

ASPECTS OF THE LIFE HISTORY AND FEEDING ECOLOGY
OF WALLEYE (STIZOSTEDION VITREUM VITREUM)
IN THE MID-COLUMBIA RIVER

by

Alec G. Maule

A THESIS

Submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Completed December 3, 1982

Commencement June 1983

APPROVED:

Redacted for privacy

Professor of Fisheries in charge of major

Redacted for privacy

Head of Department of Fisheries and Wildlife

Redacted for privacy

Dean of Graduate School

Date thesis is presented December 3, 1982

Typed by LaVon Mauer for Alec G. Maule

ACKNOWLEDGMENTS

I wish to thank Cris Stainbrook, Patrick Hulett, Randy Hjort, Bruce Mundy and Larry La Bolle for their assistance in the field, Richard Carmichael for identifying invertebrates, and Ryan Maule for preparing the figures. Special appreciation goes to Judith and Amy Maule, my wife and daughter for their financial and emotional support. Funding for this research was provided by the United States Army Corps of Engineers Contract DACW57-79-0067 and the Milne Computer Center, Oregon State University, Corvallis, Oregon.

TABLE OF CONTENTS

	<u>Page</u>
Introduction	1
Feeding Ecology	2
Abstract	2
Introduction	3
Methods	6
Results	8
Discussion	17
Life History	22
Abstract	22
Introduction	22
Methods	23
Results	26
Discussion	31
References	36
Appendices	40

LIST OF FIGURES

<u>Figure</u>		<u>Page</u>
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 1980-1981.	4
2.	Length frequency distribution of walleye collected from the John Day pool of the Columbia River, April-September, 1980-1981.	9
3.	Percent change in Index of Relative Importance (IRI) (Pinkas et al. 1971) of various prey items found in walleye stomachs. Positive or negative value indicates an increase or decrease in IRI from spring to summer, 1980 (top) or from summer, 1980 to summer, 1981 (bottom).	14
4.	Index of fullness and numbers of juvenile salmonids and shad consumed per walleye captured during 2-hr intervals. Data collected from the John Day pool of the Columbia River, April-September, 1980 and 1981. (Sample size in parentheses.)	16

5. Change in percent of total Index of Relative Importance (IRI) (Pinkas et al. 1971) of prey with change in walleye fork length. Walleye collected in the John Day pool of the Columbia River, April-September, 1980-1981. (Sample size in parentheses.) 18

6. Length frequencies of potential walleye prey collected in the John Day pool of the Columbia River, April-September, 1981. (Sample size in parentheses.) 19

7. Percent mature walleye by age and length and by sex for specimens collected in the John Day pool of the Columbia River, April-September 1980-1981. Curves were drawn by eye. (Sample size in parentheses.) 30

8. 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). 32

LIST OF TABLES

<u>Table</u>		<u>Page</u>
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.	5
2.	Percent by volume, percent by number and percent frequency of occurrence of food items found in the stomachs of walleye collected in the John Day pool of the Columbia River, April-September, 1980. Sample size equals 189 walleye, with 38.1% empty stomachs. (Raw data are in parentheses.)	10
3.	Percent by volume, percent by number and percent frequency of occurrence of food items found in the stomachs of walleye collected in the John Day pool of the Columbia River, April-September, 1981. Sample size equals 236 walleye, with 39.0% empty stomachs. (Raw data are in parentheses.)	11
4.	Catch-per-unit effort (CPUE) for various juvenile (Juv) and adult fishes caught in the John Day pool of the Columbia River, April-September, 1980-1981.	13
5.	Average backcalculated fork length (FL), SE, and annual growth increment for walleye collected in the John Day pool of the Columbia River, April-September, 1980-1981.	28

6. Fecundity of walleye from the John Day pool of the Columbia River, March 30 to April 18, 1981, compared to fecundities from Norris Reservoir, Tennessee (Smith 1941), Lake Gogebic, Michigan (Eschmeyer 1950), and western Lake Erie (Wolfert 1969).

ASPECTS OF THE LIFE HISTORY AND FEEDING ECOLOGY OF WALLEYE
(Stizostedion vitreum vitreum) IN THE MID-COLUMBIA RIVER

INTRODUCTION

The walleye (Stizostedion vitreum vitreum) is a highly piscivorous, coolwater fish whose native range centers in the Great Lakes region (Scott and Crossman 1973). Little is known about the walleye's introduction into the Columbia River, but they are now found throughout most of the length of the river. In recent years, interest has focused on the potential sport fishery for walleye and on the impact of walleye on native salmonid populations.

In this thesis, I report on a study of walleye captured in the John Day pool of the Columbia River and present my findings in the form of two manuscripts. The manuscripts contain data on the feeding ecology and life history of walleye, independently, and have been prepared for submission to the Transactions of the American Fisheries Society. Out of necessity, there is some redundancy in the two manuscripts, particularly in their introduction and methods sections. In using this format, my intent is to provide a concise presentation of the data and conclusions of my study.

FEEDING ECOLOGY OF WALLEYE (Stizostedion vitreum vitreum)
IN THE MID-COLUMBIA RIVER, WITH EMPHASIS ON THE INTERACTIONS
BETWEEN WALLEYE AND JUVENILE ANADROMOUS FISHES¹

Alec G. Maule

Oregon Cooperative Fisheries Research Unit

Department of Fisheries and Wildlife, Oregon State University

Howard F. Horton

Department of Fisheries and Wildlife, Oregon State University

Corvallis, Oregon 97331

ABSTRACT

Annual and seasonal variation in diet, diel feeding periodicity and prey size selectivity of walleye (Stizostedion vitreum vitreum) in the John Day pool of the Columbia river were studied in the spring and summer of 1980 and 1981. All walleye were captured by either gillnet or electroshock methods. Members of Cottidae, Catostomidae and Cyprinidae were of primary dietary importance to walleye, and young-of-the-year (YOY) salmonids and YOY shad (Alosa sapidissima) were of secondary, seasonal dietary importance. Seasonal appearance and annual changes in the abundances of YOY prey fishes contributed to the annual and seasonal variation in diet. Walleye in this study were

¹ Technical Paper No. _____, Oregon Agricultural Experiment Station.

crepuscular feeders, but YOY salmonids and YOY shad were primarily consumed from late night to midday. An abundance of alternate prey and advantageous behavioral responses to dimming light appear to buffer juvenile anadromous fishes from walleye predation.

INTRODUCTION

The walleye (Stizostedion vitreum vitreum) is widely distributed in the United States and Canada and has been studied throughout most of its native range (Colby et al. 1979). The walleye is exotic to the Pacific northwest and its biology here has not been fully investigated. The exact circumstances of the walleye introduction into the Columbia River system are not documented; however, this piscivorous, coolwater fish is found throughout the mid-Columbia River (Fig. 1) and downstream of Bonneville Dam (Durbin²). As the populations of walleye in the Columbia River have increased, interest in them has focused on the potential sport fishery for walleye and on the impact of walleye on native salmonid populations (Carlander et al. 1978; Brege 1981).

The construction of dams has transformed the Columbia River into a series of low velocity impoundments with physical characteristics (Table 1) which are well suited for walleye (Colby et al. 1979). Thus, the Columbia River fits the model for ideal walleye habitat proposed by Kitchell et al. (1977a). This same transformation has

² Durbin, K. 1977. News column. Oregon Department of Fish and Wildlife, Portland, Oregon, USA.

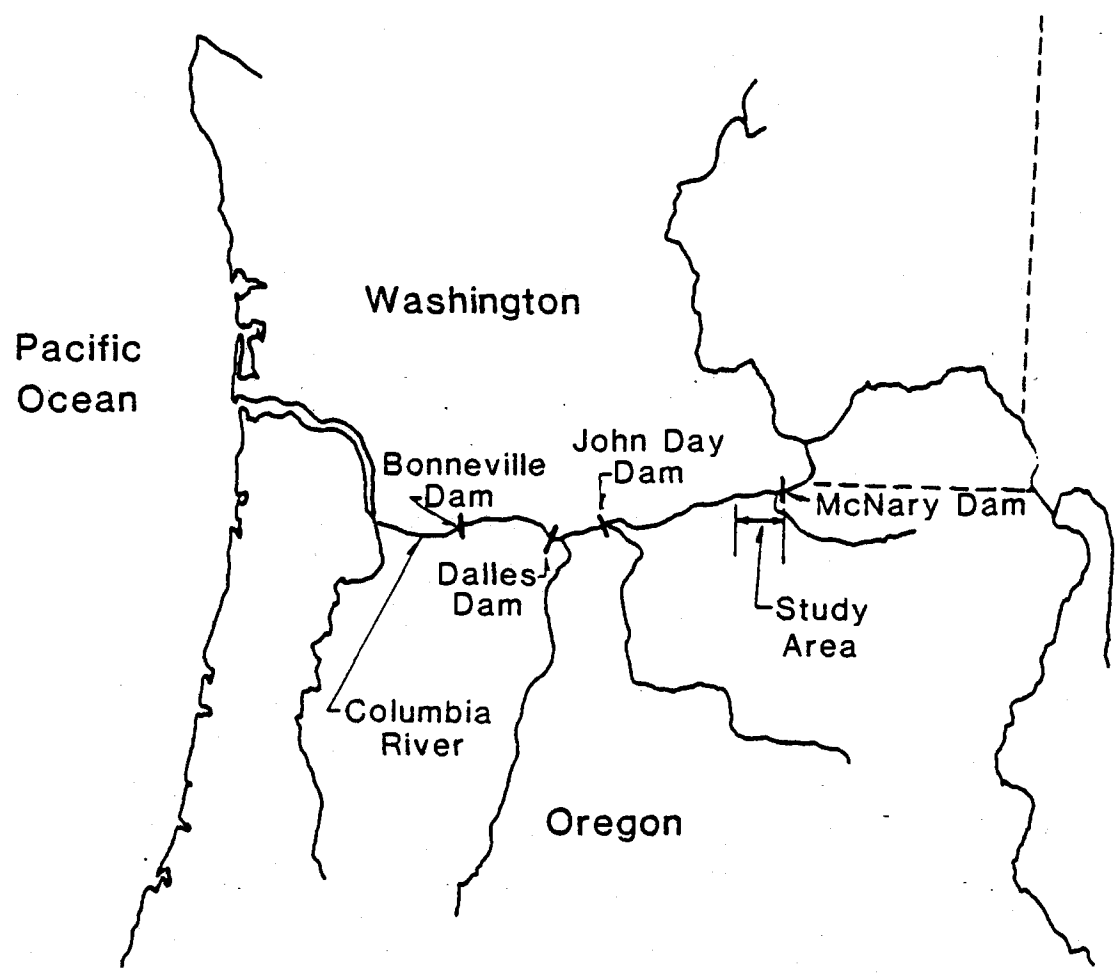


Figure 1. Map of the lower and mid-Columbia River showing the locations of the major dams and the John Day pool study area where walleye were collected during 1980-1981.

