j that were no more than 90% digested during time period i.

Regression equations.—Several regression equations are needed to accomplish the various steps of the calculation procedure outlined above.
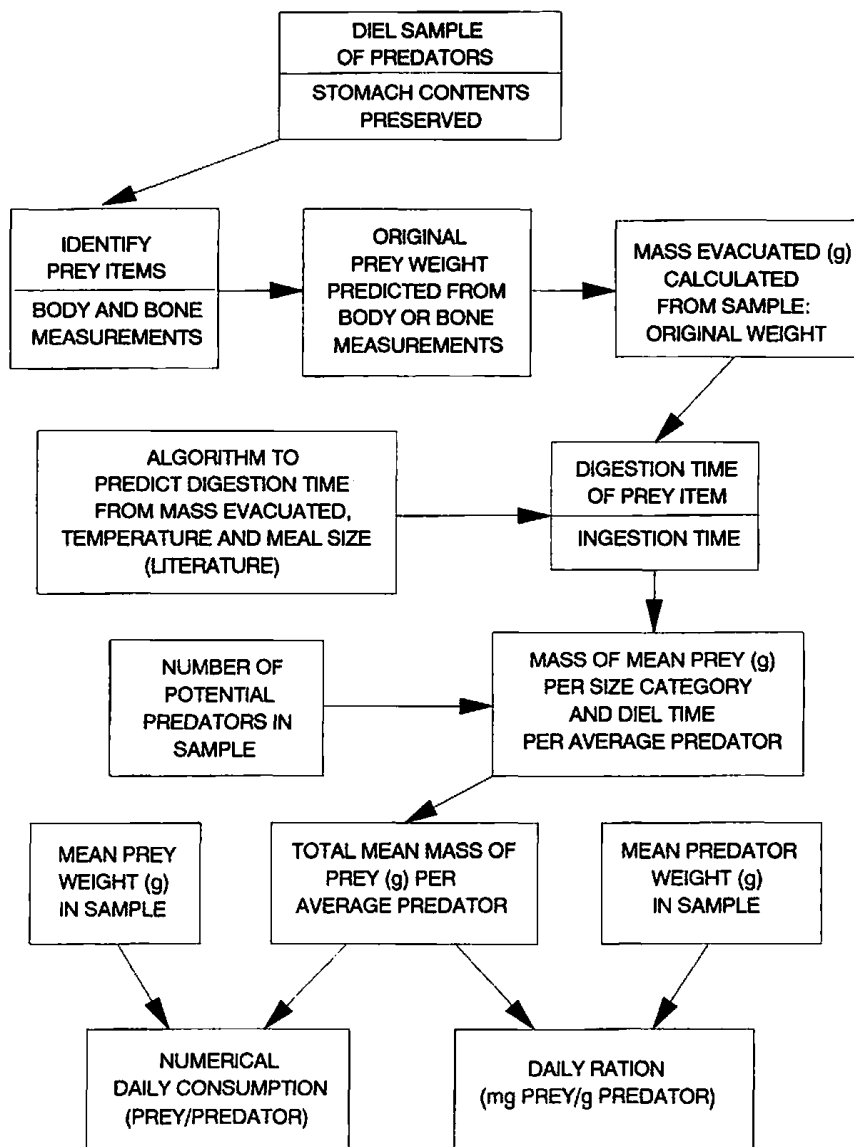
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┌─────────────────────┐
│     DIEL SAMPLE     │
│    OF PREDATORS     │
├─────────────────────┤
│  STOMACH CONTENTS   │
│      PRESERVED      │
└─────────────────────┘
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┌──────────────────┐      ┌──────────────────┐      ┌──────────────────┐
│     IDENTIFY     │      │     ORIGINAL     │      │ MASS EVACUATED (g)│
│    PREY ITEMS    │      │    PREY WEIGHT   │      │    CALCULATED    │
├──────────────────┤ ───▶ │  PREDICTED FROM  │ ───▶ │   FROM SAMPLE:   │
│  BODY AND BONE   │      │   BODY OR BONE   │      │ ORIGINAL WEIGHT  │
│  MEASUREMENTS    │      │   MEASUREMENTS   │      │                  │
└──────────────────┘      └──────────────────┘      └──────────────────┘
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┌──────────────────────┐      ┌──────────────────┐
│     ALGORITHM TO     │      │  DIGESTION TIME  │
│ PREDICT DIGESTION TIME│      │   OF PREY ITEM   │
│  FROM MASS EVACUATED, │ ───▶ ├──────────────────┤
│ TEMPERATURE AND MEAL SIZE│   │  INGESTION TIME  │
│     (LITERATURE)     │      │                  │
└──────────────────────┘      └──────────────────┘
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┌──────────────────┐      ┌──────────────────────┐
│    NUMBER OF     │      │  MASS OF MEAN PREY (g)│
│    POTENTIAL     │      │   PER SIZE CATEGORY  │
│   PREDATORS IN   │ ───▶ │    AND DIEL TIME     │
│     SAMPLE       │      │  PER AVERAGE PREDATOR│
└──────────────────┘      └──────────────────────┘
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┌──────────────────┐  ┌──────────────────┐  ┌──────────────────┐
│    MEAN PREY     │  │ TOTAL MEAN MASS OF│  │  MEAN PREDATOR   │
│    WEIGHT (g)    │  │    PREY (g) PER   │  │    WEIGHT (g)    │
│    IN SAMPLE     │  │  AVERAGE PREDATOR │  │    IN SAMPLE     │
└──────────────────┘  └──────────────────┘  └──────────────────┘
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┌──────────────────┐            ┌──────────────────┐
│    NUMERICAL     │            │   DAILY RATION   │
│ DAILY CONSUMPTION│            │(mg PREY/g PREDATOR)│
│  (PREY/PREDATOR) │            │                  │
└──────────────────┘            └──────────────────┘
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FIGURE 1.—Flow diagram showing the processes involved in calculating consumption rates with the technique developed by Swenson (1972).

Fork length of prey was measured directly if possible, but estimated from other body measurements for moderately digested prey fish (Table 2), and from bone measurements of well digested prey (Hansel et al. 1988). Original prey weights were estimated from fork length with exponential regressions (Table 3).

The mass of each prey fish evacuated was calculated as the difference between the estimated original weight of the item and its digested weight. We used the linear regression equation of Beyer et al. (1988) to estimate unpreserved digested weight from formalin-preserved weight. Time of digestion (hours) for each prey item was estimated

from predator species-specific evacuation rate regressions, solved for time (Table 4). Depending on predator species, digestion time was predicted from mass of the prey item evacuated, temperature, prey weight, predator weight, meal size, or combinations thereof. Time of ingestion of each fish was back-calculated from the time of predator capture and the stage of digestion of the item.

Meal size, based on stomach contents of each individual predator, was calculated as a weight (g) for northern squawfish and smallmouth bass, or as a ration (mg/g) for walleye. Meal weight (S) was the sum of (1) the original weight of the specified prey fish item (O_i), (2) the original weights of any

TABLE 3.—Power regression model ($Y = aX^b$) statistics for weight (Y, g) regressed on fork length (X, mm), solved by least squares, for 11 species of prey fish in John Day Reservoir; r^2 values were 0.98–0.99 except as footnoted.

