

declined below 13° C and sturgeon movements ceased by mid-October. If photoperiod were involved, sturgeon movements in 1977 should have stopped at about the same time as they did in 1975 and 1976. Complete cessation of movement >0.5 km in autumn may be related to cold-induced inactivity.

Linear regression analyses comparing distances moved by sturgeon with river flows at Priest Rapids Dam produced scatter diagrams with regression coefficients approaching zero. In contrast to results of studies in the Snake River, Idaho (Coon et al.⁵), river flow apparently had no influence on long-distance sturgeon movements in the Columbia River at Hanford.

The complex interaction of water temperature, light cycle, feeding, urge to spawn, and other factors undoubtedly influence sturgeon movements in the mid-Columbia River. Although temperature is a major influence stimulating seasonal movements, light cycle and feeding probably influence diel movements.

Acknowledgments

We thank C. D. Becker, who critically reviewed the manuscript; and R. P. Olson, S. W. Cubberly, D. W. Crass, and R. W. Cordo, who assisted data collection in the field. V. B. Kuechle, Bioelectronics Laboratory at Cedar Creek, University of Minnesota, kindly provided information on temperature transmitter precision. The study was supported by the U.S. Department of Energy under Contract EY-76-C-06-1830 with Battelle Memorial Institute, Pacific Northwest Laboratories.

Literature Cited

- BAJKOV, A. D.
1949. A preliminary report on the Columbia River sturgeon. *Fish. Comm. Oreg. Res. Briefs* 2(2):3-10.
1951. Migration of white sturgeon (*Acipenser transmontanus*) in the Columbia River. *Fish. Comm. Oreg. Res. Briefs* 3(2):8-21.
- BELL, M. C.
1973. Fisheries handbook of engineering requirements and biological criteria. *Fish.-Eng. Res. Program, Corps Eng., N. Pac. Div., Portland, Oreg.*
- CARL, G. C., W. A. CLEMENS, AND C. C. LINDSEY.
1967. The fresh-water fishes of British Columbia. 3d ed. *B.C. Prov. Mus. Handb.* 5, 192 p.

⁵Coon, J. R., R. R. Ringe, and T. C. Bjornn. 1977. Abundance, growth, distribution and movements of white sturgeon in the mid-Snake River. *Forest, Wildl. Range Exp. Stn., Univ. Idaho, Contrib.* 97, 63 p.

- CRAIG, J. A., AND R. L. HACKER.
1940. The history and development of the fisheries of the Columbia River. *U.S. Bur. Fish. Bull.* 49:133-216.
- HAYNES, J. M.
1978. Movements and habitat studies of chinook salmon and white sturgeon. Ph.D. Thesis, Univ. Minnesota, Minneapolis, 168 p.
- HAYNES, J. M., R. H. GRAY, AND J. C. MONTGOMERY.
1978. Seasonal movements of white sturgeon (*Acipenser transmontanus*) in the mid-Columbia River. *Trans. Am. Fish. Soc.* 107:275-280.
- JORDAN, D. S., AND B. W. EVERMANN.
1908. American food and game fishes. Doubleday, Page and Co., Garden City, N.Y., 572 p.
- SCOTT, W. B., AND E. J. CROSSMAN.
1973. Freshwater fishes of Canada. *Fish. Res. Board Can., Bull.* 184, 966 p.
- SEMAKULA, S. N., AND P. A. LARKIN.
1968. Age, growth, food, and yield of the white sturgeon (*Acipenser transmontanus*) of the Fraser River, British Columbia. *J. Fish. Res. Board Can.* 25:2589-2602.
- SNEDECOR, G. W., AND W. G. COCHRAN.
1972. Statistical methods. 6th ed. Iowa State Univ. Press, Ames, 587 p.

JAMES M. HAYNES

*Department of Biological Sciences
State University College
Brookport, NY 14420*

ROBERT H. GRAY

*Environment, Health and Safety Research Program,
Pacific Northwest Laboratory
Richland, WA 99352*

FEEDING PERIODICITY AND DIEL VARIATION IN DIET COMPOSITION OF SUBYEARLING COHO SALMON, *ONCORHYNCHUS KISUTCH*, AND STEELHEAD, *SALMO GAIRDNERI*, IN A SMALL STREAM DURING SUMMER

Throughout their native range in northwestern North America, juvenile coho salmon, *Oncorhynchus kisutch*, and steelhead, *Salmo gairdneri*, occur sympatrically in streams (Milne 1948). In these instances, social interaction between the two species leads to spatial segregation during the spring and summer, with coho salmon generally occupying pools and steelhead riffles (Hartman 1965; Allee 1974). A recent investigation of naturalized populations in the Great Lakes region has observed similar patterns of spatial segregation (Johnson and Ringler 1980).

