

NOTES

FEEDING ECOLOGY OF WALLEYE, *STIZOSTEDION VITREUM VITREUM*, IN THE MID-COLUMBIA RIVER, WITH EMPHASIS ON THE INTERACTIONS BETWEEN WALLEYE AND JUVENILE ANADROMOUS FISHES¹

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 walleye introduction into the Columbia River system are not documented; however, this piscivorous, cool-water fish is found throughout the mid-Columbia River (Fig. 1) and downstream of Bonneville Dam (Durbin²). As populations of walleye in the Columbia River have increased and their range extended, 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).

¹Technical Paper No. 6722, Oregon Agricultural Experiment Station, Oregon State University, Corvallis, Oreg.

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

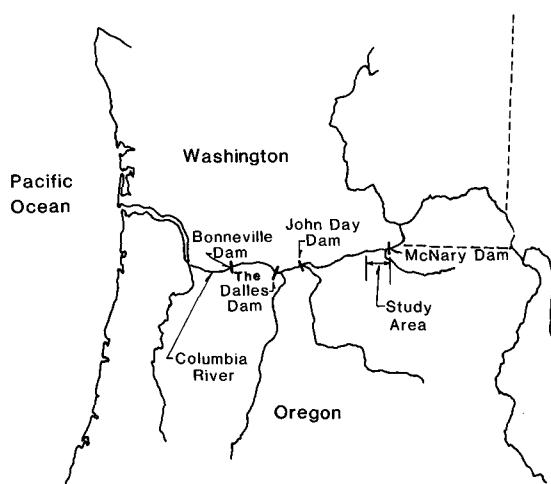


FIGURE 1.—Map of the lower and mid-Columbia River showing the locations of the major dams and the John Day pool study area where walleye were collected during 1980 and 1981.

Construction of dams has transformed the Columbia River into a series of low velocity impoundments with physical characteristics (Table 1) that 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. (1977). This transformation has increased the time required for emigration of juvenile salmonids and increased their mortality partly due to increased predation (Raymond 1979).

The purpose of this study was to describe the spring and summer feeding ecology of walleye in the John Day pool of the Columbia River. Emphasis was placed on walleye interaction with juvenile salmonids and young-of-the-year American shad, *Alosa sapidissima*, an anadromous fish that is morphologically and behaviorally similar to outmigrant salmonids and is abundant in the Columbia River in the late summer. We concentrated on seasonal variation in walleye diets, diel feeding periodicity, and food selection as influenced by walleye size. Preliminary findings regarding the spring diets of these walleye were reported by Maule (1982).

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 temperature		
Apr.-July-Sept. (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
Midpool depth (m)	11 - 48	11 - 20
Pool length (km)	≈120	23

Methods

We collected walleye for this study in the first 23 km of the John Day pool immediately downstream from McNary Dam on the Columbia River (Fig. 1) from 2 April to 30 September 1980 and from 30 March to 30 September 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 with either a 38.1 × 1.8 m sinking gill net with multifilament, variable, stretched mesh of 3.81, 5.08, 6.35, 7.52, and 10.16 cm, or a 76.2 × 3.7 m monofilament, floating gill net with 15.25 cm stretched mesh. All gill net sets were set at a maximum of 2.5-h duration in order to minimize regurgitation or digestion of stomach contents of the walleye. In 1981 we used gill nets and a 6.15 m electroshock boat with a 3,500-W generator and front mounted electrodes utilizing pulsed direct current at 1-4 A. Potential prey fish were periodically sampled with a 30.48 × 2.44 m beach seine of 6.35 mm stretched mesh. When we caught potential prey by means of gill nets, seines, or electroshock gear, we recorded numbers and fork lengths by species. Gear selectivity prohibited reliable estimates of numerical abundance of species, however, we used catch per unit of effort (CPUE) to estimate change in intraspecific abundance through time.

For each walleye captured, we recorded fork length (FL, mm), weight (g), sex, and stage of maturity, took scale samples, and preserved the stomach in 10% buffered Formalin³. Subsequently, each stomach was examined and each prey item was identified to the lowest possible taxon and its volume was recorded. A reference bone collection of potential prey species aided in the identification of partially digested prey. The most useful bones

were pharyngeal teeth, opercles, preopercles, and jaw bones. Characteristics of the internal morphology, e.g., the black peritonium of bridgelp suckers, *Catostomus columbianus*, or the number of pyloric ceca in salmonids (Scott and Crossman 1973), were also useful in identifying prey items.