Prey species	N	Length range (mm)	Regression statistic	
			a	b
American shad	40	39–98	4.600×10^{-6}	3.106
Chinook salmon	148	34–184	8.910×10^{-6}	3.031
Steelhead[a]	122	93–206	8.395×10^{-6}	3.003
Bridgelip sucker	52	89–214	5.321×10^{-6}	3.161
Largescale sucker	58	61–229	6.531×10^{-6}	3.131
Chiselmouth	52	98–242	22.080×10^{-6}	2.907
Peamouth	40	57-194	9.638×10^{-6}	3.038
Northern squawfish	50	40-238	12.677×10^{-6}	2.970
Sand roller[b]	46	30-110	16.943×10^{-6}	2.984
Smallmouth bass	36	34–93	10.046×10^{-6}	3.117
Prickly sculpin	49	40–137	5.309×10^{-6}	3.187

[a] $r^2 = 0.89$.
[b] $r^2 = 0.96$.

other prey fish items in the stomach that were within 10% of the original weight and 20% of the percent digestion of the specified prey item (O_j), and (3) the digested weight of all other food items in the stomach (D_k):

$$S = O_i + O_j + D_k .\qquad(2)$$

Meal ration (R) was meal size as a proportion of predator weight (P):

$$R = S \cdot 1,000/P.\qquad(3)$$

The total daily ration of all food items combined was determined from the gravimetric proportion of fish to non-fish food items in the diet (Table 5). Total ration (R_t) was calculated by extrapolation:

$$R_t = R_f/G;\qquad(4)$$

R_f is the ration of prey fish and G is the gravimetric fraction of fish in the diet.

Results

Daily Ration

Northern squawfish (≥250 mm in length) ate a higher mean seasonal proportion of fish in the McNary restricted zone (91%) than in the John Day pool (58%), as did channel catfish: 89 versus 56% (Table 5). Diets of smallmouth bass (≥200 mm in length), averaged 82% fish; walleyes of all sizes ate almost exclusively fish (99.8%). Northern squawfish and channel catfish showed similar temporal trends in total daily ration (fish and non-fish) that were different from those of walleye and smallmouth bass. In the McNary Dam restricted zone, northern squawfish had the highest mean total daily ration during July (33.0 mg/g); likewise, channel catfish exhibited their highest ration during July–August (16.7 mg/g). In the remainder of John Day Reservoir, both predators showed a feeding pattern with peaks in May and July; max-

TABLE 4.—Algorithms for calculating predator-specific digestion times (h) based on evacuation rate regression equations for northern squawfish, smallmouth bass, walleye, and channel catfish. E - prey mass evacuated (g); S = prey meal weight (g); R = prey meal ration (mg/g); D = prey weight digested (%); P = predator weight (g); T = temperature (°C).

Predator species	Algorithm to solve for digestion time (h)
Northern squawfish[a]	$1,330.753\ E^{1.081}\ S^{-0.469}\ T^{-1.606}\ P^{-0.273}$
Smallmouth bass[b]	$268.529\ (E + 0.01)^{0.696}\ S^{-0.364}\ e^{-0.139T}\ P^{-0.175}$
Walleye[c]	
Prey <1.1 g	$(-7.540 + 0.178\ D + 0.088\ R)/0.0283\ T^{1.1899}$
Prey 1.1–2.5 g	$(-4.476 + 0.208\ D + 0.031\ R)/0.0415\ T^{1.1899}$
Prey >2.5 g	$(-0.065 + 0.231\ D + 0.047\ R)/0.0415\ T^{1.1899}$
Channel catfish[d]	$0.327\ D + 0.293\ T$

[a] Beyer et al. (1988).
[b] J. Beyer and C. C. Burley (unpublished data, U.S. Fish and Wildlife Service, 1988).
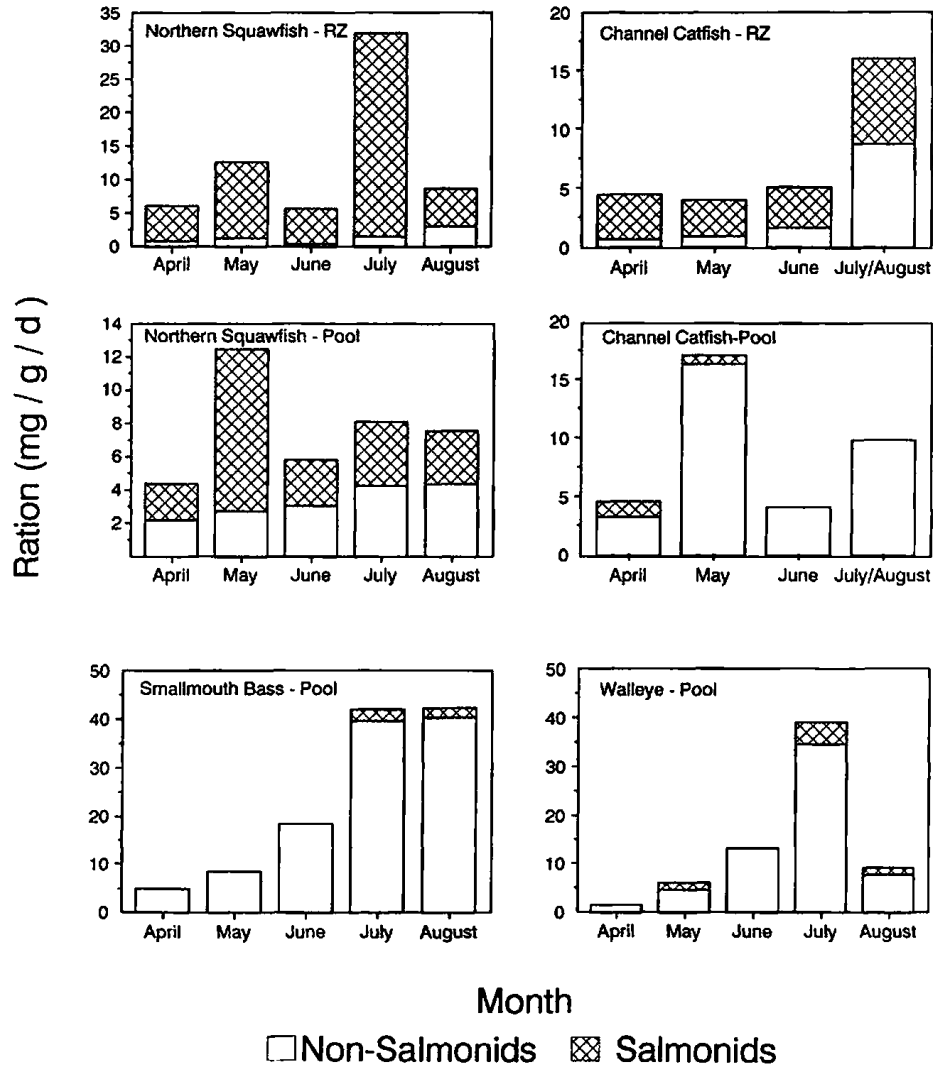[c] Swenson and Smith (1973); Wahl and Nielsen (1985).
[d] Shrable et al. (1969).