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/second)	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 temperature Apr-Jul-Sep (maximum)	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

increased the time required for juvenile salmonid outmigration and increased outmigrant mortality due, in part, to increased predation (Raymonds 1979).

The purpose of this study was to describe the feeding ecology of walleye in the John Day pool of the Columbia River. Emphasis was placed on walleye interaction with young-of-the-year (YOY) salmonids and YOY American shad (Alosa sapidissima), an anadromous fish which is morphologically and behaviorally similar to outmigrant salmonids and is abundant in the Columbia River in the late summer. We specifically looked at annual and seasonal variation in the importance of food items in the walleye diets, diel feeding periodicity, and variation in the importance of food items based on walleye size. This information will benefit resource agency personnel when they make management decisions concerning walleye and anadromous fish populations in the Columbia River.

METHODS

We collected walleye for this study in the first 23 km of the John Day pool immediately downstream of McNary Dam on the Columbia River (Fig. 1). We sampled walleye from 2 Apr to 30 Sep 1980 and from 30 Mar to 30 Sep 1981. During each month we attempted to collect a minimum of 10 walleye during each of four generalized times of day: dawn, midday, dusk and night. In 1980 we captured walleye in either a 38.1- x 1.8-m sinking gillnet with multifilament, variable, stretch mesh of 3.81, 5.08, 6.35, 7.52 and 10.16 cm, or a 76.2- x 3.7-m monofilament, floating gillnet with 15.25-cm stretch mesh. All

gillnet sets were for a maximum of 2.5 hour duration to minimize regurgitation or digestion of stomach contents. In 1981 we used gillnets and a 6.15-m electroshock boat with a 3500 watt generator and front mounted electrodes utilizing pulsed D.C. current at 1-4 A. Potential prey fish were periodically sampled with a 30.48- x 2.44-m beach seine with 6.35-mm stretch mesh. Whenever potential prey were caught using gillnets, seines or electroshock gear, we recorded numbers and fork lengths by species. Due to gear selectivity, not all prey are adequately represented nor can these data be used to estimate interspecific relative abundances. We do, however, use catch per unit of effort (CPUE) data as indices of change in intraspecific abundance through time.

We recorded the fork length (FL, mm), weight (g), sex and stage of maturity for each walleye captured. We took scale samples and then removed the stomach which was preserved in 10% buffered Formalin. At a later date, each stomach was examined and each prey item was identified to the lowest possible taxon and its volume was recorded. To aid in the identification of partially digested prey we used a bone collection of potential prey species. The most useful bones were pharyngeal teeth, opercles, pre-opercles and jaw bones. Characteristics of the internal morphology, e.g., the black peritonium of bridgelip suckers (Catostomus columbianus) or the number of phloric caeca in salmonids (Scott and Crossman 1973), were also useful in identifying prey items.

Stomach content data were separated into a variety of sub-populations and tested for statistically significant differences

in both numbers and volumes of individual prey items. Statistical significance was computed using a nonparametric, multivariate test, $L_{N,t}$, which has approximately a Chi-squared distribution with $p(v-1)$ degrees of freedom, where p is the number of conditions (prey taxa) and v is the number of populations (Koch 1969). To identify changes in the importance of food items we examined changes in the Index of Relative Importance (IRI) which is equal to the sum of the percent by volume and the percent by number, multiplied by the percent frequency of occurrence (Pínkas et al. 1971).

RESULTS

Annual and Seasonal Diet

The walleye size ranges were similar for both years, approximately 200-750 mm FL, and all size groups were well represented (Fig. 2). Tables 2 and 3 contain a listing of the food items found in walleye stomachs in 1980 and 1981, respectively. In both years fish accounted for over 99% of the total prey volume. Although invertebrates represented 4-13% of the numbers of prey items, they contributed little to the total caloric intake of the walleye because of their almost negligible volume. The single most important dietary item was the prickly sculpin (Cottus asper), followed by the largescale sucker (Catostomus macrocheilus), and bridgelip sucker, and the cyprinids, primarily chiselmouth (Acrocheilus alutaceus) and peamouth (Mylocheilus caurinus). All of these species are generally associated with the benthos (Scott and Crossman 1973; Wydoski and Whitney 1979).

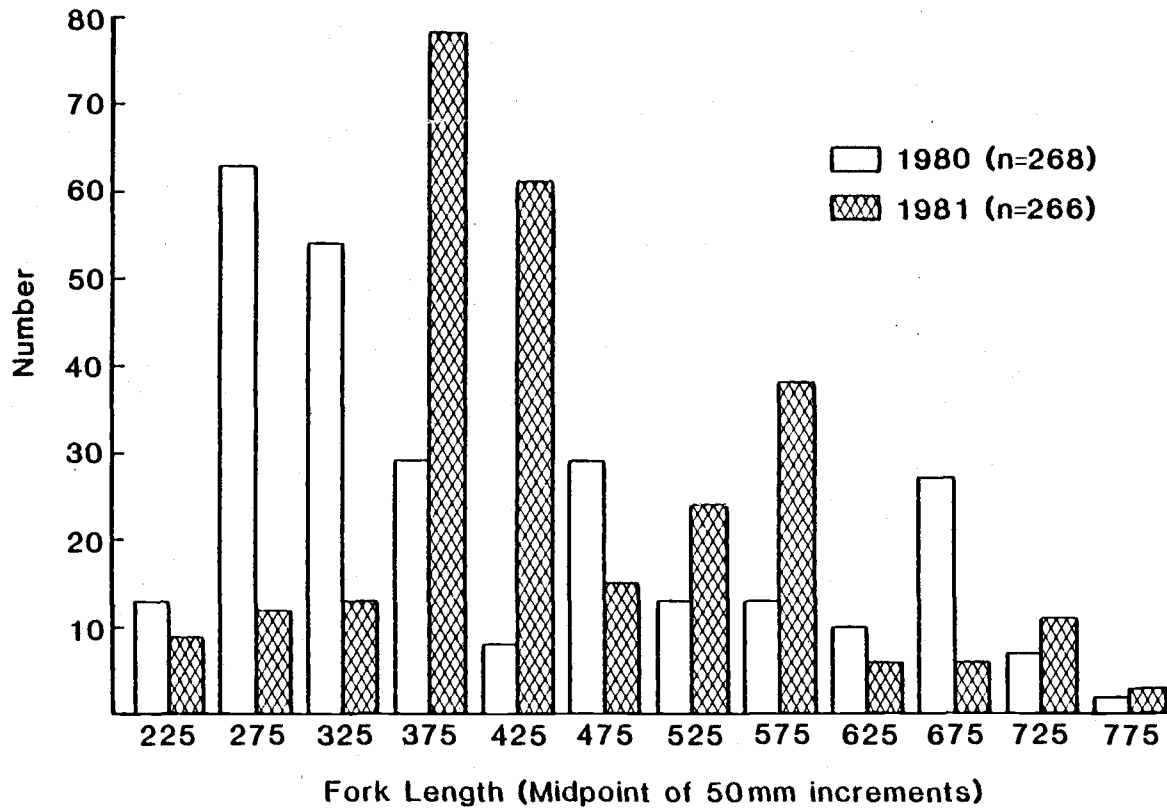


Figure 2. Length frequency distribution of walleye collected from the John Day pool of the Columbia River, April-September, 1980-1981.

Table 2. Percent by volume, percent by number and percent frequency of occurrence of food items found in the stomachs of walleye collected in the John Day pool of the Columbia River April-September, 1980. Sample size equals 189 walleye, with 38.1% empty stomachs. (Raw data are in parentheses.)