We separated stomach content data into subpopulations based on season and year of capture, and tested for statistically significant differences in numbers and volumes of individual prey items. We computed statistical significance using a non-parametric, 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 (Pinkas et al. 1971).

Results

Seasonal Diet

The walleye size ranges were similar for both years, about 200-750 mm FL (Fig. 2). In both years fish accounted for over 99% of the total prey volume (Tables 2, 3). Based on IRI (Table 4), prickly sculpin, *Cottus asper*, was the most important species found in walleye stomachs. Excluding un-

³Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 2.—Percent by volume, percent by number, and percent frequency of occurrence of foods 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) ¹	% number ¹	% occurrence
Salmonidae (juvenile)	5.5 (89)	8.7 (22)	12.8 (15)
<i>Oncorhynchus tshawytscha</i>	1.7 (27)	2.7 (7)	8.5 (10)
Unidentifiable Salmonidae	3.8 (62)	6.0 (15)	4.3 (5)
Castostomidae	39.4 (638)	6.0 (15)	12.0 (14)
<i>Catostomus columbianus</i>	7.3 (118)	2.0 (5)	4.3 (5)
<i>C. macrocheilus</i>	12.8 (200)	1.2 (3)	2.6 (3)
Unidentifiable Castostomidae	19.3 (320)	2.8 (7)	5.1 (6)
Cyprinidae	15.2 (247)	5.6 (14)	12.0 (14)
<i>Acrocheilus alutaceus</i>	2.2 (36)	3.2 (8)	6.8 (8)
<i>Mylocheilus caurinus</i>	11.8 (192)	1.2 (3)	2.6 (3)
<i>Ptychocheilus oregonensis</i>	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)
<i>Cottus asper</i>	33.7 (544)	30.6 (77)	32.5 (38)
<i>Lampetra</i> spp.	0.1 (2)	0.4 (1)	0.1 (1)
<i>Alosa sapidissima</i> (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)

¹Volumes and numbers of individual prey taxa were significantly different from those of 1981 ($P < 0.005$).

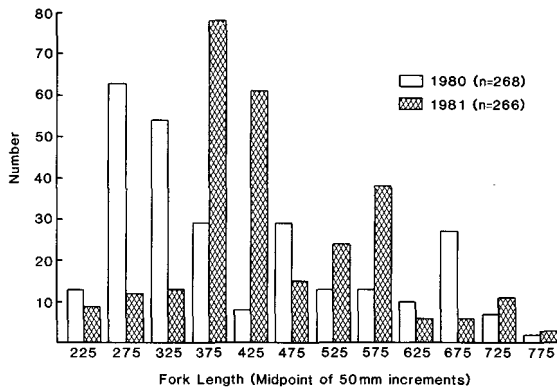


FIGURE 2.—Length-frequency distribution of walleye collected from the John Day pool of the Columbia River, April through September 1980 and 1981.

identifiable fish remains, the next most important foods were catostomids (largescale suckers, *Catostomus macrocheilus*, and bridgelip suckers) and cyprinids (primarily chiselmouth, *Acrocheilus alutaceus*, and peamouth, *Mylocheilus caurinus*). These species are generally associated with the benthos (Scott and Crossman 1973; Wydoski and Whitney 1979). In 1980, juvenile salmonids, primarily chinook salmon, *Oncorhynchus tshawytscha*, and juvenile American shad were equal to cyprinids in importance; however, in 1981, the importance of salmonids and shad was greatly reduced (Table 4).

All statistical tests were conducted with foods at the lowest taxon, and the data for individual species are presented in Tables 2, 3, and 4; however, in the interest of concise reporting we discuss results based on the following groups: catostomids, cyprinids, salmonids, cottids, shad, and invertebrates. Numbers and volumes of individual prey were significantly different between 1980 and 1981 ($P < 0.005$); to further investigate these differences, we tested for seasonal variation within and between years. We found no significant difference in numbers or volumes of prey between spring (April-June) 1980 and spring 1981 ($P > 0.25$); however, there were significant differences in diets (numbers and volumes) between summer (July-September) 1980 and summer 1981 ($P < 0.05$) and between the spring and summer of each year ($P < 0.01$).