FIGURE 2.—Mean daily ration (mg of prey per gram of predator per day), by month, of northern squawfish, walleyes, smallmouth bass, and channel catfish feeding on salmonid and non-salmonid prey fish in McNary Dam restricted zone (RZ) and the rest of John Day Reservoir (pool), 1983–1986.

imum peaks were about 17.5 mg/g for northern squawfish and 25.5 for channel catfish. Walleye exhibited an exponential increase in total ration from April to July (peak, 39.7 mg/g), and a decline in August. Smallmouth bass also showed an exponential increase in total ration from April to July, but maintained the maximum ration of about 51.5 mg/g in August.

The mean total daily ration over the entire season was remarkably consistent for all predators except smallmouth bass. Northern squawfish, channel catfish, and walleye had total mean daily rations of 14.1, 12.6, and 14.2 mg/g, respectively. The mean daily ration of smallmouth bass was about twice that of the other species, i.e., 28.7 mg/g.

Daily fish ration (salmonid and non-salmonid) of each predator varied from month to month; the mean daily prey fish ration (mg prey/g predator) was generally lowest in April and highest in July (Figure 2). From April to August, the non-salmonid fish ration of northern squawfish increased from about 1.0 to 3.0 mg/g in McNary Dam restricted zone, and from about 2.1 to 4.5 in the reservoir. The salmonid component of the northern squawfish ration was relatively high in May and July in both reservoir areas; however, it peaked in the reservoir in May (9.7) and in the McNary Dam restricted zone in July (30.3 mg/g).

The channel catfish ration of fish in the McNary Dam restricted zone was nearly constant from April to June (about 4.5 mg/g); but it tripled dur-

TABLE 5.—Proportions of the diets of four fish predators (northern squawfish, ≥250 mm fork length; walleyes, all sizes; smallmouth bass, ≥200 mm fork length; and channel catfish, all sizes) that were composed of fish (percent by weight) in John Day Reservoir, April–August 1983–1986. RZ is the restricted zone below McNary Dam; John Day pool is the rest of the reservoir.

Predator species and reservoir area	Gravimetric percentage of fish in the diet				
	Apr	May	Jun	Jul	Aug
Northern squawfish					
McNary Dam RZ	92.5	97.8	84.0	96.6	86.2
John Day pool	78.1	74.3	43.4	44.8	49.3
Walleye					
John Day pool	99.6	99.7	99.9	99.8	99.9
Smallmouth bass					
John Day pool	85.1	81.8	76.7	82.2	82.9
Channel catfish[a]					
McNary Dam RZ	72.9	95.3	88.0	98.0	
John Day pool	75.3	64.1	42.2	42.6	

[a] For channel catfish, data for July and August are combined.

ing July–August (16.3). In John Day Reservoir, the fish ration of channel catfish was about 4.5 mg/g during both April and June, but was greater in May (16.7) and July–August (10.0). In both the restricted zone and reservoir, the proportion of the total fish ration of channel catfish that was composed of salmonids decreased progressively from April to July–August; i.e., from 87% to 46% in the restricted zone and from 29% to nil in the John Day Reservoir.

The non-salmonid fish component of the ration of walleye and smallmouth bass increased at an accelerating rate from April to July, reaching 35.1

mg/g for walleyes and 39.9 mg/g for smallmouth bass. During August, however, the non-salmonid fish component ration of walleyes decreased to 8.0 mg/g whereas that of smallmouth bass remained high, i.e., 40.6 mg/g. The salmonid component of the walleyes' ration was highest in July (4.6 mg/g) and relatively high during May and August (about 1.5 mg/g), but low in April and June (<0.4). Likewise, the salmonid component of smallmouth bass ration was highest in July and August (about 2.3 mg/g).

Consumption Rates—Numerical

Consumption estimates showed that the maximum predation rate on juvenile salmonids was by northern squawfish in the restricted zone during July (Table 6). Over the entire season, daily northern squawfish consumption of salmonids was more than 5 times higher in the restricted zone than in the rest of the reservoir, averaging 0.68 versus 0.13 prey/predator. Likewise, the mean daily consumption of juvenile salmonids by channel catfish over the season was 10 times higher in the restricted zone (0.50 prey/predator) than in the remainder of the reservoir (0.05). In the John Day Reservoir, walleye exhibited the highest mean seasonal consumption rate on juvenile salmonids (0.19 prey/predator), which was similar in magnitude to that of northern squawfish. Of the predators studied, smallmouth bass had the lowest mean seasonal consumption of salmonids in the reservoir (0.04 prey/predator daily). Too few walleyes and smallmouth bass were sampled in the restricted zone to enable us to make monthly consumption estimates.

TABLE 6.—Mean daily consumption (prey/predator) of juvenile salmonids estimated for four piscivores in the restricted zone (RZ) of McNary Dam tailrace and the rest of John Day Reservoir (pool), April–August 1983–1986.

Predator species[a] and location	N	Salmonids per predator per day				
		Apr	May	Jun	Jul	Aug
Northern squawfish						
McNary RZ	2,371	0.139	0.490	0.358	2.027	0.392
Pool	1,996	0.043	0.251	0.086	0.154	0.094
Walleye						
McNary RZ[b]	38					
Pool	1,021	0.021	0.113	0.118	0.447	0.232
Smallmouth bass						
McNary RZ[b]	24					
Pool	2,856	0.003	0.009	0.019	0.118	0.070
Channel catfish[c]						
McNary RZ	394	0.149	0.283	0.162	1.385	
Pool	262	0.065	0.078	0.054	0.000	

[a] Predator lengths: northern squawfish, ≥250 mm; smallmouth bass, ≥200 mm; walleye and channel catfish, all sizes.
[b] Too few predators to enable monthly estimates.
[c] For channel catfish, data for July and August are combined.

TABLE 7.—Mean daily consumption (prey/predator) of salmonid and non-salmonid prey by northern squawfish, walleyes, smallmouth bass, and channel catfish in six areas of John Day Reservoir, 1983–1986. The six areas and their distances (km) downstream from McNary Dam are: McNary Dam restricted zone (RZ), 1; McNary tailrace, 5; Irrigon, 20; Arlington, 75; John Day forebay, 118; John Day Dam RZ, 123. N and W are numbers and mean weights of predators; n and w are mean numbers and weights of prey consumed daily per predator.