It is generally accepted that social interaction among closely related fish species may lead to interactive segregation, with each species segre-

gating into a habitat which it is best suited to exploit (e.g., Nilsson 1967). In this respect, interactive segregation of juvenile coho salmon and steelhead enables the surface and drift forager, coho salmon, to inhabit pools and the more bottom-oriented steelhead to occupy riffles. Johnson and Ringler (1980) pointed out that in sympatry with coho salmon, steelhead are found in areas (riffles) where the standing crop of benthic invertebrates is the greatest, an obvious advantage in conjunction with their benthic habits. Conversely, coho salmon which feed predominantly from the drift presumably have a relatively long time interval in which to observe drifting prey because of decreased water velocities in pools.

Johnson and Ringler (1980) demonstrated that in sympatry the diet of subyearling coho salmon was closely associated with the composition of the drift, and the diet of subyearling steelhead was more closely associated with the bottom fauna. They found a low degree of overlap in the diurnal summer diet of coho salmon and steelhead due to the utilization of drifting terrestrial invertebrates by coho salmon and benthic invertebrates by steelhead. They speculated that since the composition of invertebrates on or within the substratum of a stream is much more stable over a 24-h period than the composition of the invertebrates drifting over it, that the diet of the drift feeder (coho salmon) would be more variable than the diet of the benthic forager (steelhead) over a 24-h period. The purpose of this study was to test this hypothesis while also gathering information sufficient to determine diel feeding periodicity, daily meal, and daily ration of juvenile coho salmon and steelhead.

Methods

Subyearling coho salmon and steelhead were collected from a 200 m section of Orwell Brook, Oswego County, N.Y. The stream discharges into the Salmon River which empties into Mexico Bay in the southeastern portion of Lake Ontario. Orwell Brook is a high quality spawning and nursery stream for salmonids migrating from Lake Ontario (Johnson 1980). The 200 m stream section generally consisted of a series of pools, runs, and riffles. The surface substrate consisted of gravel and pebbles. Maximum and minimum water temperatures recorded during the study period were 21°C at 1600 h (31°C air temperature) and 16°C at 0400 h (17°C air temperature).

The study was carried out in July 1979 since previous studies had shown that subyearling coho salmon and steelhead are most abundant in Orwell Brook at this time (Johnson 1980). Maximum numbers of coho salmon and steelhead in the stream were desired in order to facilitate collections and to prevent depletion of the populations of each species. Fish were collected at 4-h intervals commencing at 0800 h on 13 July and ending at 0400 h on 14 July 1979. During the study period sunrise occurred at 0436 h and sunset at 1943 h e.s.t. A minimum of 20 individuals of each species on 13 July 1979 was collected during each 4-h interval. Fish were collected with a 3 m seine, slit, and immediately placed in 10% Formalin¹ in order to halt digestive processes. Prior to the removal of their digestive tracts all fish were weighed (grams) and measured (millimeters total length, TL). Correction factors were used to account for weight gain and length shrinkage caused by preservation (Parker 1963; Stauffer²). Dietary items were identified to the family level for aquatic invertebrates and to the ordinal level for terrestrial invertebrates.

Dry weight estimates were obtained for individuals of each family of aquatic prey and each order of terrestrial prey (invertebrate taxa which had no life state occurring in the aquatic environment) to determine the relative contribution of food organisms in the fishes' diet. A representative number of individuals of each prey taxa (usually 10) were used to derive a dry weight estimate. Food items were placed in small pre-weighed pans and then dried at 105°C for 24 h. The pans were then placed in a desiccator for 6 h, and reweighed. The dry weight of the organisms in the pan was divided by the number of individuals in the pan giving an average dry weight estimate of an individual of that taxa. Dry weight determinations were used to estimate diet composition for both coho salmon and steelhead for each 4-h interval. In addition, dry weight estimates for each taxon were summed for the 24-h period to derive an estimate of diel diet composition.