We examined seasonal changes in IRI to detect which prey could account for significant differences in walleye diet (Table 4). From 1980 to 1981 there is a reduction in the importance of salmonids, cottids, and shad, and an increase in importance of catostomids, cyprinids, and invertebrates. Seasonal changes are not consistent; however, there are reductions in importance of cottids, increases in importance of cyprinids, and no changes in importance of invertebrates from spring to summer each year. Our CPUE data (Table 5) reflect annual and seasonal changes in the abundance of juvenile shad, juvenile

TABLE 3.—Percent by volume, percent by number, and percent frequency of occurrence of foods 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) ¹	% number ¹	% occurrence
Salmonidae (juvenile)	3.6 (62)	4.4 (14)	7.0 (10)
<i>Oncorhynchus tshawytscha</i>	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)
<i>Catostomus columbianus</i>	11.6 (201)	2.5 (8)	4.2 (6)
<i>C. macrocheilus</i>	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)
<i>Acrocheilus alutaceus</i>	28.3 (490)	5.7 (18)	11.1 (16)
<i>Mylocheilus caurinus</i>	1.8 (32)	2.5 (8)	5.6 (8)
<i>Ptychocheilus oregonensis</i>	1.7 (30)	1.6 (5)	2.8 (4)
<i>Cyprinus carpio</i>	0.3 (6)	0.3 (1)	0.7 (1)
<i>Carassius auratus</i>	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)
<i>Cottus asper</i>	22.5 (390)	25.6 (81)	36.8 (53)
<i>Alosa sapidissima</i> (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)

¹Volumes and numbers of individual prey taxa were significantly different from those of 1980 ($P < 0.005$).

TABLE 4.—Index of Relative Importance (IRI) (Pinkas et al. 1971) of foods found in spring (April through June) and summer (July through September)

Prey taxon	1980		
	Combined ¹	Spring	Summer
Salmonidae	182 (1.7)	293 (2.5)	148 (1.2)
<i>Oncorhynchus tshawytscha</i>	37 (0.9)	99 (1.7)	104 (2.4)
Unidentifiable Salmonidae	42 (1.0)	51 (0.9)	4 (0.1)
Catostomidae	545 (5.0)	548 (4.6)	749 (6.1)
<i>Catostomus columbianus</i>	40 (0.9)	12 (0.2)	121 (2.7)
<i>C. macrocheilus</i>	36 (0.8)	12 (0.2)	66 (1.5)
Unidentifiable Catostomidae	113 (2.6)	226 (3.9)	37 (0.8)
Cyprinidae	250 (2.3)	98 (0.8)	491 (4.0)
<i>Acrocheilus alutaceus</i>	37 (0.8)	2 (<0.1)	162 (3.7)
<i>Mylocheilus caurinus</i>	34 (0.8)	62 (1.1)	16 (0.4)
<i>Ptychocheilus oregonensis</i>	1 (<0.1)		4 (0.1)
Other Cyprinidae	3 (0.1)		6 (0.1)
Miscellaneous fishes	9,879 (90.7)	10,859 (91.5)	10,795 (88.3)
<i>Cottus asper</i>	2,090 (48.6)	3,621 (62.8)	1,335 (30.7)
<i>Alosa sapidissima</i>	91 (2.1)		480 (11.1)
Other (unidentifiable fish; <i>Lampetra</i> spp., Ictaluridae)	1,784 (41.3)	1,677 (29.0)	2,012 (46.4)
Invertebrates	34 (0.3)	74 (0.6)	40 (0.3)

¹IRI's are not additive across columns.

TABLE 5.—Catch-per-unit-effort (CPUE) for various juvenile (Juv.) and adult fishes caught in the John Day pool of the Columbia River, April-September 1980-81.