Predator species, prey group, and statistic	Station kilometer downstream from McNary Dam					
	1	5	20	75	118	123
Northern squawfish						
N	2,373	414	236	448	497	409
W(g)	997	854	802	737	685	783
Salmonid prey						
n	0.605	0.146	0.028	0.053	0.138	0.236
w(g)	18.5	24.7	26.8	31.6	32.6	33.6
Non-salmonid prey						
n	0.094	0.331	0.181	0.180	0.206	0.357
w(g)	12.6	20.4	21.4	23.8	27.6	25.1
Walleye						
N	38	659	338	27	0	0
W(g)	3,109	2,149	2,505	1,135		
Salmonid prey						
n	0.000	0.072	0.144	0.745		
w(g)		20.9	16.3	13.0		
Non-salmonid prey						
n	0.529	0.676	1.128	1.320		
w(g)	27.0	18.4	21.9	15.5		
Smallmouth bass						
N	24	166	1,033	836	635	192
W(g)	517	515	544	462	292	225
Salmonid prey						
n	0.051	0.014	0.052	0.023	0.011	0.083
w(g)	0.3	16.4	3.7	6.2	16.7	13.3
Non-salmonid prey						
n	0.358	1.428	0.927	0.652	0.473	0.321
w(g)	5.0	8.5	9.6	10.8	15.4	10.2
Channel catfish						
N	394	59	149	52	2	0
W(g)	2,111	1,606	1,957	931		
Salmonid prey						
n	0.239	0.048	0.053	0.000		
w(g)	32.4	10.1	26.2			
Non-salmonid prey						
n	0.130	0.531	0.549	0.197		
w(g)	21.1	20.9	39.7	14.9		

Spatial Trends

Mean daily consumption rates of each predator, as well as the mean weights of predators and of the prey fish they consumed, varied among localities in John Day Reservoir (Table 7). Mean daily salmonid and non-salmonid fish rations showed different spatial trends for each predator species. Northern squawfish ingested a high ration of salmonids at McNary Dam restricted zone (11.3 mg/g), relatively low rations (<4.3) throughout the main body of the John Day Reservoir, and increased ration (about 6.5) at John Day Dam restricted zone and forebay. The non-salmonid component of northern squawfish ration, however, was lowest at McNary Dam restricted zone, relatively high throughout the main body of the

John Day Reservoir and highest at John Day Dam forebay restricted zone.

The spatial trend of consumption by channel catfish resembled that by northern squawfish, except that channel catfish were not captured (and thus assumed to be rare) in the John Day forebay and the restricted zone. Their ration of salmonids was highest at McNary Dam restricted zone (3.7 mg/g), and the consumption of non-salmonids was highest (11.8) at Irrigon, about 20 km downstream. Walleyes' ration of salmonids, unlike that of northern squawfish, was very low (<1.0 mg/g) in the upper 20 km of the reservoir (McNary Dam to Irrigon), but high 75 km downstream at Arlington (8.5). Similarly, the consumption of non-salmonids increased progressively from 4.1 mg/g at McNary Dam restricted zone and tailrace to

9.5 at Arlington. We collected no walleyes in extensive sampling at John Day Dam restricted zone and forebay, and therefore assume that they were rare there and that walleye predation was negligible in this region. Consumption of salmonids by smallmouth bass was very low throughout the reservoir (<0.5 mg/g), but was elevated (4.9) in the John Day Dam forebay restricted zone. Conversely, the ration of non-salmonids was high (>15.3 mg/g) throughout the remaining reservoir, except that rates were relatively low (5.0) near McNary Dam.

Predator Size Relations

Each predator showed trends in consumption rates with changes in predator size. Overall prey fish consumption by northern squawfish increased progressively with size (Figure 3). Daily consumption (numbers) and ration (weight) leveled off at about 0.6 prey/predator and 12.0 mg/g for northern squawfish more than 400 mm in length. As northern squawfish grew, salmonids composed an increasing proportion of the total ration—over 75% for northern squawfish greater than 250 mm. Mean weight of prey fish eaten was directly related to northern squawfish size; non-salmonid prey fish were slightly larger than salmonids eaten, except for predators 450 mm and larger.

Like northern squawfish, channel catfish increased their prey consumption rate as they grew, but daily ration peaked (at 17.1 mg/g) in channel catfish 400–450 mm long (Figure 4). The prey of channel catfish shorter than 450 mm was mostly non-salmonids; larger channel catfish had a fish ration that was about 50% salmonids, and those of 650 mm or more ate only salmonids. Mean weight of fish eaten by channel catfish generally increased with the size of the predator, but this relation was variable for large channel catfish.

Fish consumption by walleyes peaked at predator fork lengths around 350 mm (1.2 prey/predator), then slightly declined and leveled off at about 0.7 prey (Figure 5). The corresponding ration showed a more pronounced peak (42.5 mg/g) at 250 mm and then declined to about 6.5 for walleyes larger than 350 mm. The proportion of the walleye rations composed of salmonids decreased with size from about 39% at 300 mm to about 1% for predators 700 mm in length (the few larger walleyes in our samples had eaten no salmonids). Mean weight of salmonids eaten by walleyes longer than 400 mm was nearly constant, whereas the weight of non-salmonid prey fish increased in large walleyes. In smallmouth bass, prey fish ra-
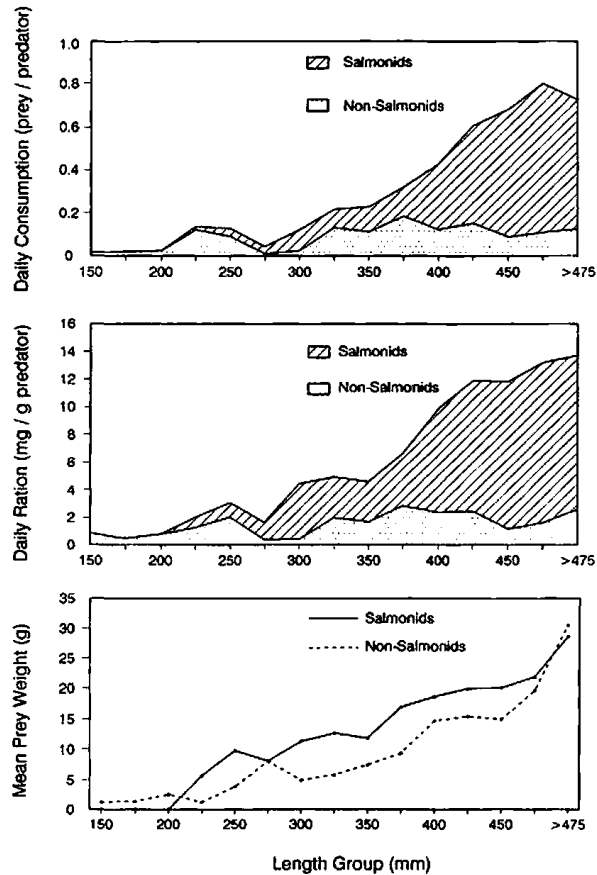
FIGURE 3.—Mean size-specific consumption rates of northern squawfish feeding on salmonid and non-salmonid prey in John Day Reservoir (all locations), 1983–1986.

tion was highest at 200 mm (30.4 mg/g), and then declined (Figure 6). Consumption was relatively constant in predators 126–250 mm in length (about 0.75 prey/predator), then slightly increased in larger fish. The salmonid component of smallmouth bass consumption ranged from about 1 to 7% for predator lengths of 50–375 mm; no salmonids had been eaten by the few larger smallmouth bass in our samples. Mean salmonid prey weight ranged from about 4 to 11 g in smallmouth bass 126–375 mm long; non-salmonid prey fish increased in size over most of the predator's length range.