To examine diel patterns of food consumption of both coho salmon and steelhead the total dry weight of the stomach contents per dry weight of

¹Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

²Stauffer, T. M. 1971. Salmon eggs as food for stream salmonids and sculpins. Mich. Dep. Nat. Resour., Fish. Res. Rep. 1776, 10 p. Institute for Fisheries Research, Museums Annex Building, Ann Arbor, MI 48109.

the fish was plotted for each 4-h interval. Dry weight estimates for each fish were based on the entire carcass. These estimates were derived experimentally using a dry weight to wet weight conversion (21.1%) based on the combined results of 15 individuals of each species.

Daily meal and daily ration of subyearling coho salmon and steelhead were determined by summing interval values for the 24-h period. The amount of food consumed at each 4-h interval, was estimated from the Elliott and Persson (1978) formula:

$$C_t = \frac{(S_t - S_0 e^{-Rt})Rt}{1 - e^{-Rt}}$$

where C_t = amount of food consumed in t hours
 S_t = mean stomach contents at the end of the interval
 S_0 = mean stomach contents at the beginning of the interval
 R = exponential rate of gastric evacuation in t hours.

Estimates of R were derived using available information for subyearling rainbow trout (Windell et al. 1976).

Variability in the diet of coho salmon and steelhead over the 24-h period, and diet similarity between coho salmon and steelhead between sampling periods spaced 4 h apart were examined using the overlap formula of Morisita (1959) modified by Horn (1966):

$$C_\lambda = \frac{2 \sum_{i=1}^s X_i \cdot Y_i}{\sum_{i=1}^s X_i^2 + \sum_{i=1}^s Y_i^2}$$

where C_λ = overlap coefficient
 s = food categories
 X_i = proportion of the total diet of fish

species X contributed by food category i

Y_i = proportion of the total diet of fish species Y contributed by food category i .

C_λ can range from 0, when samples contain no food in common, to 1, when there is identical representation of food between samples.

Results

A total of 130 coho salmon and 142 steelhead were examined for diet composition and feeding periodicity (Table 1). Subyearling coho salmon which emerge approximately 6 wk earlier than subyearling steelhead were substantially larger at the time of collection. Terrestrial invertebrates were the major components (51.3-62.3%) in the diurnal diet of coho salmon fry, whereas aquatic invertebrates were the major prey utilized at night (89.5-96.9%) (Table 2). Predation on terrestrial invertebrates was greatest between 1600 and 2000 h and greatest on benthic invertebrates between 2000 and 2400 h. Of the aquatic taxa immature chironomids were the most important item (17.1%) during the 24-h period although some diel variation in importance is suggested. Other less important aquatic items include adult chironomids (7.7%), caenid (7.0%), and leptophlebiid (6.8%) mayfly nymphs along with hydropsychid caddisfly larvae (6.0%). Homopterans (6.5%), dipterans (5.4%), and coleopterans (4.8%) were the major terrestrial invertebrates consumed. Overall, aquatic invertebrates composed 74.7% and terrestrial invertebrates 25.3% of the diel diet of coho salmon (Table 2).

Aquatic invertebrates were the principal food of subyearling steelhead throughout the 24-h period (Table 2). Although steelhead did not utilize terrestrial invertebrates to the extent that coho salmon did during diurnal feeding, temporal patterns in the consumption of terrestrial prey were

TABLE 1.—Number examined, mean total length (millimeters \pm 95% confidence limits), mean dry weight of fish (gram) and stomach contents (milligrams), and C_λ of subyearling coho salmon and steelhead. Data are from sampling intervals spaced 4 h apart, 13-14 July 1979, in Orwell Brook, N.Y.

Time	Coho salmon				C_λ	Steelhead			
	Number	Length	Weight	Stomach contents		Number	Length	Weight	Stomach contents
0800	20	70.9 \pm 4.1	0.63	1.83	0.70	24	49.7 \pm 2.7	0.23	1.40
1200	25	66.1 \pm 5.7	.53	2.01	.53	20	55.2 \pm 2.6	.32	1.66
1600	20	62.5 \pm 5.1	.45	.90	.42	28	53.7 \pm 1.6	.30	2.58
2000	21	71.0 \pm 3.5	.68	2.65	.64	24	55.1 \pm 2.5	.32	4.26
2400	22	68.4 \pm 3.9	.58	5.80	.82	24	51.1 \pm 2.4	.25	1.45
0400	22	64.4 \pm 4.6	.49	3.77	.91	22	49.0 \pm 2.8	.22	1.08

TABLE 2.—Percentage dry weight dietary composition of subyearling coho salmon and steelhead sampled at 4-h intervals over a 24-h period, 13-14 July 1979, in Orwell Brook, N. Y.