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

Dates	Hours	Gill nets		
		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.-Sept. 1980	330	0.37	0.54	0.74
Jul.-Sept. 1981	154	0.31	0.84	0.61

peamouth, and juvenile chinook salmon. However, Sims et al. (1982) reported no significant seasonal differences in the estimated numbers of juvenile salmonids emigrating past the John Day Dam (53,000 and 44,000 daily from 21 April to 30 June and from 1 July to 28 September 1981, respectively), 90 km downstream of our study area. Similar estimates are not available for 1980, but the smolt emigration past the John Day Dam was estimated at 8.3 million (Sims et al. 1981) and 7.7 million (Sims et al. 1982) in 1980 and 1981, respectively. Unfortunately cottids, the most important food, were rare in our CPUE data for 1980, and in 1981, the electroshock CPUE was <0.1, a level too low to detect changes.

Seasonal shifts in walleye diets are often the result of high spring-time availability of aquatic insects and/or increased availability of prey fish in the summer (Eschmeyer 1950; Parsons 1971). In this study, invertebrates represented 4-13% of the

numbers of prey items (Tables 2, 3), however they contributed little to the total caloric intake of the walleye because of their almost negligible volume and poor assimilation by walleye (Kelso 1972). Moreover, invertebrates did not exhibit significant seasonal variation in walleye dietary importance (Table 4).

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-h intervals) in Figure 3. The shape of this curve suggests the

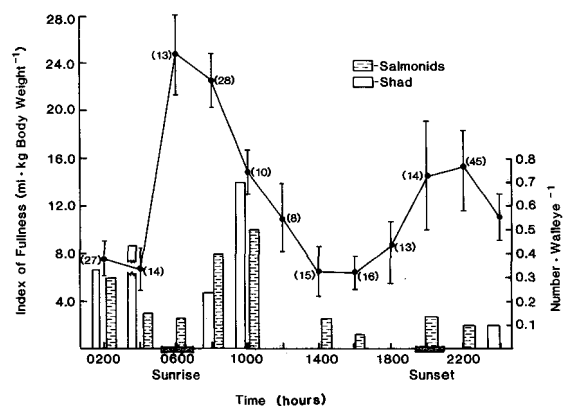


FIGURE 3.—Index of fullness and numbers of juvenile salmonids and shad consumed per walleye captured during 2-h intervals. Data collected from the John Day pool of the Columbia River, April to September 1980 and 1981. (Sample size in parentheses.)

stomachs of walleye collected in the John Day pool of the Columbia River in the 1980 and 1981. Numbers in parentheses are percent IRI.

Prey taxon	1981		
	Combined ¹	Spring	Summer
Salmonidae	56 (0.6)	53 (0.5)	58 (0.6)
<i>Oncorhynchus tshawytscha</i>	8 (0.2)	4 (0.1)	
Unidentifiable Salmonidae	11 (0.3)	26 (0.5)	58 (1.5)
Catostomidae	795 (8.8)	88 (0.9)	816 (8.3)
<i>Catostomus columbianus</i>	59 (1.4)	65 (1.1)	69 (1.7)
<i>C. macrocheilus</i>	3 (0.1)	1 (<0.1)	8 (0.2)
Unidentifiable Catostomidae	350 (8.4)	418 (7.3)	293 (7.3)
Cyprinidae	1,211 (13.4)	649 (6.3)	2,776 (28.4)
<i>Acrocheilus alutaceus</i>	377 (9.0)	462 (8.1)	298 (7.5)
<i>Mylocheilus caurinus</i>	24 (0.6)	1 (<0.1)	162 (4.1)
<i>Ptychocheilus oregonensis</i>	9 (0.2)	2 (<0.1)	41 (1.0)
Other Cyprinidae	34 (0.8)	1 (<0.1)	234 (5.9)
Miscellaneous fishes	6,808 (75.5)	9,480 (91.3)	6,028 (61.6)
<i>Cottus asper</i>	1,770 (42.2)	2,376 (41.7)	1,314 (32.9)
<i>Alosa sapidissima</i>	<1 (<0.1)		2 (<0.1)
Other (unidentifiable fish; <i>Lampetra</i> spp., Ictaluridae)	1,544 (36.8)	2,336 (41.0)	1,511 (37.9)
Invertebrates	150 (1.7)	113 (1.1)	106 (1.1)

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. Numbers of juvenile salmonids and shad consumed per walleye at various times of the day peaked from late night to midmorning, drop to a low level at midday, and remain low through the evening peak in walleye feeding.