Diel Feeding Chronology

Consumption rates varied with time of day; diel patterns were generally consistent throughout the season. Feeding by northern squawfish in John Day pool began increasing at dawn and remained strong into the afternoon (0400–1600 hours; Figure 7). The diel feeding chronology in the McNary Dam restricted zone was bimodal, having a noc-
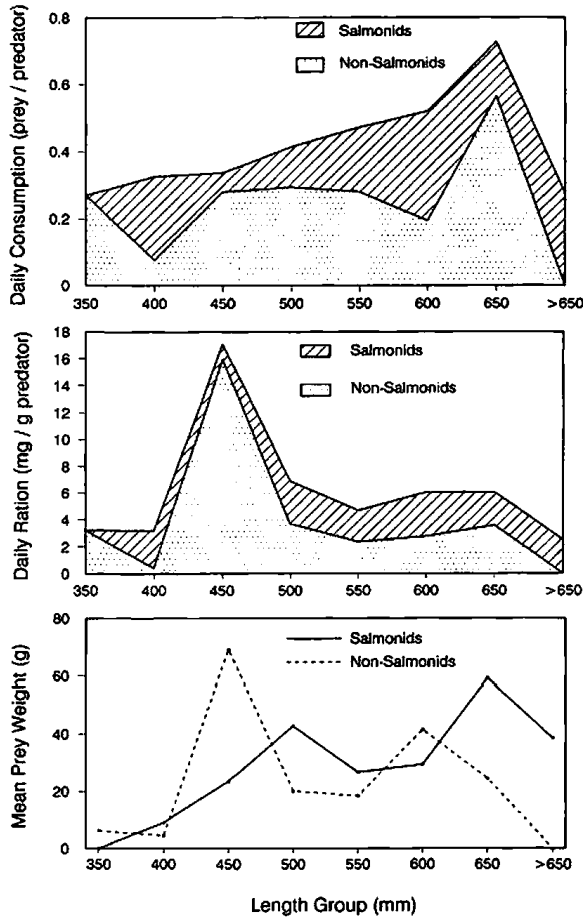
FIGURE 4.—Mean size-specific consumption rates of channel catfish feeding on salmonid and non-salmonid prey in John Day Reservoir (all locations), 1983–1986.
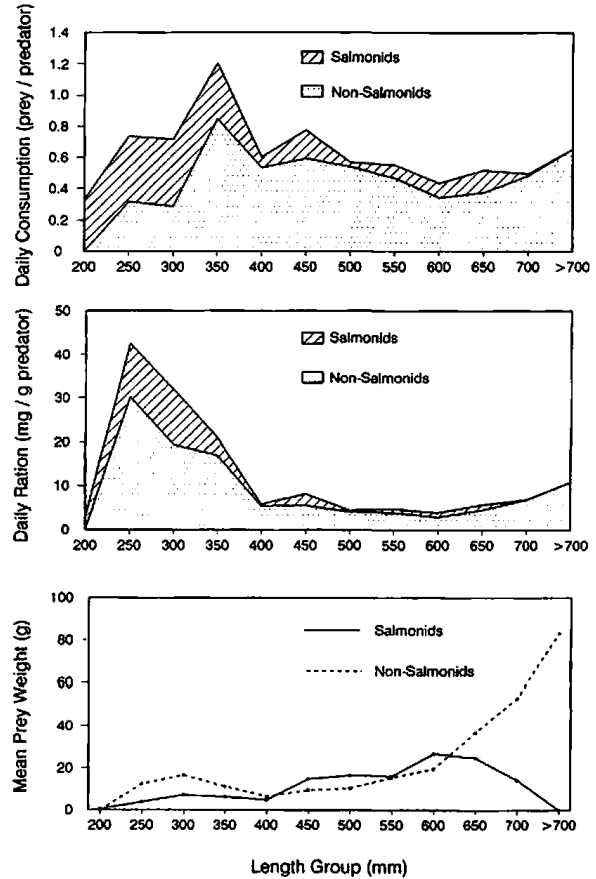

FIGURE 5.—Mean size-specific consumption rates of walleyes feeding on salmonid and non-salmonid prey in John Day Reservoir (except McNary Dam restricted zone), 1983–1986.

turnal peak at 2400–0400 hours and another peak after sunrise at 0600–1000 hours. Northern squawfish fed almost entirely on juvenile salmonids in the McNary Dam restricted zone, but fed on almost equal numbers of salmonids and non-salmonids in the rest of the reservoir; the feeding periodicity was similar for both types of prey.

The other three predators generally had differing diel feeding patterns (Figure 8). Walleyes fed primarily during the day from 0800 to 1600 hours, but also fed actively at night, two sharp peaks occurring at 2200–2400 hours and 0200–0400 hours. There was no obvious diel trend in the quantity of salmonids eaten by walleyes; however, the proportion of salmonids eaten was highest at 0400–0800 hours and lowest at 1800–2000 hours. Smallmouth bass fed throughout the diel cycle. Feeding rate was lowest at night (2200–0600 hours), increased from 0600 to 1400 hours, was relatively low from 1400 to 2000 hours, and ex-

hibited a peak near sunset (2000–2200 hours). A weak bimodal crepuscular feeding pattern was seen in channel catfish; feeding peaked near sunrise and sunset. No diurnal preference for salmonid versus non-salmonid prey was apparent; that is, no one predator fed mostly on salmonids at night and switched to mostly non-salmonids during the day.

Discussion

We described consumption rates as a function of predator size, month, reservoir area, and diel time period to illustrate important aspects of the dynamics of predation. Many factors affect spatiotemporal trends in consumption rates of fish predators in John Day Reservoir: metabolic requirements, distribution, feeding behavior, spawning, and prey availability. Temperature is probably the most influential single variable regulating consumption rates of fish in nature. Little is known about the thermal relations of northern squawfish; the upper lethal temperatures for
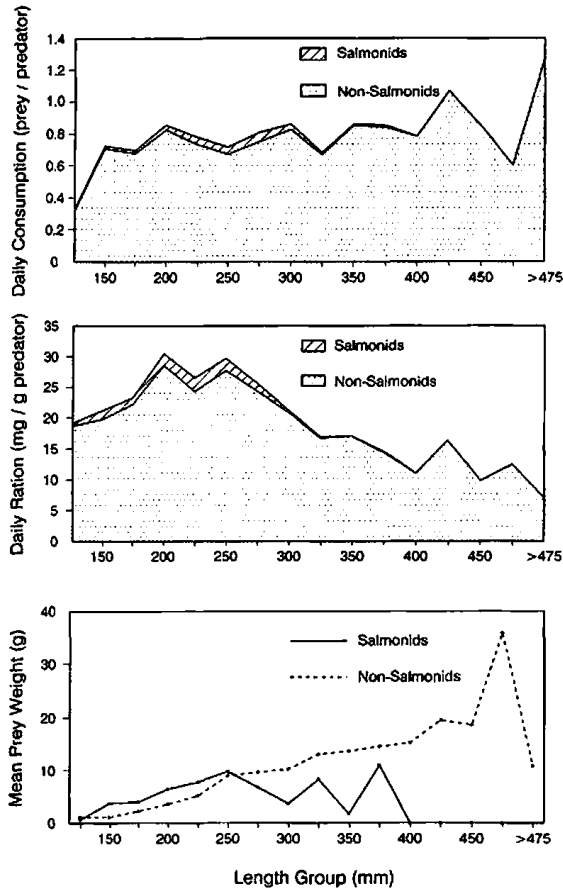
FIGURE 6.—Mean size-specific consumption rates of smallmouth bass feeding on salmonid and non-salmonid prey in John Day Reservoir (except McNary Dam restricted zone), 1983–1986.
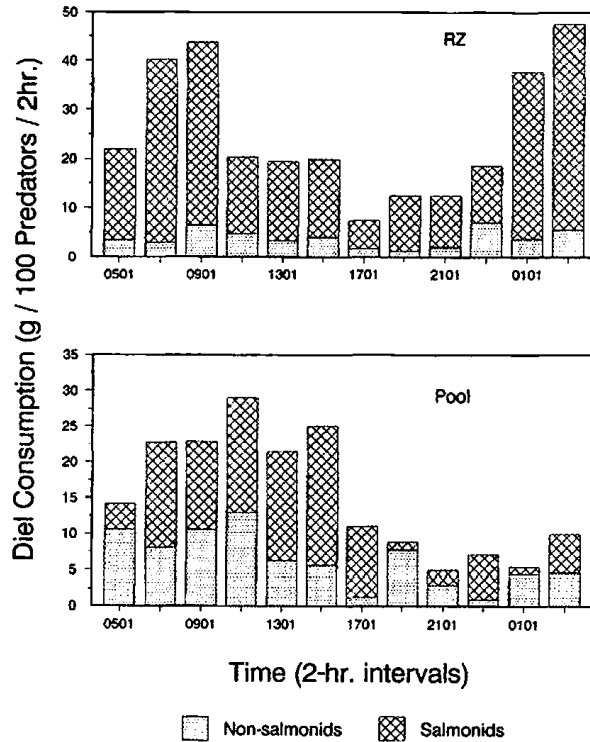

