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PROBABLE CAUSES OF THE RAPID GROWTH AND HIGH FECUNDITY OF WALLEYE, *STIZOSTEDION VITREUM VITREUM*, IN THE MID-COLUMBIA RIVER[1]

The introduction of walleye, *Stizostedion vitreum vitreum*, into the Pacific Northwest of the United States is not documented; however, they are now found throughout the mid-Columbia River (Fig. 1) and downstream of Bonneville Dam (Durbin[2]). The construction of dams has transformed the Columbia River from a free-flowing river into a series of low water-velocity impoundments with physical characteristics (Table 1) that closely match the model for ideal walleye habitat proposed by Kitchell et al. (1977a).

We studied basic life history factors of mid-Columbia River walleye for 2 yr to determine how well these exotic predators have adapted to their new environment. We found that our walleye grew at a rate approaching the highest previously reported, that they were highly fecund, and that they matured at an early age. We evaluated these high growth and reproductive rates against environmental and genetic variables. We believe these data will help to identify the ever increasing role of walleye in the aquatic ecosystem of the Columbia River and similar river-reservoir systems.

[1]Technical paper no. 6723, Oregon Agricultural Experiment Station, Oregon State University, Corvallis, OR 97331.

[2]Durbin, K. 1977. News column. Oregon Department of Fish and Wildlife, P.O. Box 3503, Portland, OR 97208. Mimeogr., 3 p.

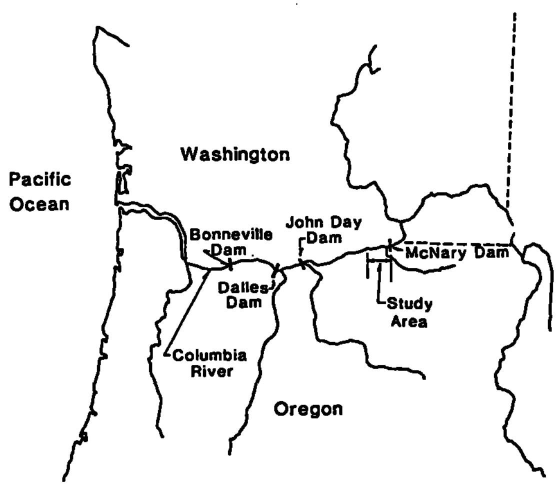

FIGURE 1.—Map of the lower and mid-Columbia River showing the locations of the major dams and the John Day pool study area where walleye were collected during 1980-81.

TABLE 1.—Summary of limnological data for the John Day pool of the Columbia River, from Hjort et al. (1981). All data collected in August 1979 except for surface temperatures, which were taken in 1981.

Characteristic	Range for John Day pool	Range for study area
Water velocity (m/s)	0.1-1.4	0.5-1.4
Secchi depth (m)	1.0-2.2	1.5-1.7
Dissolved O_2 (ppm)		
surface-bottom	16.0-8.0	14.0-10.0
Average surface temp.		
Apr.-July-Sept. (max.)	7.0°-24.5°-20.5°(24.8°)C	
Temperature profile		
surface-bottom	22.0°-20.8°C	21.0°-21.0°C
Pool width (km)	0.8-4.2	0.8-1.8
Mid-pool depth (m)	11-48	11-20
Pool length (km)	120	23

Methods

We collected walleye for this study in the first 23 km (tailrace) downstream of McNary Dam in the John Day pool of the Columbia River at lat. 45°55'N (Fig. 1). Walleye were collected from 2 April to 30 September 1980 and from 30 March to 30 September 1981. In 1980, we captured walleye with either a 38.1 × 1.8 m sinking gill net with 3.81, 5.08, 6.35, 7.52, and 10.16 cm variable stretch mesh, or a 76.2 × 3.7 m monofilament floating gill net with 15.25 cm stretch mesh. All gill net sets were of a maximum 2.5-h duration. In 1981 we used these gill nets and a 6.15 m electroshock boat with a 3,500-W generator and front-mounted electrodes, utilizing pulsed DC current of 1-4 A to capture walleye. Sampling was conducted in the day and night.

We recorded the fork length (FL, mm), weight (g), sex and whether or not the fish were sexually mature (Eschmeyer 1950), and removed a scale sample from beneath the tip of the left pectoral fin of each walleye. Many authors report difficulty using scales to determine the age of older walleye (Carlander and Whitney 1961; Campbell and Babaluk 1979); therefore, we took a subsample of sagitta (n = 86), which we preserved in 50:50 glycerine and water.