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

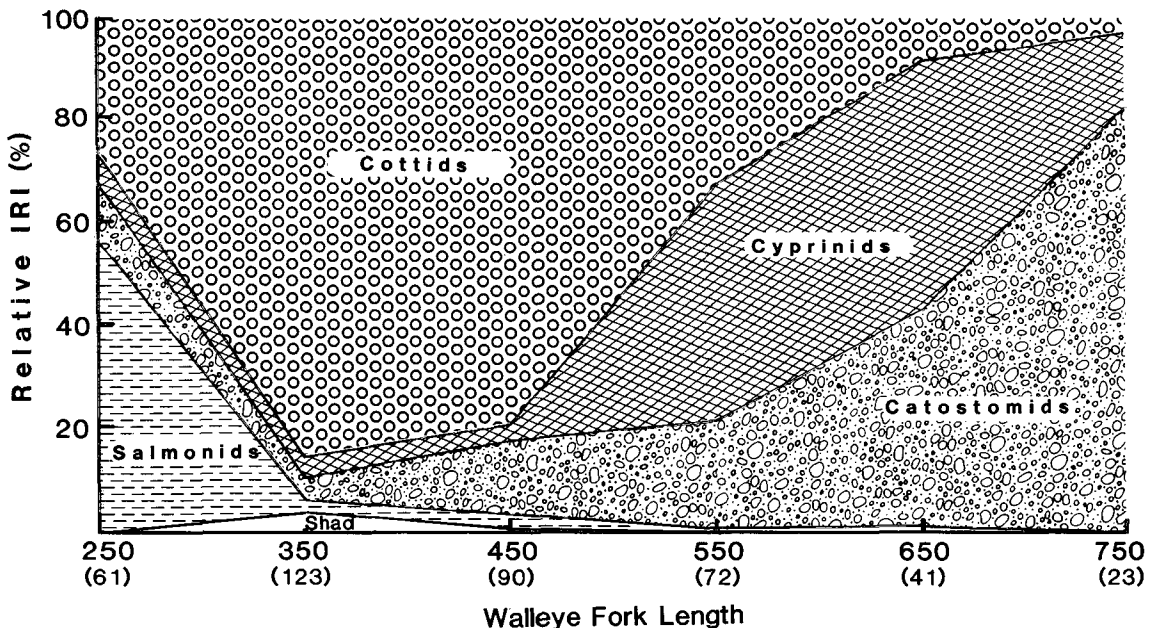


FIGURE 4.—Change in percent of total Index of Relative Importance (IRI) (Pinkas et al. 1971) of prey components as a function of walleye fork length (100 mm increments). Walleye collected in the John Day pool of the Columbia River, April through September 1980 and 1981. (Sample size in parentheses.)

charted in Figure 4. Small walleye (200-400 mm FL) primarily consume salmonids, cottids, and shad, while midrange walleye (400-600 mm FL) rely more heavily on cyprinids, cottids, and catostomids. For large walleye (>600 mm FL), suckers are the most important prey and the importance of cyprinids and cottids is reduced. Figure 5 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., cottids, juvenile shad, and juvenile salmonids are small (25-125 mm FL); cyprinids, excluding juvenile peamouth, are midrange in length (125-300 mm FL); and catostomids are present in a large range of sizes (150-450 mm FL) with peaks >300 mm FL.