FIGURE 7.—Diel consumption rates (g/100 predators per 2 h) of northern squawfish feeding on salmonid and non-salmonid prey fish in McNary Dam restricted zone (RZ) and the rest of John Day Reservoir (pool), 1983–1986.

northern squawfish acclimatized at 18.9 to 22.2°C were 26.4, 29.3, and 32.0°C for 0, 50, and 100% mortality, respectively (Black 1953). Northern squawfish apparently prefer temperatures of 16–22°C, but are often found in warmer waters (Brown and Moyle 1981). The mean consumption rate of northern squawfish in July (2.0 prey/predator) at 19.0°C was four times that in May (0.5 prey/predator) at a mean temperature of about 11.5°C. Walleyes prefer temperatures of 21–23°C, which is within the range for optimum growth (20–25°C); their physiological optimum is 22.6°C, and their upper incipient lethal level is 31.6°C (Koenst and Smith 1976; Hokanson 1977). Maintenance rations of walleyes showed an exponential relationship with temperature over the range of 4 to 20°C (Kelso 1972). This observation is consistent with the exponential increase in walleye daily rations exhibited in John Day Reservoir from April to July (Figure 2). Optimum physiological temperatures for smallmouth bass are substantially high-

er than those of northern squawfish and walleyes. Depending on seasonal acclimatization and age group, the final preferendum of smallmouth bass can range from 12 to 31°C (Ferguson 1958; Barans and Tubb 1973; Reutter and Herdendorf 1974). The temporal consumption rates of smallmouth bass (Figure 2) showed an exponential increase from April to July, and a leveling off in August. Channel catfish, given a wide range of temperatures, prefer temperatures of 33.8°C (experimental) to 33.9–35.0°C (field) (Stauffer et al. 1976).

The maximum daily temperature at McNary Dam is usually highest (about 22°C) in August (U.S. Army Corps of Engineers, unpublished data); corresponding subsurface maximum temperatures in shallows and backwaters of John Day Pool are about 26°C (U.S. Fish and Wildlife Service, unpublished data). Thus the highest water temperatures in John Day Reservoir are at or below the thermal preference and optimum temperature for consumption and growth of all predators except northern squawfish; that is, the thermal range gives northern squawfish the greater opportunity to select their physiological optimum habitat.
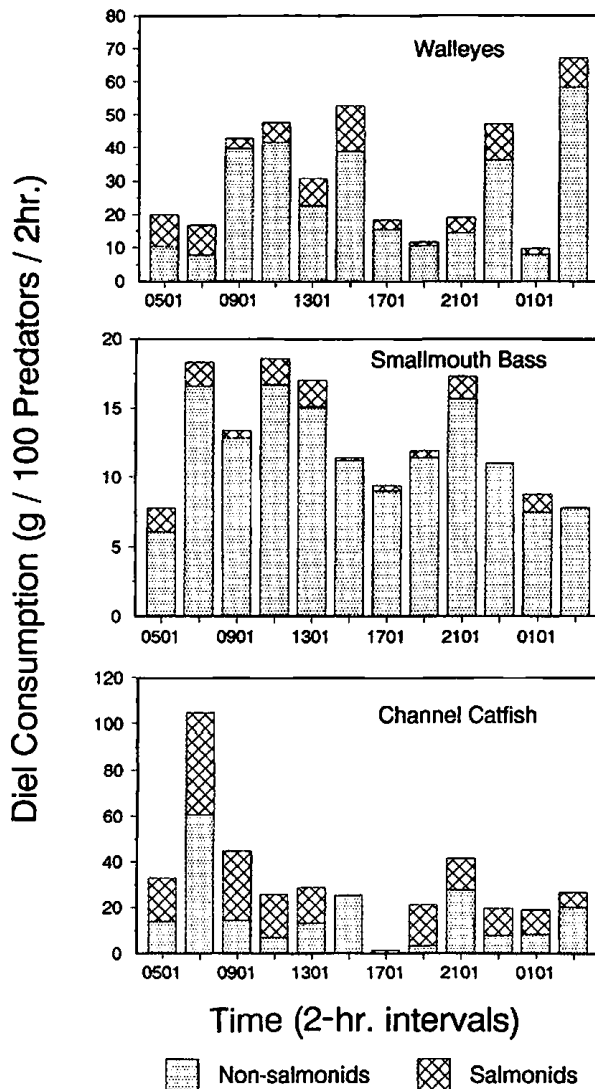
FIGURE 8.—Diel consumption rates (g/100 predators per 2 h) of walleyes, smallmouth bass, and channel catfish feeding on salmonid and non-salmonid prey fish in John Day Reservoir, 1983–1986.

Spawning may depress consumption rates of predators. Spawning of northern squawfish in John Day Reservoir peaks in June (S.V. and L.A.P., unpublished data), when consumption rates were relatively low and the percentage of empty stomachs was relatively high. Consumption rates of male centrarchids are depressed during the spawning season due to their territorial nest guarding behavior (Heidinger 1976; Adams et al. 1982). In the Hanford reach of the Columbia River, smallmouth bass spawning was protracted (April–July) and some males guarded nests until late July (Montgomery et al. 1980); hatching of their eggs was observed during July and August in the Hanford reach at temperatures of 15.5–29.5°C (Hen-

derson and Foster 1956). Male channel catfish are also known to build and guard nests; a discontinuation of feeding has been observed during the spawning season of channel catfish (Bailey and Harrison 1948; Clemens and Sneed 1957).