We mounted scales between two glass microscope slides and viewed them using a microfiche projector at 43×. We identified annuli using the criteria described by Carlander and Whitney (1961). We found that the easiest way to detect annuli on sagittae was to burn the whole otolith in a flame, immerse it in oil or alcohol, and examine it under a dissecting microscope. Reburning was often necessary until very distinct, dark annuli appeared. Christensen (1964) proposed a similar technique; however, he broke the burned otolith and examined the cross section. There was 92% agreement between at least one otolith reading and one scale reading so we terminated the collection of otoliths. We examined scales and otoliths twice and a person experienced in reading walleye scales (W. R. Nelson, U.S. Fish and Wildlife Service, Vancouver, WA) examined a subsample of scales (n = 63).

Age determinations for walleye collected in 1980 were based on either two scale readings, three scale readings, two scale readings and two otolith readings, or three scale readings and two otolith readings. All age determinations of walleye collected in 1981 were based on two scale readings. There was 90% agreement between at least two of the five possible age determinations for walleye collected in 1980, and 75% agreement between the two age determinations for walleye collected in 1981. After the final age determination, we measured the scale radius and scale length to each annulus (43×) at about 45° off of a straight line from the focus through the anterior field. In this area of the scale it was much easier to detect the annuli because of crowding and anastomosis of circuli in the lateral fields.

We back-calculated length at each annulus (i.e., year of life) assuming a straight line body-scale relationship (r^2 = 0.69) and using the Fraser-Lee method as recommended by Carlander (1982):

$$L_i = a + \frac{(L_c - a)}{S_c} S_i$$

where L_c = fish fork length at capture
L_i = calculated fork length at age i
S_c = scale radius at capture
S_i = scale measurement at annulus i
a = intercept of body-scale regression = 55 mm.

We converted these back-calculated fork lengths to total lengths (TL) using a conversion factor of 1.06 FL, which is the unweighted mean of the TL/FL relationships reported by Colby et al. (1979). This conversion allowed us to more easily compare our data with data from other areas.

During the spring 1981 spawning season, we removed the ovaries from 27 mature, but unspawned walleye. We preserved the ovaries in Bouin's solution and subsequently estimated the number of eggs by means of the gravimetric method recommended by Wolfert (1969). We performed regressions of life history characteristics by use of an interactive statistical computer program.

Results

We sampled over 250 walleye in each year, and they varied in length from 208 to 765 mm FL (220-810 mm TL) (Fig. 2). The weight (WT)/length (FL) relationship for 324 walleye was best described by the equation:

$$\text{Log}_e \text{WT} = -11.426 + 3.010 \text{Log}_e \text{FL} \ (r^2 = 0.966).$$

The slopes and intercepts of similar weight-length regressions for walleye collected in 1980 versus 1981 and males versus females were not significantly different ($F = 4.61$; $\alpha = 0.01$; df = 2; 247).

We had no difficulty detecting annuli in the scale samples from older walleye because of their rapid growth and apparently short life span (Table 2). Although females are larger than males in each year of life, the difference is not statistically significant until after the second year.

The mean fecundity of 27 walleye, between 520 to 764 mm FL and 1,720 to 5,905 g weight, was 82,900 eggs/kg body weight (Table 3). We found fecundity (FEC) linearly related to fish weight (WT):

$$\text{FEC} = -28{,}100 + 93.8 \text{ WT}, \quad r^2 = 0.969$$

and curvilinearly related to fork length (FL):

$$\text{Log}_e \text{FEC} = -8.4 + 3.2 \text{ Log}_e \text{FL}, \quad r^2 = 0.905.$$

A majority of males and females were mature by age III (Fig. 3); however, the maturity at fork length data show a more gradual increase than do the maturity

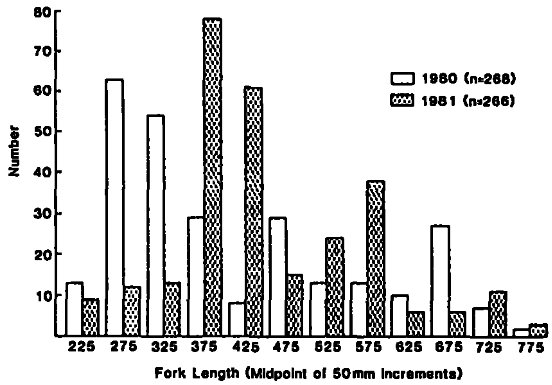

FIGURE 2.—Length-frequency distribution of walleye collected from the John Day pool of the Columbia River, April-September 1980-81.

TABLE 2.—Average back-calculated fork length (FL), SE, and annual growth increment for walleye collected in the John Day pool of the Columbia River, April-September 1980-81.