Prey Taxon	% Volume (ml) ^a	% Number ^a	% Occurrence
Salmonidae (juvenile)	5.5 (89)	8.7 (22)	12.8 (15)
<u>Oncorhynchus tshawytscha</u>	1.7 (27)	2.7 (7)	8.5 (10)
Unidentifiable Salmonidae	3.8 (62)	6.0 (15)	4.3 (5)
Catostomidae	39.4 (638)	6.0 (15)	12.0 (14)
<u>Catostomus columbianus</u>	7.3 (118)	2.0 (5)	4.3 (5)
<u>C. macrocheilus</u>	12.8 (200)	1.2 (3)	2.6 (3)
Unidentifiable Catostomidae	19.3 (320)	2.8 (7)	5.1 (6)
Cyprinidae	15.2 (247)	5.6 (14)	12.0 (14)
<u>Acrocheilus alutaceus</u>	2.2 (36)	3.2 (8)	6.8 (8)
<u>Mylocheilus caurinus</u>	11.8 (192)	1.2 (3)	2.6 (3)
<u>Ptychocheilus oregonensis</u>	0.4 (6)	0.4 (1)	0.9 (1)
Unidentifiable Cyprinidae	0.8 (13)	0.8 (2)	1.7 (2)
Miscellaneous fishes	40.0 (646)	75.4 (190)	85.6 (101)
<u>Cottus asper</u>	33.7 (544)	30.6 (77)	32.5 (38)
<u>Lampetra spp.</u>	0.1 (2)	0.4 (1)	0.1 (1)
<u>Alosa sapidissima</u> (juvenile)	1.9 (30)	9.9 (25)	7.7 (9)
Unidentifiable	4.3 (70)	34.5 (87)	45.3 (53)
Invertebrates	0.04 (0.7)	4.4 (11)	7.7 (9)
Ephemeroidea	0.03 (0.56)	2.4 (6)	5.1 (6)
Chironomidae	<0.01 (0.04)	1.2 (3)	0.9 (1)
Talitridae	<0.01 (0.05)	0.4 (1)	0.9 (1)
Gammaridae	<0.01 (0.05)	0.4 (1)	0.9 (1)

^aVolumes and numbers of individual prey taxa were significantly different from those of 1981 (P < 0.005).

Table 3. Percent by volume, percent by number and percent frequency of occurrence of food items found in the stomachs of walleye collected in the John Day pool of the Columbia River, April-September, 1981. Sample size equals 236 walleye, with 39.0% empty stomachs. (Raw data are in parentheses.)

Prey Taxon	% Volume (ml) ^a	% Number ^a	% Occurrence
Salmonidae (juvenile)	3.6 (62)	4.4 (14)	7.0 (10)
<u>Oncorhynchus tshawytscha</u>	2.8 (48)	3.2 (10)	1.4 (2)
Unidentifiable Salmonidae	0.8 (14)	1.2 (4)	5.6 (8)
Catostomidae	32.5 (563)	11.4 (36)	18.1 (26)
<u>Catostomus columbianus</u>	11.6 (201)	2.5 (8)	4.2 (6)
<u>C. macrocheilus</u>	1.2 (21)	0.6 (2)	1.4 (2)
Unidentifiable Catostomidae	19.7 (321)	8.3 (26)	12.5 (18)
Cyprinidae	34.1 (590)	13.0 (41)	25.7 (37)
<u>Acrocheilus alutaceus</u>	28.3 (490)	5.7 (18)	11.1 (16)
<u>Mylocheilus caurinus</u>	1.8 (32)	2.5 (8)	5.6 (8)
<u>Ptychocheilus oregonensis</u>	1.7 (30)	1.6 (5)	2.8 (4)
<u>Cyprinus carpio</u>	0.3 (6)	0.3 (1)	0.7 (1)
<u>Carassius auratus</u>	0.5 (8)	0.6 (2)	1.4 (2)
Unidentifiable Cyprinidae	1.5 (24)	2.3 (7)	4.1 (6)
Miscellaneous fishes	29.3 (508)	58.2 (184)	77.8 (112)
<u>Cottus asper</u>	22.5 (390)	25.6 (81)	36.8 (53)
<u>Aloa sapidissima</u> (juvenile)	0.1 (1)	0.3 (1)	0.7 (1)
Ictaluridae	0.2 (4)	0.3 (1)	0.7 (1)
Unidentifiable	6.5 (113)	32.0 (101)	39.6 (57)
Invertebrates	0.5 (8.23)	13.0 (41)	11.1 (16)
Ephemeroidea	0.3 (5.98)	12.0 (38)	10.4 (15)
Chironomidae	0.01 (0.20)	0.3 (1)	0.7 (1)
Gammaridae	<0.01 (0.05)	0.3 (1)	0.7 (1)
Astacidae	0.1 (2.00)	0.3 (1)	0.7 (1)

^a Volumes and numbers of individual prey taxa were significantly different from those of 1980 (P < 0.005).

YOY salmonids, primarily chinook salmon (Oncorhynchus tshawytscha), and YOY American shad were of secondary, seasonal importance.

All statistical tests were conducted with prey items at the lowest possible taxa; however, for simplicity we will discuss the results based on the following groups: suckers, cyprinids, salmonids, sculpin and shad. The numbers and volumes of individual prey were significantly different between 1980 and 1981 ($P < 0.005$) and to further investigate these differences we tested for seasonal variation within and between years. We found no significant dietary difference between spring (April-June) 1980, and spring 1981 ($P > 0.25$); however, there were significant differences in diets between summer (July-September) 1980 and summer 1981 ($P < 0.05$), and between the spring and summer of each year ($P < 0.01$). The seasonal changes in 1980 and changes from summer 1980 to summer 1981 are shown in Figure 3. The percent change in the IRI is scaled from -100.0% to +100.0%; negative values indicate reduced importance and positive values indicate increased importance. The percent change in the IRI indicates the magnitude of change in importance and not the relative importance of prey categories. The CPUE data (Table 4) reflects large annual and seasonal differences in the abundance of YOY chinook and YOY shad, and seasonal differences in YOY peamouth, which can account for the percent change in the IRI's of these groups (Fig. 3). Unfortunately sculpins, the most important dietary item, were very rare in the CPUE data for 1980 and, in 1981 the electroshock CPUE was less than 0.1, a level too low to detect changes. Therefore, we cannot explain the seasonal change in the dietary importance of sculpin.

Table 4. Catch-per-unit effort (CPUE) for various juvenile (Juv) and adult fishes caught in the John Day pool of the Columbia River, April-September, 1980-1981.

Dates	Seines			
	Effort	CPUE		Juv peamouth
	Sets	Juv chinook	Juv shad	
Apr-Jun 1980	45	16.65	0	0
Apr-Jun 1981	37	10.70	0	0
Jul-Sep 1980	35	2.65	92.76	6.88
Jul-Sep 1981	39	1.36	42.87	5.77

Dates	Gillnets			
	Hours	Chiselmouth	Largescale sucker	Bridgelip sucker
Apr-Jun 1980	122	0.23	0.86	0.40
Apr-Jun 1981	212	0.32	0.90	0.67
Jul-Sep 1980	330	0.37	0.54	0.74
Jul-Sep 1981	154	0.31	0.84	0.61

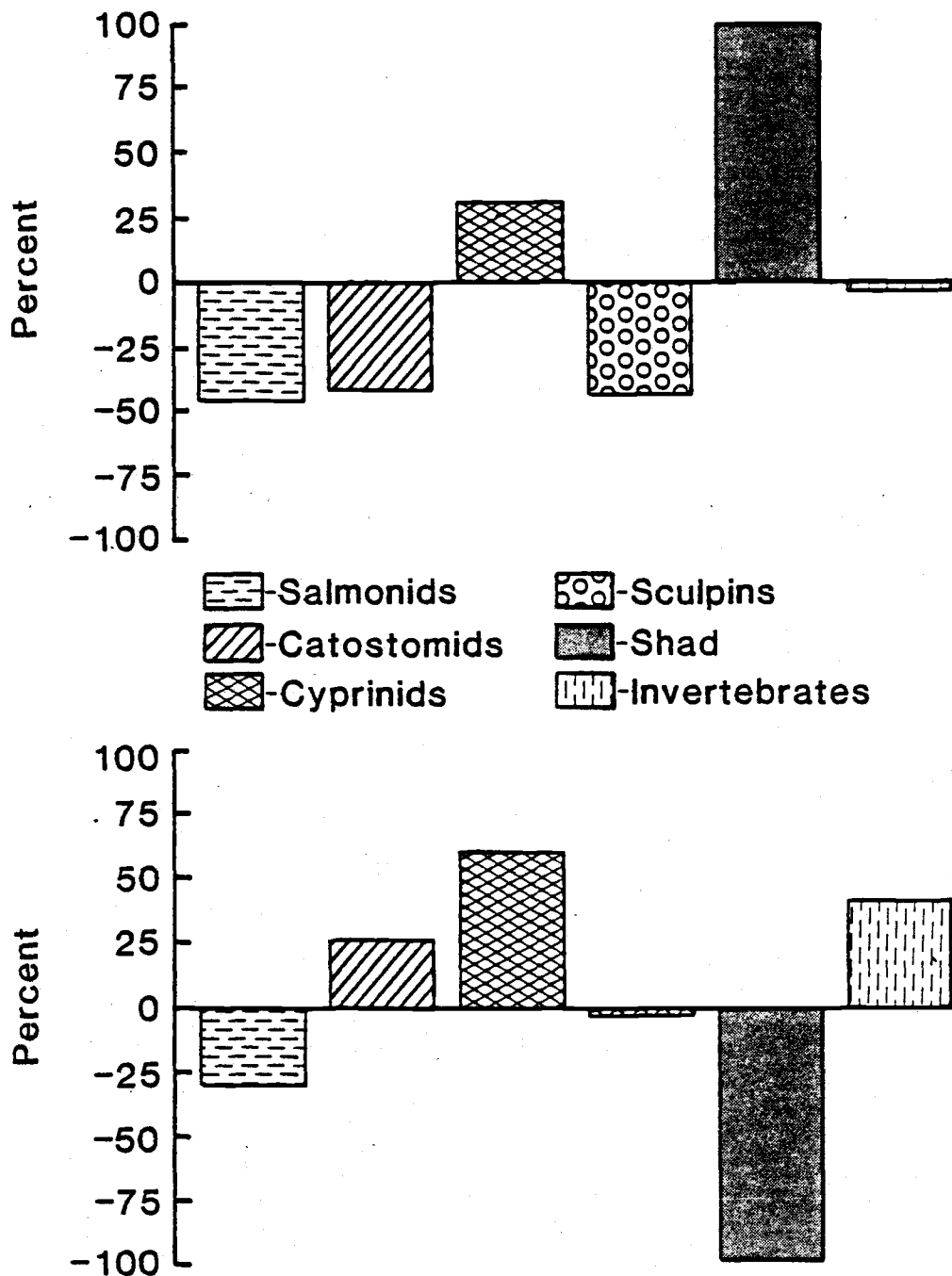


Figure 3. Percent change in Index of Relative Importance (IRI) (Pinkas et al. 1971) of various prey items found in walleye stomachs. Positive or negative value indicates an increase or decrease in IRI from spring to summer, 1980 (top) or from summer, 1980 to summer, 1981 (bottom).