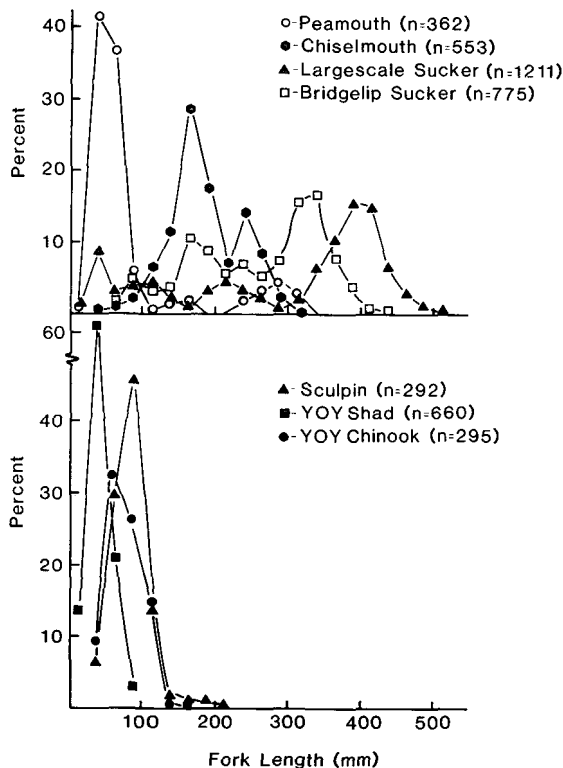


FIGURE 5.—Length frequencies of potential walleye prey collected in the John Day pool of the Columbia River, April through September 1981. (Sample size in parentheses.)

Discussion

Walleye have been described as opportunistic (Eschmeyer 1950; Ryder and Kerr 1978), crepuscular, or nocturnal feeders which primarily search

the bottom for prey (Ali et al. 1977; Ryder 1977) and, in areas of abundant prey, select prey based on size preference (Parsons 1971; Wagner 1972). Walleye of the mid-Columbia River fit this general description; however, the species composition of their diet is different from that reported elsewhere. This difference is undoubtedly due to differing arrays and abundances of potential prey. Our data suggest no significant change in annual or seasonal variation in abundances of adult catostomids and cyprinids (chiselmouth) (Table 5); therefore, we believe that the variations in walleye diets (Tables 2, 3, 4) are the result of changes in availability of juvenile prey fish (Table 5).

Our data do not clearly explain the dietary role of juvenile anadromous fish that normally have seasonal abundances in excess of 10 million fish (Sims et al. 1981, 1982). We hypothesize that different behavioral responses of walleye, juvenile salmonids and shad, and alternate prey result in the walleye's apparent low dietary utilization of juvenile anadromous fish. The walleye's subretinal tapetum lucidum greatly enhances its visual acuity at twilight, when many potential prey have reduced visual acuity and are inactive (Ali et al. 1977; Ryder 1977). Yellow perch, *Perca flavescens*, are 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) suggested that were it not for their complimentary behavior at dawn and dusk, walleye and yellow perch interaction would not be as significant as it appears to be. In dimming light, emigrating juvenile Pacific salmon rise to the surface, increase swimming activity, and move downstream (Hoar 1958; Ali 1959). Similar behavior has been reported for juvenile 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 juvenile salmonids and shad are buffered from walleye predation by an abundance of alternate prey (Tables 2, 3, 5) of a wide size range (Figs. 4, 5) and by a separation in space and time during one of the walleye's peak feeding periods (Fig. 3).

We caught no walleye <200 mm FL (Fig. 2), even though our gear captured numerous specimens of other species <100 mm FL (Fig. 5). We

believe that inclusion of this smaller size group of walleye would not seriously alter our results or conclusions as they relate to predation on juvenile salmonids. They might, however, increase the importance of shad in walleye diets. Walleye <200 mm FL will primarily be juvenile walleye and will not reach 150 mm TL until mid-September (Bregé 1981; Maule 1983). The length frequencies of juvenile chinook salmon which we sampled peaked at about 100 mm FL and, generally, chinook salmon complete their emigration by early fall (Raymond 1979; Sims et al. 1981). Juvenile shad, however, are generally smaller than juvenile salmonids (Fig. 5) and emigrate in late fall (Stainbrook 1983). Whereas juvenile salmonids may be buffered from the juvenile walleye predation by a size and time separation, juvenile shad may become a more important juvenile walleye food in late summer through fall.

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. The impact of walleye on the anadromous fish populations cannot be addressed without adequate estimates of walleye and prey fish abundances.

Acknowledgments

We thank Hiram Li and Carl Bond for their reviews of the manuscript. Funds were provided by the U.S. Army Corps of Engineers contract DACW57-79-C-0067, the Oregon Agricultural Experiment Station, and the Milne Computer Center, Oregon State University, Corvallis, Oreg.