	Age							
	I	II	III[1]	IV[1]	V[1]	VI[1]	VII[1]	VIII
Males								
FL (mm)	241	363	434	484	533	562	596	
SE	2	3	6	7	9	10	7	
N (cumulative)	134	86	35	25	21	18	8	
increment (mm)	241	122	71	50	49	29	34	
Females								
FL (mm)	243	371	466	527	590	643	684	701
SE	2	3	4	4	5	5	6	11
N (cumulative)	197	150	122	95	69	57	28	8
increment (mm)	243	128	95	61	62	54	41	17
Combined[2]								
FL (mm)	244	368	458	515	575	623	664	701
SE	2	2	3	4	4	5	8	11
N (cumulative)	446	277	189	142	104	85	40	8
increment (mm)	244	124	90	57	60	8	41	37

[1]Females versus males significantly different, $P < 0.01$, Student's t-test.
[2]Includes some fish whose sex was not determined.

TABLE 3.—Fecundity of walleye from the John Day pool of the Columbia River, 30 March to 18 April 1981, compared with fecundities from Norris Reservoir, TN (Smith 1941), Lake Gogebic, MI (Eschmeyer 1950), and western Lake Erie (Wolfert 1969).

		Eggs/kg body weight[1]	
Location	*N*	Range[1]	Mean[1]
John Day pool	27	69,000-101,000	82,900 ± 1,550 (1SE)
Norris Reservoir		28,400-32,700	29,700
Lake Gogebic	34	57,900-67,800	61,800
Western Lake Erie	78	56,300-123,200	82,500

[1]Values converted from eggs/pounds body weight and rounded to nearest 100 eggs, except John Day pool.

data by age and, inexplicably, males were not 100% mature at any length (Fig. 3).

Discussion

The transplanted walleye population of the John Day pool of the Columbia River grows at a rate approaching the highest previously reported (Fig. 4). Concomitant with rapid growth these walleye are very fecund (Table 3) and mature at an early age (Fig. 3). We suggest that these life history characteristics result from the combination of a favorable temperature regimen and a nonlimiting food supply. High growth rates are generally found in walleye populations of more southerly latitudes where higher temperatures and longer growing seasons occur. Figure 4 contains data from Norris Reservoir, TN (Stroud 1949), Lake Gogebic, MI (Eschmeyer 1950), Lac la Ronge, Saskatchewan (Rawson 1957); as well as the composite high and low length-at-age values reported by Colby et al. (1979). Relative to the latitude of the John Day pool (lat. 45°55'N), Norris Reservoir is south (lat. 36°15'N), Lac la Ronge is north (lat. 55°07'N), and Lake Gogebic is at approximately the same latitude (lat. 46°47'N). The mean growing degree-days (GDD) above 5°C (GDD >5°C)

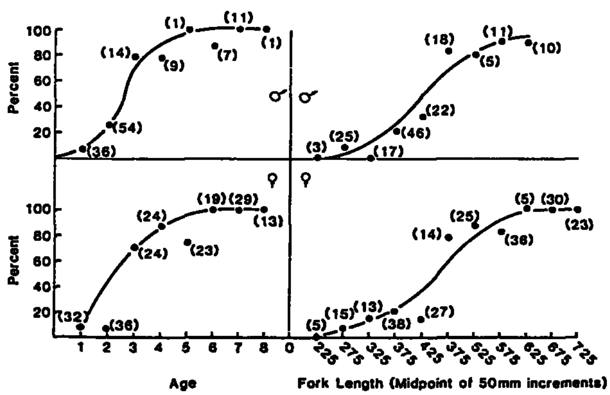

FIGURE 3.—Percent mature walleye by age and length and by sex for specimens collected in the John Day pool of the Columbia River, April-September 1980-81. Curves were drawn by eye. (Sample size in parentheses.)

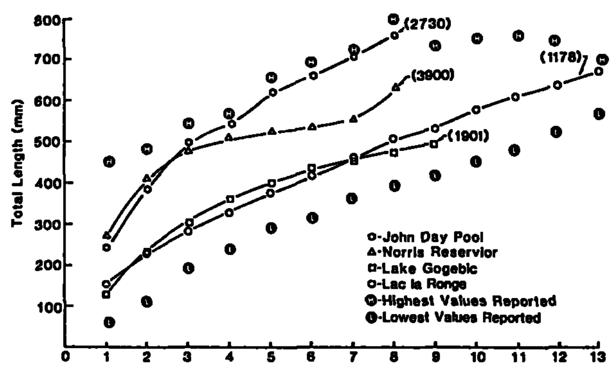

FIGURE 4.—Comparison of length-at-age for walleye from the John Day pool, Columbia River; Norris Reservoir, Tennessee (Stroud 1949); Lake Gogebic, Michigan (Eschmeyer 1950); Lac la Ronge, Saskatchewan (Rawson 1957) and the composite high and low values reported by Colby et al. (1979). Numbers in parentheses are the mean growing degree-days above 5°C, John Day value is from Anonymous (1969), all others are from Colby and Nepszy (1981).