Seasonal shifts in walleye diets are often the result of high spring-time availability of aquatic insects and/or increased availability of YOY prey fish in the summer (Eschmeyer 1950; Parsons 1971). In this study, invertebrates are of tertiary dietary importance (Table 2 and 3) and do not exhibit significant seasonal variation in dietary importance (Fig. 3). Our data suggests no change in the abundances of adult suckers and cyprinids (chiselmouth), therefore we believe that the dietary variations are the result of the changes in the availability of YOY prey fish.

Diel Periodicity

The mean index of fullness, measured as the volume of stomach contents (ml) divided by walleye body weight (kg), for all walleye sampled is plotted against time of capture (2-hour intervals) in Figure 4. The shape of this curve suggests the same bimodal feeding periodicity as reported for other walleye populations during times of high prey densities (Swenson 1977). We found no annual or seasonal variation in this periodicity. The numbers of YOY salmonids and YOY shad consumed per walleye at various times of the day peaks from late night to midmorning then drops to a low level at midday and remains low through the evening peak in walleye feeding. We believe that behavioral mechanisms may reduce the availability of YOY salmonids and YOY shad at dusk.

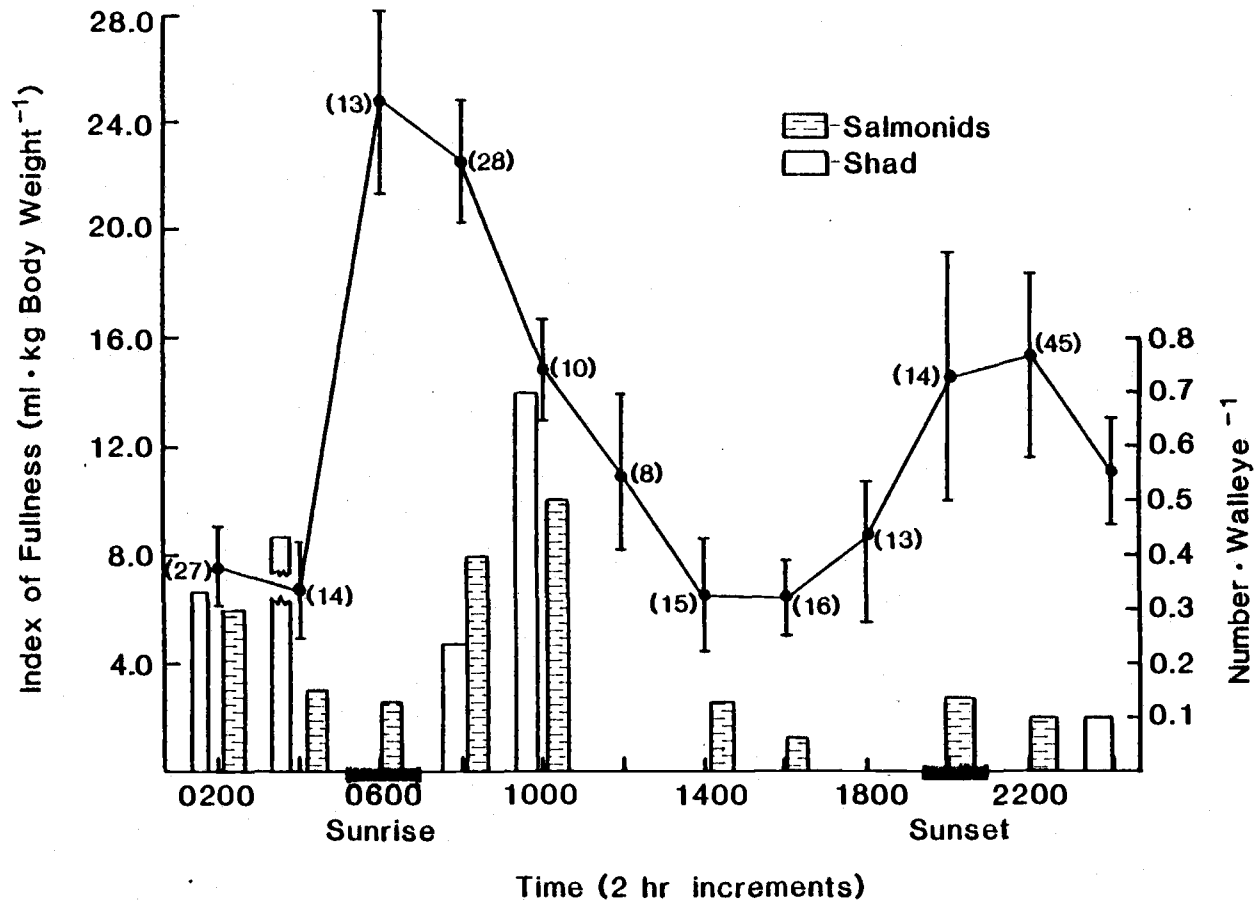


Figure 4. Index of fullness and numbers of juvenile salmonids and shad consumed per walleye captured during 2-hr intervals. Data collected from the John Day pool of the Columbia River, April-September, 1980 and 1981. (Sample size in parentheses.)

Size of Prey Consumed

Parsons (1971) showed a positive relationship between walleye length and length of prey consumed in Lake Erie. Walleye in the mid-Columbia River exhibit the same relationship and size of prey is correlated to different prey taxa. The change in the percent of the IRI of various prey groups, as a function of walleye fork length is charted in Figure 5. Small walleye (200-400 mm FL) primarily consume salmonids, sculpins and shad, while midrange walleye (400-600 mm FL) rely more heavily on cyprinids, sculpins and suckers. For large walleye (>600 mm FL), suckers are the most important prey and the importance of cyprinids and sculpins is reduced. Figure 6 contains the length frequencies of walleye prey collected in 1981, and shows peaks which correspond to the size of walleye most likely to consume that prey, i.e. sculpin, YOY shad and YOY salmonids are small (25-125 mm FL), cyprinids are midrange in length (125-300 mm FL) and suckers are present in a large range of sizes (150-450 mm FL) with peaks > 300 mm FL.

DISCUSSION

The walleye has been described as an opportunistic (Eschmeyer 1950; Ryder and Kerr 1978), crepuscular or nocturnal feeder which primarily searches the bottom for prey (Ali et al. 1977; Ryder 1977) and, in areas of abundant prey, selects food items based on size preference (Parsons 1971; Wagner 1972). The walleye of the mid-Columbia River fits this general description; however, the species