Predator Size Relations

Consumer size is an important consideration for predator–prey relations in terms of distribution, swimming ability, capture efficiency, size of prey fish eaten, metabolic requirements, food conversion efficiency, growth rates, spawning, sex ratio, and intraspecific behavioral interactions. Swimming ability of fish varies with size and species, and this is relevant to the distribution and movements of fish in John Day Reservoir—especially with respect to predators inhabiting the swift currents of McNary Dam tailrace. Poe et al. (1991) found prey size selectivity was related to predator size in John Day Reservoir. Food conversion efficiency and growth rates of fish generally decreased with size.

The northern squawfish was the only predator in John Day Reservoir for which the ration increased with fish size over almost the entire length range (Figure 3). This aspect of the consumption relations, in conjunction with the size structure of the population has important ramifications in the dynamics of predation in John Day Reservoir (Rieman and Beamesderfer 1990). The mean size of northern squawfish collected in McNary Dam restricted zone (997 g) was significantly greater ($P < 0.01$) than in the remainder of the John Day pool (772 g). The differential distribution of larger fish observed at McNary Dam is probably related to both swimming ability and size-related dominance feeding. Channel catfish are known to have a feeding hierarchy; in aquaculture, large fish are dominant at demand feeders and small fish have to wait (Randolph and Clemens 1976). Large channel catfish and possibly northern squawfish may be dominant over their smaller counterparts at prime feeding locations at McNary Dam.

Mean prey fish ration of walleye peaked at predator lengths of 200–300 mm (Figure 5); this is probably because walleyes are piscivorous at an early age and grow rapidly when young. Maintenance ration is independent of walleye weight over the range of 170–889 g (Kelso 1972), so the decreasing ration with size that we observed is probably related to the observed decreasing growth rates of older fish (P. J. Connolly and B. E. Rieman, Oregon Department of Fish and Wildlife, unpublished data). The ration of total prey fish and of

salmonids in smallmouth bass was highest at a length of 200 mm, and then declined. This observation is consistent with the size-specific consumption relations for largemouth bass, i.e., their maximum daily ration declined exponentially with predator weight (Niimi and Beamish 1974).

Diel Feeding Chronology

Several factors affect the time of day at which fish predators feed, including hunger and appetite, metabolic requirements, innate behavioral periodicity, optimization of sensory organs (e.g., vision), timing and intensity of light sources (e.g., sun, moon, and artificial light), other physical environmental factors (e.g., temperature, flow, turbidity), and factors in the biotic environment—especially prey availability. Keast and Welsh (1968) documented different diel feeding periodicities for different fishes (percids, centrarchids, and ictalurids). Thus, the observed diel feeding periodicity of predators in a given environment is probably a function of both innate behavioral patterns and the vulnerability of prey fish.

Northern squawfish have been described as sight feeders (Eggers et al. 1978); however, little information is available on detailed feeding behavior of northern squawfish or on their visual acuity as a function of light. We have observed that, under laboratory conditions, feeding activity was enhanced by low light levels (unpublished data). In two British Columbia lakes, northern squawfish feeding peaked in the hours of dusk and darkness (Steigenberger and Larkin 1974). The diel feeding activity we determined in John Day Reservoir indicated a pronounced difference in the feeding chronology between the McNary Dam restricted zone and the John Day pool. We hypothesize that this difference was at least partly due to differences in prey availability. On a daily basis, the consumption rates of northern squawfish in the McNary Dam restricted zone were related to smolt density (Vigg 1988).

The diel activity pattern of the prey fishes in John Day Reservoir is not well understood; however, some information on diel passage of juvenile salmonids through dams is available. Most (85–95%) of yearling chinook salmon and steelhead pass McNary Dam between dusk and dawn (Long 1968). Similarly, Johnson et al. (1986) found that usually 75–95% of the passage of salmonid smolts through turbines occurred at night at John Day Dam. Farther downriver at Bonneville Dam's first powerhouse, two peaks in salmon and steelhead smolt passage were observed: a minor mode after

dawn (0600–1000 hours) and a much stronger one at dusk (after 2000 hours; Gessel et al. 1986). Thus, the nocturnal mode in northern squawfish feeding we observed at McNary Dam restricted zone may be related to the increased availability of juvenile salmonids passing the dams during this period.

Another explanation for the nocturnal feeding mode of northern squawfish at McNary Dam may be that artificial lighting at the dam extends the "twilight" period for visual feeding and diminishes the nocturnal "cover" of the smolts. Low light conditions generally give sight-feeding predators an advantage over their prey (Howick and O'Brien 1983; Helfman 1986). Predation by Sacramento squawfish on chinook salmon smolts at the Red Bluff Diversion Dam, California, may have been reduced when dam lights were turned off (U.S. Fish and Wildlife Service, unpublished observations).

The daytime feeding of northern squawfish in the John Day Reservoir may reflect the diel feeding and activity pattern of both anadromous salmonid and resident juvenile prey fishes in the reservoir. From the results of concurrent sampling of the turbines at John Day Dam and diel purse seining in John Day Reservoir, it was concluded that the juvenile salmonids moved through John Day Reservoir during the daylight and passed dams at night (National Marine Fisheries Service, unpublished data). Juvenile salmonids may be more vulnerable to predation during the time of day when they are most actively feeding. Juvenile coho salmon in the coastal marine environment had food in their stomachs throughout the day, but fullness substantially increased in late afternoon and shortly after sunset (Brodeur and Pearcy 1987). Daytime feeding and associated increases in activity levels have been observed for a variety of juvenile fishes: largemouth bass (Elliot 1976); yellow perch and pumkinseed (Hansen and Leggett 1986); prickly sculpin (Rickard 1980). It is not clear how dam passage has affected diel migratory behavior of juvenile salmonids.

Walleyes are generally considered to be visual feeders, but they feed most actively in low light. The morphology of the retina in the walleye is adapted for functioning efficiently in low light (Ali and Anctil 1977). Mathias and Li (1982) characterized larval and juvenile walleyes as visual "strike" feeders whose feeding intensity was highest at dusk (2200 hours) and lowest at dawn (0400 hours). Adult walleyes are negatively phototactic and their daily movements are related primarily to levels of subsurface illumination (Marshall 1977;

Ryder 1977). The diel feeding periodicity we observed for walleyes in John Day Reservoir was bimodal, consisting of daytime and nocturnal feeding. Thus the innate pattern, related to functional morphology, may be moderated by environmental factors. In a previous study, walleyes in John Day Reservoir showed a consistent crepuscular pattern in the index of stomach fullness throughout the year; peaks were at sunrise (0600–0800 hours) and after sunset (2000–2200 hours) (Maule and Horton 1984). This chronology, however, did not account for differential seasonal digestion rates that would have enabled back-calculation of time when food items were ingested. The more variable diel chronology we observed was similar to that reported for walleyes by Swenson and Smith (1973). Walleye feeding pattern in Lake of the Woods was uniform throughout the diel period during June, but was consistently highest at night and in early morning (2000–0800 hours) during July–September; predominance of nocturnal feeding and species composition of prey showed that walleyes were pelagic feeders, especially in July and August (Swenson and Smith 1973; Swenson 1977).