(Colby and Nepszy 1981) for each area are included in Figure 4 as a measure of solar energy input to the system. Colby and Nepszy (1981) found that walleye growth was directly correlated to GDD >5°C and that the optimum range was from 2,500 to 4,000 GDD >5°C. While the GDD >5°C for the John Day pool is within this range, the walleye growth reported here is greater than would be predicted using this variable.

Water temperature may be the most important factor governing the growth of fishes (Brett 1979). Kitchell et al. (1977b) presented a bioenergetics model for walleye growth and indicated that thermal optima and maxima for weight specific consumption are 22°C and 27°C, respectively, and 27°C and 32°C, respectively, for weight specific respiration. Water temperatures in the John Day pool during the growing season remain at or near the thermal optimum for consumption and, perhaps more importantly, do not approach the thermal maxima for consumption or respiration (Table 1). Many northern lakes may not reach the thermal optima (Rawson 1957; Swenson 1977) and the southern lakes or lakes which stratify in the summer may exceed the thermal maxima (MacLean and Magnuson 1977) not only reducing consumption but increasing respiration. Dendy (1948) reported that in June 1944 the surface temperature of Norris Reservoir was about 30°C and that walleye appeared to prefer water temperature of about 24°C, even though these areas had oxygen concentrations <3.0 mg/L. Conversely, water temperature of Lac la Ronge did not exceed 20°C (Rawson 1957), well below the thermal optima.

Exceptions to the north-south trend in high walleye growth occur in systems of high exploitation (Forney 1965) and/or where there have been decreases in interspecific competition (Wolfert 1969; Forney 1977) which results in density dependent increases in growth rates. The quantity and quality of food are important factors in walleye growth (Kelso 1972; Kerr and Ryder 1977; Kitchell et al. 1977b) and fecundity (Colby and Nepszy 1981). Schupp (1978) looked at the growth of walleye from several areas within Leech Lake, MN, and found food of walleye from areas of highest average growth was almost totally young-of-the-year yellow perch, whereas small walleyes from slow growth areas had eaten mostly invertebrates and small minnows. We have found (Maule and Horton 1984) that about 99% by volume of Columbia River walleye stomach contents were fish (e.g., sculpins, suckers, cyprinids) and that 61% of walleye sampled contained food. Eschmeyer (1950) reported that 89% of the volume of stomach contents from Lake Gogebic walleye was fish, but he did not report percent empty stomachs. Dendy (1946) reported that Norris Reservoir walleye stomachs contained 99% fish by volume, but only 45% of the walleye examined contained food. Rawson (1957) studied Lac la Ronge walleye and reported that fish comprised 97% of the volume of stomach contents and that 39% of the walleye stomachs contained food.

Colby and Nepszy (1981) stated that age to maturity is indirectly correlated to growth, but that fecundity is probably a function of population density and food availability. They further suggested that the wide variability in walleye fecundities is a mechanism by which walleye can adjust production in response to environmental conditions. Table 3 includes fecundity data from Norris Reservoir (Smith 1941), Lake Gogebic (Eschmeyer 1950), and western Lake Erie (Wolfert 1969). Based on a comparison of growth, stomach content analysis, and fecundity, the mid-Columbia River walleye have a more favorable food supply than the other areas considered here.

Hackney and Holbrook (1978) suggested that there is a southern race of walleye that is characterized by rapid, large growth and short life span, and a northern race characterized by slow growth and long life span. They suggested that the pattern of rapid walleye growth seen after the impoundment of southern waters, followed by decreased growth rates some years later is due to a shift from the southern race to the northern race as the result of walleye stocking programs. The movements of young-of-the-year walleye downstream past Columbia River dams has been documented (Brege 1981). Assuming that this is a means by which walleye have colonized the Columbia River, it is biologically similar to impounding waters already containing walleye populations, in that new habitat is available for population growth. Although we cannot discount the possibility that the extreme life history characteristics reported here are the result of genetic stock differences, we suggest that they can more reasonably be explained by a favorable temperature regimen and an abundant, high quality food supply.

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