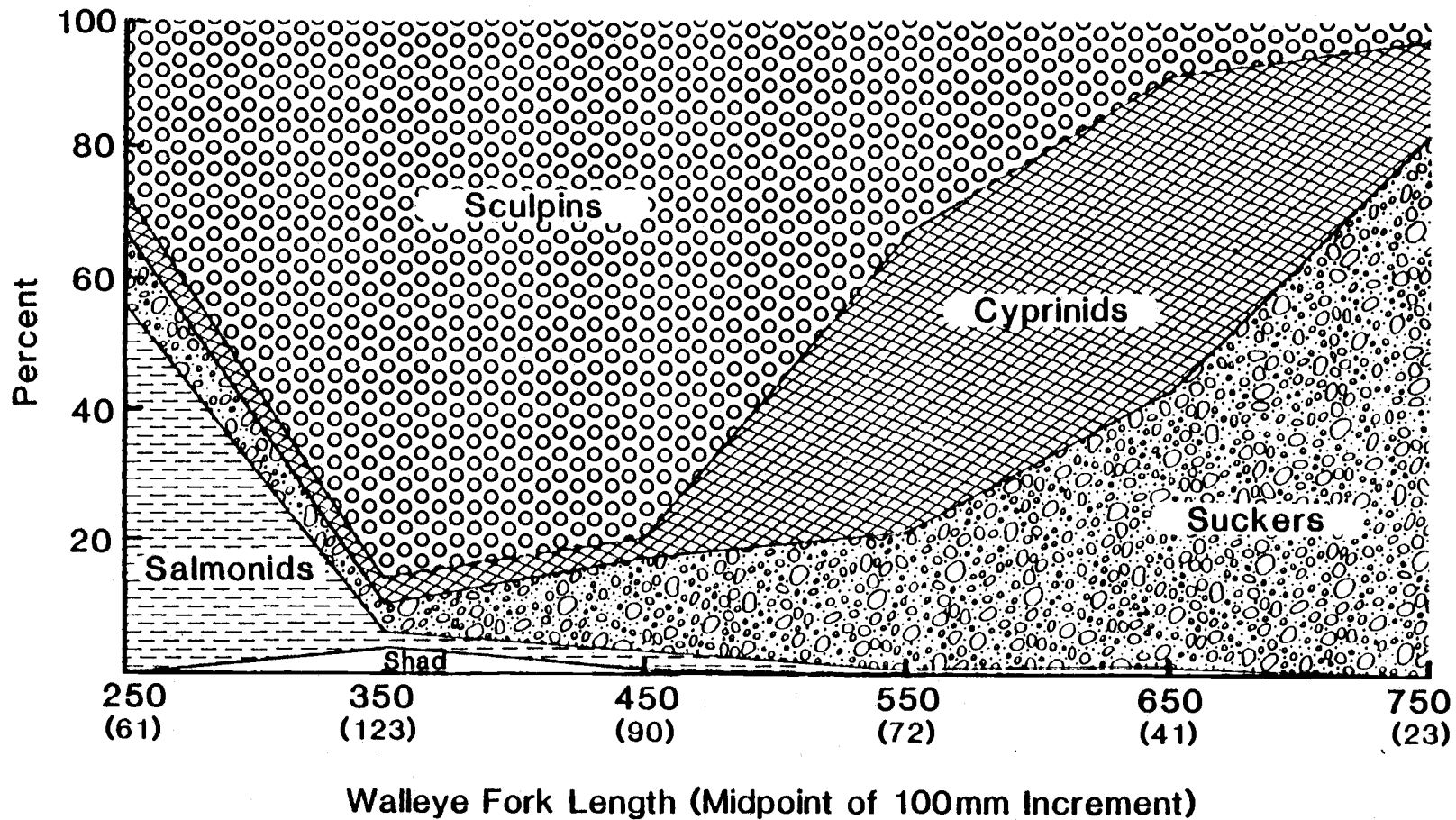


Figure 5. Change in percent of total Index of Relative Importance (IRI) (Pinkas et al. 1971) of prey with change in walleye fork length. Walleye collected in the John Day pool of the Columbia River, April-September, 1980-1981. (Sample size in parentheses.)

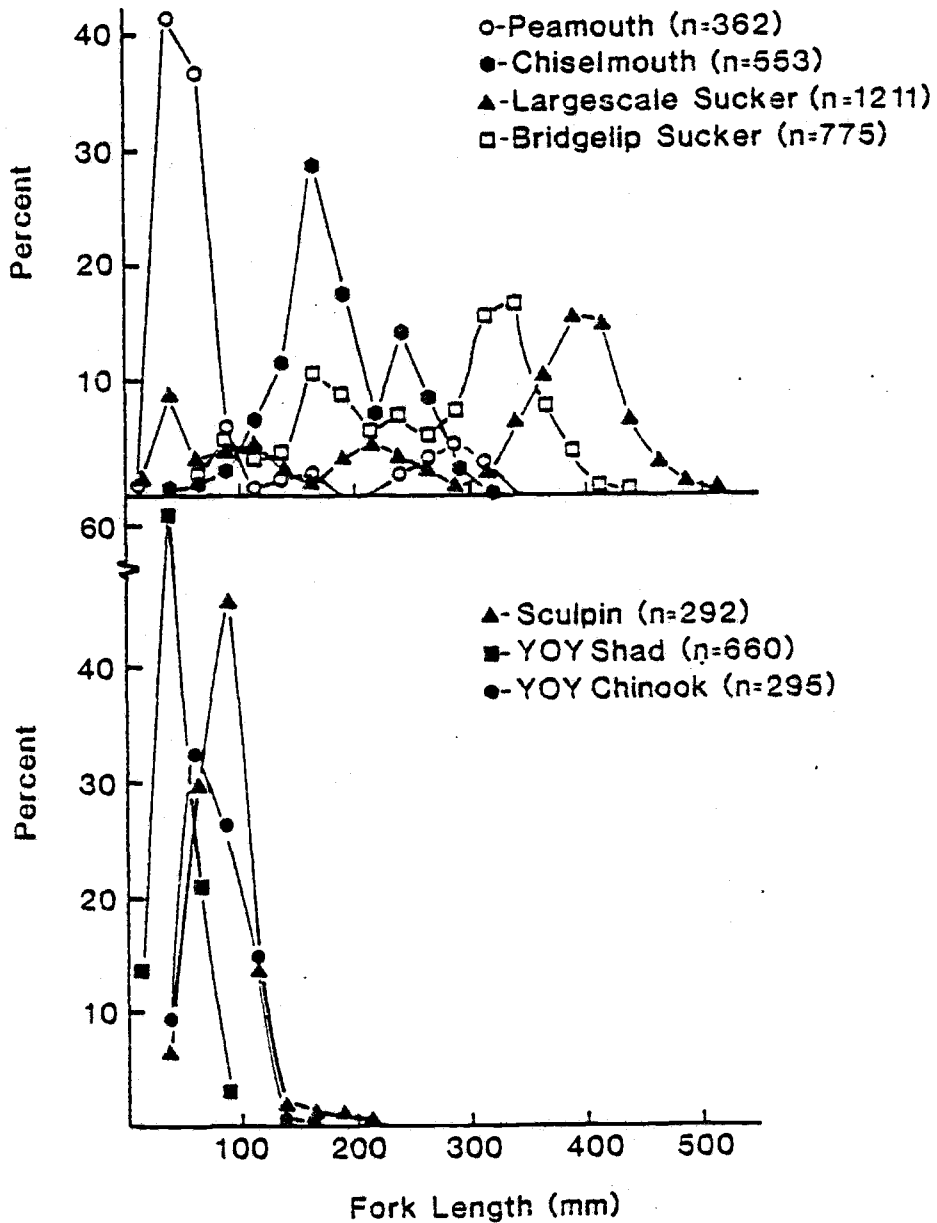


Figure 6. Length frequencies of potential walleye prey collected in the John Day pool of the Columbia River, April-September, 1981. (Sample size in parentheses.)

composition of their diet is different from those reported elsewhere. This difference is undoubtedly due to differing arrays and abundances of potential prey. The annual and seasonal variations in walleye diets in this study (Fig. 3) apparently are due to the variation in YOY prey fish abundances (Table 4).

Our data do not clearly explain the dietary role of YOY anadromous fish which normally have absolute seasonal abundances in excess of 10 million fish (Raymonds 1979; Sims et al. 1981). We hypothesize that differing behavioral responses of walleye, YOY salmonids and shad, and alternate prey result in the walleye's apparent dietary underutilization of juvenile anadromous fish. The walleye's subretinal tapetum lucidum greatly enhances their visual acuity at twilight, when many potential prey have reduced visual acuity and are inactive (Ali et al. 1977; Ryder 1977). The yellow perch (Perca flavescens) is the walleye's primary prey over most of their co-extensive habitats (Colby et al. 1979), and the yellow perch's behavior in dim light is described as settling to the bottom and becoming inactive (Ryder 1977). Ali et al. (1977) suggest that were it not for their complimentary behavior at dawn and dusk, walleye and yellow perch interaction would be second order, at best. In dimming light, juvenile Pacific salmon rise to the surface, increase swimming activity and move downstream (Hoar 1958; Ali 1959). Similar behavior has been reported for YOY shad (Loesch et al. 1982). Emery (1973) studied the diel movements of 21 species of Catostomidae, Clupeidae, Cottidae, Cyprinidae and Percidae, and all but two species of Clupeidae were on or near the bottom at twilight and during the

night. Emery (1973) further reported that these fish could be more closely approached by a diver at night than during the day. Therefore it appears that YOY salmonids and shad are buffered from walleye predation by an abundance of alternate prey (Tables 2, 3 and 4) of a wide size range (Figs. 5 and 6), and by a separation in space and time during one of the walleye's peak feeding periods (Fig. 4).

We caution that this hypothesis is based on the current fish abundances within the John Day pool of the Columbia River. Should these abundances change, i.e., an increase in walleye abundance or a decrease in alternate prey, then we would expect a change in the walleye-juvenile anadromous fish interactions. Furthermore, we have specifically addressed the question of the importance of juvenile anadromous fish in the diets of walleye. The impact of walleye on the anadromous fish populations cannot be addressed without an estimate of the walleye population.

ASPECTS OF THE LIFE HISTORY OF WALLEYE

(Stizostedion vitreum vitreum)

IN THE MID-COLUMBIA RIVER

Alec G. Maule

Oregon Cooperative Fisheries Research Unit

Department of Fisheries and Wildlife, Oregon State University

Howard F. Horton

Department of Fisheries and Wildlife, Oregon State University

Corvallis, Oregon 97331

ABSTRACT

The exotic walleye (Stizostedion vitreum vitreum) population in the John Day pool of the Columbia River was investigated for the first time in the spring and summer of 1980 and 1981. Backcalculated fork lengths-at-age for ages 1 thru 8 were 243.8, 368.2, 458.4, 515.6, 575.6, 623.6, 664.2, and 700.7 mm respectively, values which approach the highest growth previously reported. This rapid growth is accompanied by high fecundity (82,900 eggs \cdot kg body weight⁻¹) and early age at maturity (3 yr). We attribute these extreme values to optimal environmental temperatures and a nonlimiting food supply.

INTRODUCTION

The walleye (Stizostedion vitreum vitreum) is widely distributed throughout the United States and Canada, and has been studied through

most of its native range (Colby et al. 1979). Although the introduction of walleye into the Pacific northwest is not documented, this piscivorous coolwater fish has been found throughout the mid-Columbia River (Fig. 1) and downstream of Bonneville Dam (Durbin³). Interest in the walleye in the Columbia River has focused on the potential sport fishery for walleye and the impact of walleye on native salmonid populations (Carlander et al. 1978; Brege 1981).

The construction of dams on the Columbia River has transformed it from a free-flowing river into a series of low current impoundments with physical characteristics (Table 1) which closely match the model for ideal walleye habitat proposed by Kitchell et al. (1977a). The biology of the walleye in the Columbia River has not been fully investigated. The purpose of our study was to investigate some aspects of the life history of walleye from the John Day pool of the Columbia River. Specifically we looked at their age and growth, weight/length relationships, fecundity, and size and age at maturity. This information will be of benefit to resource agency personnel who make management decisions affecting walleye, and will provide baseline data important for further investigations of walleye in the Columbia River.