The largemouth bass, which is primarily a sight feeder (Nyberg 1971), has two diel peaks of feeding activity (i.e., at dawn and dusk; Perez et al. 1985). Largemouth bass and smallmouth bass exhibited endogenous crepuscular activity rhythms under controlled laboratory conditions; smallmouth bass avoided bright light, and their activity peaked at the beginning and end of the dark periods (Reynolds and Casterlin 1976). In John Day Reservoir, smallmouth bass showed a crepuscular pattern, but it was not pronounced (i.e., an extended period of morning feeding was observed). This daytime feeding may be associated with prey availability; Stauffer et al. (1976) postulated that smallmouth bass activity and distribution were direct responses to forage fish movements. In Ontario lakes, smallmouth bass fed opportunistically during the day in shallow water, but peak feeding activity occurred at dusk and dawn; at night the fish moved into deeper water and were inactive, apparently resting (Emery 1973). Similarly, Cochran and Adelman (1982) observed a nocturnal decline in consumption rates of largemouth bass in a Minnesota lake.

Channel catfish, however, may feed both at night and during the day (Bailey and Harrison 1948), apparently feeding by both sight and taste. Our results showed that feeding of channel catfish peaked at dawn and to a lesser degree at dusk (on

both salmonid and non-salmonid prey). This crepuscular pattern suggests that light intensity and visual feeding may be important in regulating feeding activity of channel catfish in John Day Reservoir.

Total Daily Ration

Total daily food intake by fish is basic to their growth relations, to population energetics, and ultimately to ecosystem production. The range of variation in consumption rates (with respect to time, area, and predator size) that we quantified for the four fish predators in John Day Reservoir is consistent with previous determinations of comparable species. The mean seasonal ration of the four piscivores in John Day Reservoir ranged from 13 to 29 mg/g. Judging from previous estimates of daily ration for temperate-zone fishes (mean, 59 mg/g; range, 18–173 mg/g) given by Pandian and Vivekanandan (1985) our estimates are probably conservative on the low side. The seasonal mean daily ration of 14.1 mg/g that we estimated for northern squawfish in John Day Reservoir is within the range that Falter (1969) estimated for this species in the St. Joe River, Idaho, during summer (10.7–15.2 mg/g).

The overall seasonal daily ration of walleyes in John Day Reservoir (14.2 mg/g) was nearly equal to that of northern squawfish. The range of the mean monthly daily rations of walleyes in John Day Reservoir (2–40 mg/g) was similar to that estimated for walleyes in Lake of the Woods (8–31 mg/g) by Swenson and Smith (1973) and in Shagawa Lake and western Lake Superior (15–40 mg/g) by Swenson (1977); in those studies however, no samples were taken in spring when consumption rates were lowest in our study. The maximum we observed in July was consistent with that reported by Swenson (1977). In Lake of the Woods, Swenson and Smith (1973) observed maximum consumption by walleyes during August and September, but attributed it to prey density.

Kelso (1972) found that the assimilation efficiency of walleyes feeding on fish was very high (about 96%), was not affected by temperature, and was constant over a range of meal sizes (7–52 mg/g); however, it decreased linearly as predator weight increased and was lower (about 83%) for invertebrate food organisms with chitinous exoskeletons. Inasmuch as walleyes of all sizes in John Day Reservoir ate more than 99% fish, we infer that a high percentage of the food ingested is available

for energetic requirements of walleyes, but that this percentage decreases with age.

Smallmouth bass are highly piscivorous in John Day Reservoir and have the highest total daily ration, 28.7 mg/g; however, their rate of consumption of salmonids was very low. The higher daily ration of this species in John Day Reservoir may be a result of the size structure of the smallmouth bass population being much smaller than that of the other predators. The lack of predation on salmonids is consistent with long-term studies in an Ontario lake, which showed that smallmouth bass introductions have had no major effect on the salmonid community (Martin and Fry 1972).

The total daily ration of channel catfish in the McNary Dam restricted zone was composed of a larger proportion of fish (89%) than it was in the John Day pool (56%). This observation is consistent with the findings of Stevens (1959) that channel catfish were highly piscivorous in the tailrace of a South Carolina reservoir. The overall daily ration of channel catfish (12.6 mg/g) was similar to that of northern squawfish and walleyes.

Limitations of the Data and Consumption Estimate

Our study was based on physiological relationships of fish predators drawn from the literature and field sampling in John Day Reservoir during four field seasons (1983–1986). During these years, predator populations, prey fish abundances, predator diets, and environmental conditions were relatively homogeneous. In order to make inferences on areal, diel, monthly, and annual consumption estimates, we made several implicit assumptions: (1) fish capture methods (primarily electroshocking) provided a representative sample of predators (i.e., not biased by vertical or horizontal strata); (2) the predators sampled were representative of the population within a given area and time; (3) three consecutive sampling days were representative of a month within a given area; (4) 5 months (April–August) were representative of the entire juvenile salmonid out-migration; (5) the relatively small areas sampled were representative of much larger regions, and adequately described the entire reservoir; and (6) species-specific digestion rates determined under restricted laboratory conditions adequately described a wide range of natural conditions with almost infinite permutations of components of factors (e.g., temperature, fish physiology, fish size, diet, species composition, meal size). Furthermore, if one wants to make infer-

ences about other years or other reservoirs within the Columbia River system, additional, more tenuous assumptions must be made.

The main advantage of Swenson's (1972) technique is that it provides a fine-scale feeding chronology that is based both on a knowledge of the predators' digestion relations and on detailed site-specific stomach contents and environmental information. It has two principal disadvantages: (1) it is extremely labor-intensive to collect enough data on diel stomach contents over a sufficiently long time period to incorporate a range of environmental conditions, and (2) it is based on pooled stomach contents and consumption per average predator, so variances cannot be directly calculated for the estimate. Furthermore, although the variance in evacuation rate relations may be substantial, it is usually not quantified rigorously enough (especially with multivariate regressions) to be incorporated into the consumption estimate variance. An alternative method based on consumption per individual predator was developed by one of us (S.V.) to calculate the sample variance of the consumption estimates; this is presented in a companion paper in which salmonid losses to predation are estimated (Rieman et al. 1991).

Management Implications

The differences in consumption rates of the four major piscivores (in terms of size relations, diel, monthly, and spatial trends) suggest ways for managing the hydropower system, salmonid out-migrations, and fishery exploitation to ameliorate the losses of juvenile salmonids to predation in John Day Reservoir. Several aspects of northern squawfish consumption relations indicated that this species has a major predatory impact on juvenile salmonids: a high overall consumption rate; exceptionally high consumption rates in the McNary Dam restricted zone, where smolts are concentrated; highest monthly consumption during July, when smolt density is greatest; highest diel consumption during the night and early morning, concurrent with peak smolt migrations; and increasing daily ration with increasing predator size. Furthermore, the northern squawfish is the most abundant of the four predators studied (Beamesderfer and Rieman 1991). Thus we recommend that management actions be focused on northern squawfish, although predation by other species is also important and may be interactive with that by northern squawfish. Management options are discussed further by Rieman et al. (1991).

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