Literature Cited

- ALI, M. A., R. A. RYDER, AND M. ANCTIL.
1977. Photoreceptors and visual pigments as related to behavioral responses and preferred habitats of perch (*Perca* spp.) and pikeperches (*Stizostedion* spp.). *J. Fish. Res. Board Can.* 34:1475-1480.
- ALI, M. S.
1959. The ocular structure, retinomotor and photo-behavioral responses of juvenile Pacific salmon. *Can. J. Zool.* 37:965-996.
- BREGÉ, D. A.
1981. Growth characteristics of young-of-the-year walleye, *Stizostedion vitreum vitreum*, in John Day Reservoir on the Columbia River, 1979. *Fish. Bull., U.S.* 79:567-569.
- CARLANDER, K. D., J. S. CAMPBELL, AND R. J. MUNCY.
1978. Inventory of percoid and esocid habitat in North America. *Am. Fish. Soc., Spec. Publ.* 11, p. 27-38.
- COLBY, P. J., R. E. MCNICOL, AND R. A. RYDER.
1979. Synopsis of biological data on the walleye: *Stizostedion vitreum vitreum* (Mitchill 1818). *Food Agric. Organ. United Nations, FAO Fish. Synop.* 119, 139 p. Rome, Italy.
- EMERY, A. R.
1973. Preliminary comparisons of day and night habits of freshwater fish in Ontario lakes. *J. Fish. Res. Board Can.* 30:761-774.
- ESCHMEYER, P. H.
1950. The life history of the walleye, *Stizostedion vitreum vitreum* (Mitchill), in Michigan. *Mich. Dep. Conserv., Bull. Inst. Fish. Res. No. 3*, 99 p.
- 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 Eng. Contract No. DACW57-79-C-0067, 180 p. Portland, Oreg.
- HOAR, W. S.
1958. The evolution of migratory behavior among juvenile salmon of the genus *Oncorhynchus*. *J. Fish. Res. Board Can.* 15:391-428.
- KELSO, J. R. M.
1972. Conversion, maintenance, and assimilation for walleye, *Stizostedion vitreum vitreum*, as affected by size, diet, and temperature. *J. Fish. Res. Board Can.* 29:1181-1192.
- KITCHELL, J. F., M. G. JOHNSON, C. K. MINNS, K. H. LOFTUS, L. GREIG, AND C. H. OLVER.
1977. Percid habitat: the river analogy. *J. Fish. Res. Board Can.* 34:1936-1940.
- KOCH, G. G.
1969. Some aspects of the statistical analysis of "split plot" experiments in completely randomized layouts. *J. Am. Stat. Assoc.* 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. *Trans. Am. Fish. Soc.* 111:41-44.
- MAULE, A. G.
1982. The spring diets of walleye in the lower Columbia River, 1980-1981. In G. M. Cailliet and C. A. Simenstad (editors), *Gutshop '81, fish food habits studies, Proceedings of the Third Pacific Workshop*, p. 205-210. Washington Sea Grant Program, WSG-WO-82-2, Univ. Washington, Seattle.
1983. Aspects of the life history and feeding ecology of walleye (*Stizostedion vitreum vitreum*) in the mid-Columbia River. M.S. Thesis, Oregon State University, Corvallis, 43 p.
- PARSONS, J. W.
1971. Selective food preferences of walleyes of the 1959 year class in Lake Erie. *Trans. Am. Fish. Soc.* 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. *Calif. Dep. Fish Game, Fish. Bull.* 152:1-105.
- RAYMOND, H. L.
1979. Effects of dams and impoundments on migrations of juvenile chinook salmon and steelhead from the Snake River, 1966 to 1975. *Trans. Am. Fish. Soc.* 108:505-529.
- RYDER, R. A.
1977. Effects of ambient light variations on behaviour of