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 45°55'N latitude (Fig. 1). The tailrace is shallow (maximum depth = 11 m) and has faster current than the forebay, an area where we had

³ Ibid

very limited success capturing walleye. Walleye were collected from 2 Apr to 30 Sep 1980 and from 30 Mar to 30 Sep 1981. In 1980, we captured walleye in either a 38.1- x 1.8-m sinking gillnet with 3.81-, 5.08-, 6.35-, 7.52-, and 10.16-cm variable stretch mesh, or a 76.2- x 3.7-m monofilament floating gillnet with 15.25-cm stretch mesh. All gillnet sets were of a maximum 2.5 hour duration. In 1981 we used gillnets and a 6.15-m electroshock boat with a 3500 watt generator and front mounted electrodes, utilizing pulsed D.C. current of 1-4 A to capture walleye.

We recorded the fork length (FL, mm), weight (g), sex and maturity (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 otoliths (n = 86) which were preserved in 50:50 glycerine and water.

Scale samples were mounted between two glass microscope slides and were viewed using a microfiche projector at 43X. 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 bunsen burner 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. Scales and otoliths were examined twice and a subsample ($n = 63$) of scales was examined by a person experienced in reading walleye scales (W.R. Nelson, United States Fish and Wildlife Service, Vancouver, Washington).

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 (43X) at approximately 45 degrees off of a line from the focus through the anterior field. In this area of the scale it was much easier to detect the annuli due to crowding and anastomosis of circuli in the lateral fields.

We backcalculated 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):

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

L_c = fish FL at capture

L_i = calculated FL at age i

S_c = scale radius at capture

S_i = scale measurement at annulus i

a = intercept of body - scale regression = 55 mm.

In Figure 4 we converted these backcalculated fork lengths to total length (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 to data from other areas.

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

RESULTS

Length and Weight

We sampled over 250 walleye in each year and the length frequencies are shown in Figure 2. The walleye varied in fork length from 208-765 mm FL (220-810 mm TL) and all intervening size groups were well represented. The weight (WT)/length (FL) relationship for 324 walleye was best described by the equation:

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

The slopes and intercepts of similar weight-length regressions for walleye collected in 1980 versus 1981 and males versus females were not significantly different at the $P < 0.01$ level (F-test).

Age and Growth

The average backcalculated lengths-at-age for all walleye, and for males and females are presented in Table 5. We had no difficulty detecting annuli in the samples from older walleye because of their rapid growth and apparently short life span. Although females are larger than males in each year of life, the difference is not statistically significant until after the second year, which corresponds to findings in some other areas (Carlander and Whitney 1961). The combined backcalculated lengths indicate that the growth rates in this study are among the highest reported (Colby et al. 1979).

Fecundity and Maturity

The mean fecundity of 27 walleye, between 520 to 764 mm FL and 1720 to 5905 grams weight, was 82,900 eggs·kg body weight⁻¹ (Table 6). As with the growth data, the walleye fecundity reported here is among the highest previously reported (Colby et al. 1979). 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):

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

Data on walleye maturity based on age, length and sex is presented in Figure 7. A majority of males and females were mature by age 3, however many previous studies report that males mature before females, and mature 2-year-old males are not uncommon (Colby et al. 1979).

Table 5. Average backcalculated fork length (FL), SE, and annual growth increment for walleye collected in the John Day pool of the Columbia River, April-September, 1980-1981.

Males	AGE							
	1	2	3 ^a	4 ^a	5 ^a	6 ^a	7 ^a	8
FL (mm)	241.0	363.4	434.5	484.2	533.0	562.3	596.4	
SE	2.4	3.4	5.7	7.1	9.0	10.2	6.8	
N (cumulative)	134	86	35	25	21	18	8	
increment (mm)	241.0	122.4	71.1	49.7	48.8	29.3	34.1	
<u>Females</u>								
FL (mm)	243.5	371.3	466.2	527.5	589.8	643.4	684.2	700.7
SE	2.4	3.1	3.6	4.3	4.6	4.9	6.2	10.9
N (cumulative)	197	150	122	95	69	57	28	8
increment (mm)	243.5	127.8	94.9	61.3	62.3	53.6	40.8	16.5
<u>Combined^b</u>								
FL (mm)	243.8	368.2	458.4	515.6	575.6	623.6	664.2	700.7
SE	1.5	2.2	3.3	4.1	4.6	5.6	7.7	10.9
N (cumulative)	446	277	189	142	104	85	40	8
increment (mm)	243.8	124.4	90.2	57.2	60.0	48.0	40.6	36.5

^a ♀ vs ♂ significantly different, $P < 0.01$, Student's t-test.

^b includes some fish whose sex was not determined.

Table 6. Fecundity of walleye from the John Day pool of the Columbia River, March 30 to April 18, 1981, compared to fecundities from Norris Reservoir, Tennessee (Smith 1941), Lake Gogebic, Michigan (Eschmeyer 1950), and western Lake Erie (Wolfert 1969).

Location	N	Eggs · kg body weight ⁻¹	
		Range ^a	Mean ^a
John Day pool	27	69,000-101,000	82,900 ± 1550 (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

^a Values converted from eggs · pounds body weight⁻¹ and rounded to nearest 100 eggs, except John Day pool.

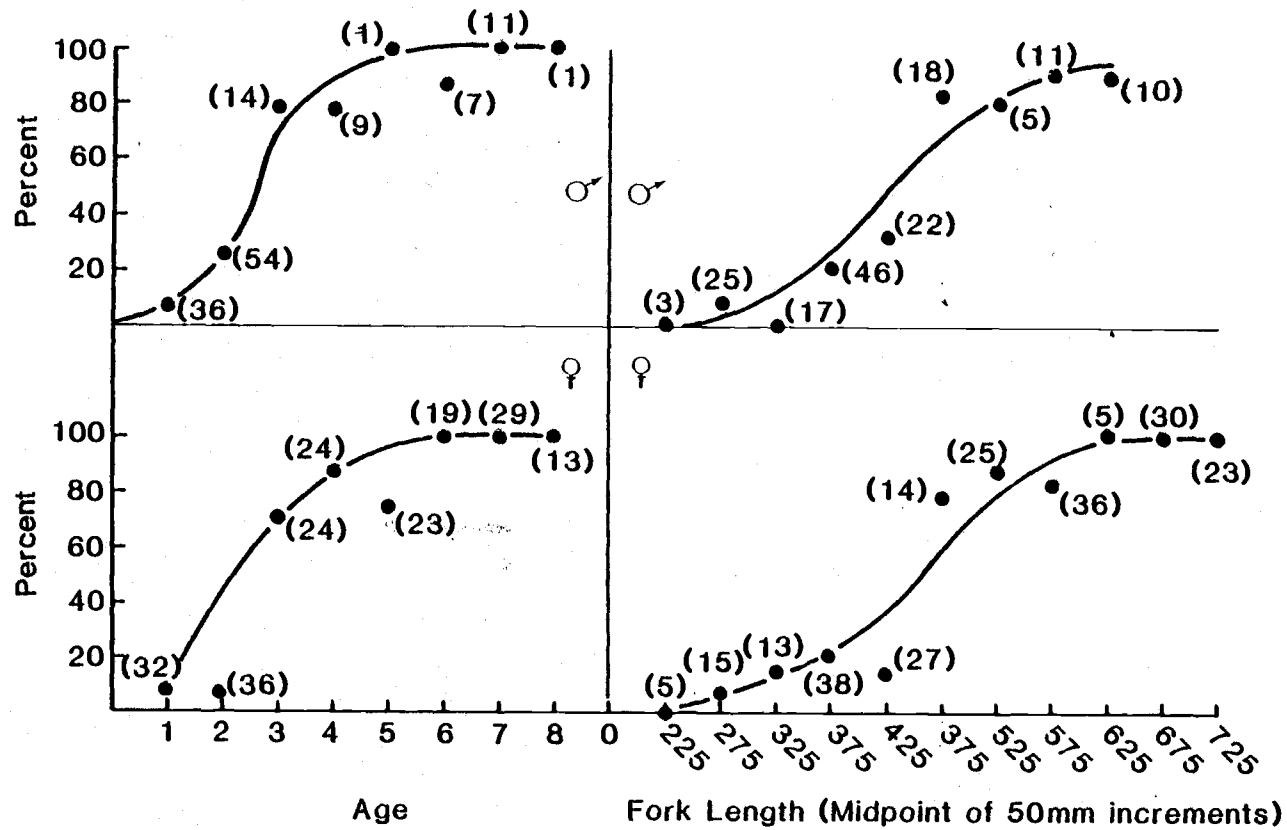


Figure 7. Percent mature walleye by age and length and by sex for specimens collected in the John Day pool of the Columbia River, April-September 1980-1981. Curves were drawn by eye. (Sample size in parentheses.)

The maturity at fork length data shows a more gradual increase than do the maturity data by age and, inexplicably, males were not 100% mature at any length (Fig. 7).

DISCUSSION

The exotic walleye population of the John Day pool of the Columbia River grows at a rate approaching the highest previously reported (Fig. 8). Concomitant with rapid growth these walleye are very fecund (Table 6) and mature at an early age (Fig. 7). We suggest that these life history characteristics are due to the combination of favorable temperature regimen and a nonlimiting food supply. High growth rates are generally found in walleye populations of more southerly latitudes where, presumably, there are higher temperatures and longer growing seasons. Figure 8 contains data from Norris Reservoir, Tennessee (Stroud 1949), Lake Gogebic, Michigan (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 ($45^{\circ}55'N$), Norris Reservoir is south ($36^{\circ}15'N$), Lac la Ronge is north ($55^{\circ}07'N$), and Lake Gogebic is at approximately the same latitude ($46^{\circ}47'N$). The mean growing degree-days above 5 C ($GDD > 5 C$) (Colby and Nepszy 1981) for each area are included in Figure 8 as a measure of system energetics. Colby and Nepszy (1981) found that walleye growth was directly correlated to $GDD > 5 C$ and that the optimum range was from 2500 to 4000 $GDD > 5 C$. While the $GDD > 5 C$ for the John Day pool is

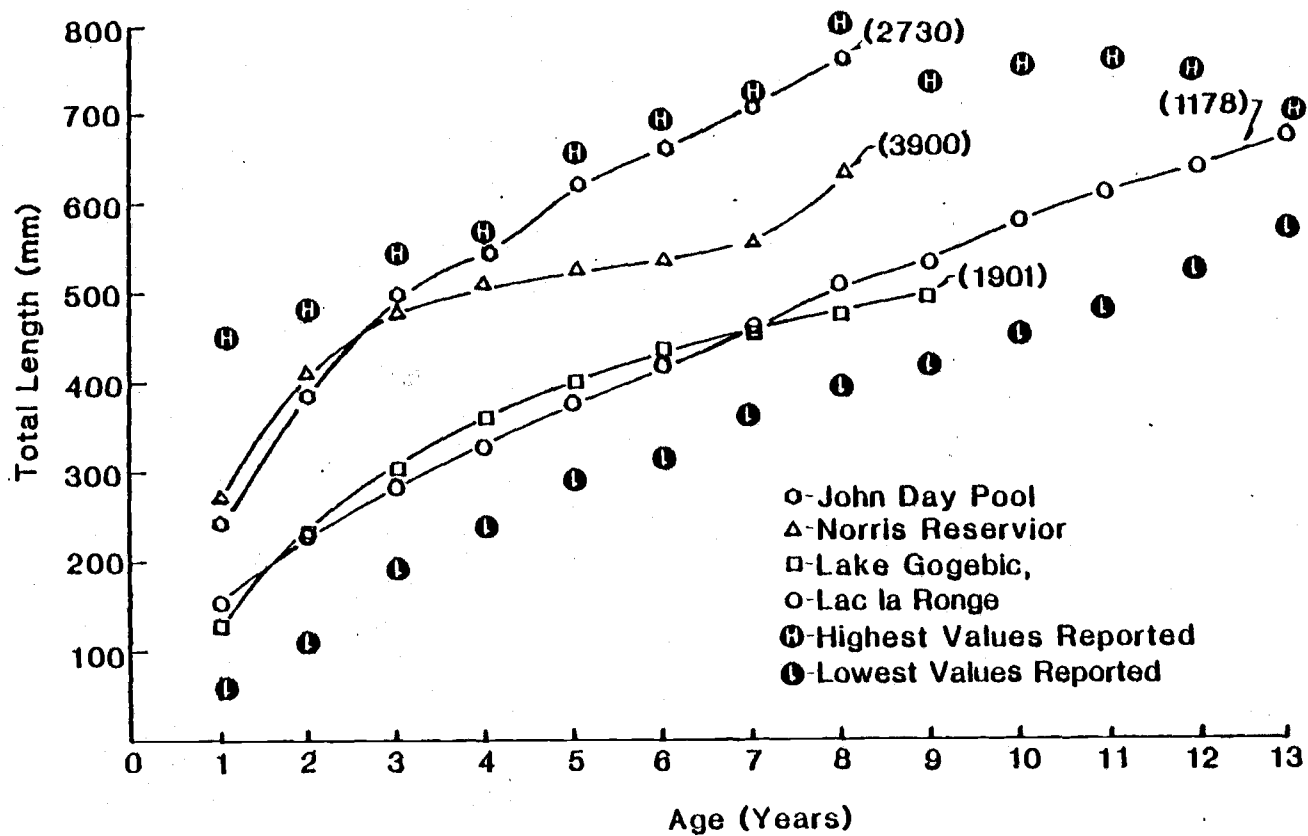


Figure 8. Comparison of length-at-age for walleye from the John Day pool, Columbia River; Norris Reservoir, Tennessee (Stroud 1949); Lake Gogebic, Michigan (Eschmeyer 1950); Lac la Ronge, Saskatchewan (Rawson 1957) and the composite high and low values reported by Colby et al. (1979). Numbers in parentheses are the mean growing degree-days above 5 C, John Day value is from Anonymus (1969), all others are from Colby and Nepszy (1981).

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) present a bioenergetics model for walleye growth and indicate 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 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 approximately 30 C and that walleye appeared to prefer water temperature of approximately 24 C, even though these areas had oxygen concentrations < 3.0 ppm. 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 increase 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, Minnesota and found the food of walleye from areas of highest average growth was almost totally young-of-the-year yellow perch while small walleyes from slow growth areas had eaten invertebrates and small minnows. We have found (Maule and Horton MS) that approximately 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 contained food.

Colby and Nepszy (1981) state that age to maturity is indirectly correlated to growth, but that fecundity is probably a function of population density and food availability. They further suggest that the wide variability in walleye fecundities is a mechanism by which walleye can adjust production in response to environmental conditions. Table 6 includes fecundity data from Norris Reservoir (Smith 1941), Lake Gogebic (Eschmeyer 1950) and western Lake Erie (Wolfert 1969), the highest fecundity reported by Colby et al. (1979). Based on a comparison of growth, stomach content analysis, and fecundity, it appears that the mid-Columbia River walleye have a more favorable food supply than the other areas considered here.

Hackney and Holbrook (1978) suggest that there is a southern race of walleye which is characterized by rapid, large growth and short life span, and a northern race characterized by slow growth and long life span. They suggest 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) and assuming that this is a means by which the walleye has colonized the Columbia River, it is biologically similar to impounding waters already containing walleye populations. 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 be explained due to favorable temperature regimen and an abundant, high quality food supply. Continued investigation of the Columbia River walleye is warranted to document their growth and fecundity through time.

REFERENCES

- Anonymous. 1969. Climatological handbook. Columbia basin states. Temperature. Volume 1 part A. Meterology Committee, Pacific Northwest River Basins Commission. Vancouver, Washington. USA.
- Ali, M.S. 1959. The ocular structure, retinomotor and photobehavioral responses of juvenile Pacific salmon. Canadian Journal of Zoology 37:965-996.
- Ali, M.A., R.A. Ryder, and M. Anctil. 1977. Photoreceptors and visual pigments as related to behavioral responses and preferred habitats of perches (Perca spp.) and pikeperches (Stizostedion spp.) Journal of the Fisheries Research Board of Canada 34:1475-1480.
- Brege, D.A. 1981. Growth characteristics of young-of-the-year walleye, Stizostedion vitreum vitreum, in John Day Reservoir on the Columbia River, 1979. Fishery Bulletin 78:567-569.
- Brett, J.R. 1979. Environmental factors and growth. Pages 599-676 in Hoar, W.S., D.J. Randall, and J.R. Brett, editors. Fish physiology. Volume VIII. Bioenergetics and growth. Academic Press, New York, New York, USA.
- Campbell, J.S., and J.A. Babaluk. 1979. Age determination of walleye, Stizostedion vitreum vitreum, (Mitchill), based on the examination of eight different structures. Fisheries and the Environment, Canada Fisheries and Marine Service Technical Report 849.
- Carlander, K.D. 1982. Standard intercepts for calculating lengths from scale measurements for some centrarchid and percid fishes. Transactions of the American Fisheries Society 111:332-336.
- _____, and R.R. Whitney. 1961. Age and growth of walleyes in Clear Lake, Iowa, 1935-1957. Transactions of the American Fisheries Society 90:130-138.
- _____, J.S. Campbell, and R.J. Muncy. 1978. Inventory of percid and esocid habitat in North America. American Fisheries Society, Special Publication 11:27-38.
- Christensen, J.M. 1964. Burning of otoliths, a technique for age determination of soles and other fish. Journal of the International Council for the Exploration of the Sea 29:73-81.
- Colby, P.J., R.E. McNicol, and R.A. Ryder. 1979. Synopsis of biological data on the walleye, Stizostedion vitreum vitreum

(Mitchill 1918). Food and Agriculture Organization of the United Nations, FAO Fisheries Synopsis 119. Rome, Italy.

- _____, and S.J. Nepszy. 1981. Variation among stocks of walleye (Stizostedion vitreum vitreum): management implications. *Canadian Journal of Fisheries and Aquatic Sciences* 38:1814-1831.
- Dendy, J.S. 1946. Food of several species of fish, Norris Reservoir, Tennessee. *Journal of the Tennessee Academy of Science* 21:275-283.
- _____. 1948. Predicting depth distribution of fish in three TVA storage type reservoirs. *Transactions of the American Fisheries Society* 75:65-71.
- Emery, A.R. 1973. Preliminary comparisons of day and night habits of freshwater fish in Ontario lakes. *Journal of the Fisheries Research Board of Canada* 30:761-774.
- Eschmeyer, P.H. 1950. The life history of the walleye, (Stizostedion vitreum vitreum (Mitchill)), in Michigan. Michigan Department of Conservation, *Bulletin of the Institute for Fisheries Science* 3.
- Forney, J.L. 1965. Factors affecting growth and maturity in a walleye population. *New York Fish and Game Journal* 12:217-232.
- _____. 1977. Evidence of inter- and intraspecific competition as factors regulating walleye (Stizostedion vitreum vitreum) biomass in Oneida Lake, New York. *Journal of the Fisheries Research Board of Canada* 34:1812-1820.
- Hackney, P.A. and J.A. Holbrook II. 1978. Sauger, walleye, and yellow perch in the southeastern United States. *American Fisheries Society Special Publication* 11:74-81.
- Hjort, R.C., B.C. Mundy, and P.L. Hulett. 1981. Habitat requirements for resident fishes in the reservoirs of the lower Columbia River. Final report. U.S. Army Corps of Engineers Contract No. DACW57-79-C-0067. Portland, Oregon, USA.
- Hoar, W.S. 1958. The evolution of migratory behavior among juvenile salmon of the genus Oncorhynchus. *Journal of the Fisheries Research Board of Canada* 15:391-428.
- Kelso, J.R.M. 1972. Conversion, maintenance and assimilation for walleye, Stizostedion vitreum vitreum, as affected by size, diet and temperature. *Journal of the Fisheries Research Board of Canada* 29:1182-1192.