- yearling, subadult, and adult walleyes (*Stizostedion vitreum vitreum*). J. Fish. Res. Board Can. 34:1481-1491.
- RYDER, R. A., AND S. R. KERR.
1978. The adult walleye in the percid community—a niche definition based on feeding behavior and food specificity. Am. Fish. Soc., Spec. Publ. 11, p. 39-51.
- SCOTT, W. B., AND E. J. CROSSMAN.
1973. Freshwater fishes of Canada. Fish. Res. Board Can., Bull. 184, 966 p.
- SIMS, C. W., R. C. JOHNSEN, AND D. A. BREGE.
1982. Migrational characteristics of juvenile salmon and steelhead trout in the Columbia River System—1981. Volume 1. Assessment of the 1981 smolt migration, 61 p. (U.S. Army Corps of Engineers contracts DACW 68-78C-0051 and DACW 57-81-F-0342.) Natl. Mar. Fish. Serv., Natl. Oceanic Atmos. Admin., Seattle, Wash.
- 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, 15 p. (U.S. Army Corps of Engineers contracts DACW57-80-F-0394 and DACW68-78-C-0051.) Natl. Mar. Fish. Serv., Natl. Oceanic Atmos. Admin., Seattle, Wash.
- STAINBROOK, C. E.
1983. Selected life history aspects of American shad (*Alosa sapidissima*) and predation on young-of-the-year shad in Lake Umatilla of the Columbia River. M.S. Thesis, Oregon State University, Corvallis, 82 p.
- SWANSON, 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. J. Fish. Res. Board Can. 34:1643-1654.
- WAGNER, W. C.
1972. Utilization of alewives by inshore piscivorous fishes in Lake Michigan. Trans. Am. Fish. Soc. 101:55-63.
- WYDOSKI, R. S., AND R. R. WHITNEY.
1979. Inland fishes of Washington. Univ. Wash. Press, Seattle, 220 p.

ALEC G. MAULE

Oregon Cooperative Fisheries Research Unit
Department of Fisheries and Wildlife
Oregon State University
Corvallis, OR 97331

HOWARD F. HORTON

Department of Fisheries and Wildlife
Oregon State University
Corvallis, OR 97331

BATHYMETRIC DISTRIBUTION, SPAWNING PERIODICITY, SEX RATIOS, AND SIZE COMPOSITIONS OF THE MANTIS SHRIMP, *Squilla EMPUSA*, IN THE NORTHWESTERN GULF OF MEXICO¹

The mantis shrimp, *Squilla empusa*, ranges in the western Atlantic Ocean from Maine through the Gulf of Mexico (Gulf) to Surinam (Manning 1969). This stomatopod occurs in high-salinity waters (Gunter 1950; Franks et al. 1972) and is one of the more common macrocrustaceans in the northern Gulf (Hildebrand 1954). *Squilla* sp. may be important predators of other crustaceans, polychaetes, and fish (Camp 1973; Caldwell and Dingle 1976), but they also serve as food for many fishes including *Rachycentron canadum*, *Lutjanus campechanus*, *Sciaenops ocellatus*, *Micropogonias undulatus*, and *Rhomboplites aurorubens* (Knapp 1951; Moseley 1966; Overstreet and Heard 1978a, b; Grimes 1979).

Despite its importance, little detail is known of the life history of *Squilla empusa*. The pelagic larval stages have been described (Morgan and Provenzano 1979; Morgan 1980), and much information has been published recently on the worldwide zoogeography and distributional interrelationships, evolutionary ecology, and life history patterns of stomatopods, primarily coral-dwelling taxa (Reaka 1979, 1980; Reaka and Manning 1980). However, the latter information does not deal with *S. empusa*, and it may not be valid to extrapolate to this species. Reaka (1979: table 5) reported that the coral-dwelling taxa were long-lived and gave estimates of 26-34 yr to reach median size (using mean growth increments and mean molting frequencies), 12-14 yr (using mean growth and maximum molting), or 4-8 yr (using maximum growth and molting). Although we could not determine age of *S. empusa* readily from length-frequency analysis, a much shorter maximum life span (1-3 yr) is part of what appears to be a common pattern of population dynamics in the white and/or brown shrimp communities where *S. empusa* occur (Chittenden and McEachran 1976; Chittenden 1977).

This paper describes bathymetric distribution, size at maturation, spawning periodicity, sex ratios, size compositions, and morphometric relationships for *S. empusa* collected in the northwestern Gulf during routine trawling operations.

¹Technical article TA 18359 from the Texas Agricultural Experiment Station, Texas A&M University, College Station, TX 77843.