- Kerr, S.R., and R.A. Ryder. 1977. Niche theory and percid community structure. *Journal of the Fisheries Research Board of Canada* 34:1952-1958.
- Kitchell, J.F., M.G. Johnson, C.K. Minns, K.H. Loftus, L.G. Greig, and C.H. Olver. 1977a. Percid habitat: the river analogy. *Journal of the Fisheries Research Board of Canada* 34:1936-1940.
- _____, D.J. Stewart, and D. Weininger. 1977b. Applications of bioenergetics model to yellow perch (Perca flavescens) and walleye (Stizostedion vitreum vitreum). *Journal of the Fisheries Research Board of Canada* 34:1922-1935.
- Koch, G.G. 1969. Some aspects of the statistical analysis of "split plot" experiments in completely randomized layouts. *Journal of the American Statistical Association* 64:485-505.
- Loesch, J.G., W.H. Kriete, Jr., and E.J. Foell. 1982. Effects of light intensity on the catchability of juvenile anadromous Alosa species. *Transactions of the American Fisheries Society* 111:41-44.
- MacLean, J.H., and J.J. Magnuson. 1977. Inferences on species interactions in percid communities. *Journal of the Fisheries Research Board of Canada* 34:1941-1951.
- Maule, A.G., and H.F. Horton. M.S. Feeding ecology of walleye (Stizostedion vitreum vitreum) in the mid-Columbia River, with emphasis on the interactions between walleye and juvenile anadromous fish. Oregon State University, Corvallis, Oregon, USA.
- Parsons, J.W. 1971. Selective food preferences of walleye of the 1959 year class in Lake Erie. *Transactions of the American Fisheries Society* 100:474-485.
- Pinkas, L., M.S. Oliphant, and I.L.K. Iverson. 1971. Food habits of albacore, bluefin tuna, and bonito in California water. California Department of Fish and Game, *Fisheries Bulletin* 152:1-105.
- Rawson, D.S. 1957. The life history and feeding ecology of the yellow walleye, Stizostedion vitreum, in Lac la Ronge, Saskatchewan. *Transactions of the American Fisheries Society* 86:15-37.
- Raymonds, H.L. 1979. Effects of dams and impoundments on migrations of juvenile chinook salmon and steelhead from the Snake River, 1966 to 1975. *Transactions of the American Fisheries Society* 108:505-529.

- Ryder, R.A. 1977. Effects of ambient light variations on behavior of yearling, subadult, and adult walleyes (Stizostedion vitreum vitreum). Journal of the Fisheries Research Board of Canada 34:1481-1491.
- _____, and S.R. Kerr. 1978. The adult walleye in the percid community--a niche definition based on feeding behavior and food specificity. American Fisheries Society, Special Publication 11:39-51.
- Schupp, D.H. 1978. Walleye abundance, growth, movements, and yield in disparate environments within a Minnesota Lake. American Fisheries Society Special Publication 11:58-65.
- Scott, W.B., and E.J. Crossman. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada, Bulletin 184. Ottawa, Canada.
- Sims, C.W., J.G. Williams, D.A. Faurot, R.C. Johnsen, and D.A. Brege. 1981. Migrational characteristics of juvenile salmon and steelhead in the Columbia River basin and related passage research at John Day Dam, Volumes I and II. (U.S. Army Corps of Engineers contracts DACW57-80-F-0394 and DACW68-78-C-0051) National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle, Washington, USA.
- Smith, C.G. 1941. Egg production of walleyed pike and sauger. Norris Reservoir fish differ from same species in other localities. Progressive Fish Culturalist 54:32-34.
- Stroud, R.H. 1949. Growth of Norris Reservoir walleye during the first twelve years of impoundment. Journal of Wildlife Management 13:157-177.
- Swenson, W.A. 1977. Food consumption of walleye (Stizostedion vitreum vitreum) and sauger (S.canadense) in relation to food availability and physical conditions in Lake of the woods, Minnesota, Shagawa Lake, and western Lake Superior. Journal of the Fisheries Research Board of Canada 34:1643-1654.
- Wagner, W.C. 1972. Utilization of alewives by inshore piscivorous fishes in Lake Michigan. Transactions of the American Fisheries Society 101:55-63.
- Wolfert, D.R. 1969. Maturity and fecundity of walleyes from the eastern and western basins of Lake Erie. Journal of the Fisheries Research Board of Canada 26:1877-1888.
- Wydoski, R.S., and R.R. Whitney. 1979. Inland fishes of Washington. University of Washington Press. Seattle, Washington, USA.

APPENDICES

APPENDIX 1.

Use of the $L_{N,t}$ Statistic in Stomach Content Analysis

The $L_{N,t}$ statistic is a nonparametric, multivariate statistical test presented by Koch (1969). A nonparametric test is preferable in stomach content analyses as the assumption of normality can not be made because the prey are not normally distributed among the predators as the result of patchy distribution of prey in the environment and selective feeding by individual predators. A multivariate test allows one to test for differences between predator populations which have consumed similar arrays of prey species. In this thesis I looked at one predator species, which I separated into populations based on time of collection (e.g. spring vs summer). The predator populations can be based on differences in species, location of collection, predator size or any other variable the researcher wishes to use.

The test can be used to test more than two populations, however, the null hypothesis is that there is no difference in the stomach contents of the populations tested. Therefore, if the null hypothesis is rejected when testing more than two populations, one can only conclude that at least one population is different from all of the rest.

The data are arranged so that each individual predator (n_{ij}) for all populations or treatments (v_i) to be tested is a row and each prey group (p^k) is a column. The values in the cells (Y_{ij}^k) are the numbers or volume of that prey found in that predator's stomach (see

Example 1). The values in each column are then assigned ranks (R_{ij}^k) such that the smallest value is ranked 1.0 the next larger value is 2.0 and so on. The midrank method is used in case of ties, for example, if there are four Y_{ij}^k equal to 0.0 then each R_{ij}^k equals 2.5, $((1+2+3+4)/4)$. This ranks matrix is then used to generate the variance-covariance matrix (VN) which is a nonsingular, diagonally symmetric $p \times p$ matrix. I wrote a Fortran program utilizing the International Mathematical and Statistical Library (IMSL) to perform the matrix algebra (Example 2). The ranks matrix is then separated into the various populations and the average rank for each column (prey) is calculated. These average ranks are maintained as row vectors (\bar{R}_i) and $L_{N,t}$ is calculated as follows:

$$L_{N,t} = \left(\frac{N-1}{N}\right) \sum_{i=1}^v n_i \left(R_i - \frac{N+1}{2} j\right)' VN^{-1} \left(\bar{R}_i - \frac{N+1}{2} j\right)$$

where: N = total number of predators in all populations

n_i = number of predators in population i

j = a column vector of p ones

VN and \bar{R}_i are matrices described above.

Unless you are dealing with an unusually large number of prey groups, the final calculation can be done on the Statistical Interactive Programming System (SIPS) or the Statistical Package for the Social Sciences (SPSS).

EXAMPLE 1

Data Array

Population or Treatment	Predator	Prey Group						
		1	2	3	.	.	.	p^k
1	1	Y_{11}^1	Y_{11}^2	Y_{11}^3	.	.	.	Y_{11}^k
	2	Y_{12}^1						
	3	Y_{13}^1						
	.	.						
	.	.						
	n_{ij}	Y_{ij}^1						
2	1	Y_{21}^1						Y_{21k}
	2	Y_{22}^1						
	.	.						
	.	.						
	.	.						
	n_{2j}	Y_{2j}^1						
v_i	1	Y_{i1}^1						Y_{ik}
	.	.						
	.	.						
	n_{ij}	Y_{ij}^1						Y_{ij}^k

EXAMPLE 2

Variance-covariance Matrix Program

```

PROGRAM RKVAR(TAPE2, INPUT, VN, OUTPUT, TAPE1=INPUT, TAPE3, VNN)
REAL R(203,12), A(203,12), ATA(78), VN(12,12)
IA=203
L=203
M=12
READ(2,10) ((R(I,J),J=1,12),I=1,203)
10 FORMAT(12F5.1)
DO 40 J=1,12
DO 50 K=1,203
A(K,J)=R(K,J)-((203+1)/2)
50 CONTINUE
40 CONTINUE
CALL VTPROF(A,L,M,IA,ATA)
CALL VCVTSF(ATA,12,VN,12)
WRITE(3,100)((VN(I,J)/203.,I=1,12),J=1,12)
100 FORMAT(12F8.1)
STOP
END

```

The above program is as I used it, the number 203 equals my total number of predators and 12 is the number of prey groups (p). ATA (78) refers to the number of elements in the VN matrix when stored in IMSL and is calculated by $ATA = p(p+1)/2$. Prior to running this program it is necessary to call up IMSL for library functions.