Taxon	Coho salmon							Steelhead						
	0400	0800	1200	1600	2000	2400	24-h total	0400	0800	1200	1600	2000	2400	24-h total
Oligochaeta	—	—	—	—	—	—	—	0.21	0.70	0.25	0.15	—	—	0.19
Ostracoda	—	—	—	—	—	—	—	—	.08	—	—	—	—	.01
Hydracarina	0.05	0.92	0.48	1.59	0.32	0.07	0.31	.27	.58	.16	.67	0.59	0.55	.52
Collembola	.06	—	.56	—	.09	—	.09	1.41	.14	.67	.10	.18	—	.29
Plecoptera:														
Chloroperlidae	.88	—	—	—	—	—	.20	1.53	—	—	—	—	—	.10
Leuctridae	4.64	6.28	—	—	—	2.46	2.62	4.12	—	—	1.24	—	1.13	.69
Perlidae	5.06	—	—	—	6.24	8.28	3.23	2.02	3.82	—	6.19	.36	.60	2.30
Unidentified	.05	—	1.96	1.25	—	.15	.33	—	1.01	1.08	—	.84	—	.54
Ephemeroptera:														
Baetidae	3.95	3.88	.81	—	.55	3.50	2.77	9.69	11.27	16.11	12.30	6.53	8.31	9.93
Caenidae	.25	1.74	.28	—	—	18.10	7.03	11.01	5.04	10.46	5.21	2.48	5.88	5.35
Ephemerellidae	2.27	3.13	—	—	—	4.38	2.47	1.19	1.39	—	1.60	.83	6.30	1.63
Ephemeridae	—	—	.98	—	—	3.88	1.55	—	—	—	—	—	—	—
Heptageniidae	.27	.29	—	2.24	—	2.71	1.21	2.94	—	—	—	—	2.99	.57
Leptophlebiidae	7.53	.47	1.15	—	—	13.33	6.83	4.00	1.31	1.89	2.00	1.18	1.94	1.75
Unidentified	1.65	.89	23.32	1.99	7.42	—	4.22	—	6.59	9.62	15.52	2.50	.77	6.30
Odonata:														
Aeshnidae	—	—	—	—	—	.54	.20	—	—	—	—	—	—	—
Trichoptera:														
Glossosomatidae	.16	.58	.14	—	—	.23	.19	—	—	—	1.76	.92	2.04	.95
Helicopsychidae	—	—	—	—	.26	—	.04	.59	—	—	—	.28	—	.14
Hydropsychidae	11.77	1.77	5.60	—	.72	6.55	5.98	4.12	5.37	2.60	.71	.66	15.91	3.51
Odontoceridae	—	—	—	—	—	—	—	2.10	—	—	1.53	—	1.06	.61
Philopotamidae	2.93	—	—	—	—	.27	.76	—	—	—	—	—	—	—
Polycentropodidae	.41	—	—	—	—	—	.09	—	—	—	.23	—	—	.05
Unidentified	4.76	8.35	2.52	—	2.81	2.64	3.66	2.24	.30	—	2.48	2.32	3.80	2.30
Hemiptera:														
Veliidae	.41	—	—	—	—	—	.10	—	—	—	—	—	—	—
Megaloptera:														
Stalidae	—	1.66	—	—	—	.12	.22	—	.20	—	—	—	—	.02
Coleoptera:														
Dytiscidae	.49	—	—	2.49	1.12	—	.41	—	—	—	—	—	—	—
Elmidae	.76	.80	—	2.12	—	1.36	.86	—	1.09	—	—	—	2.06	.37
Psephenidae	.37	4.39	—	—	—	.70	.81	—	1.22	.84	.63	.48	3.70	.99
Diptera:														
Ceratopogonidae	.10	.39	—	—	—	.17	.12	—	.11	—	—	.08	.50	.22
Chironomidae, immature	27.48	12.95	3.31	7.04	3.28	22.28	17.08	26.33	25.80	20.03	8.44	20.34	20.82	18.76
Chironomidae, adult	11.76	3.50	7.55	12.34	12.34	3.35	7.67	14.16	3.40	2.85	9.06	15.96	15.45	11.10
Dixidae	—	—	—	—	—	.19	.07	—	—	—	—	—	.88	.10
Simuliidae	.41	.75	—	—	—	.61	.40	—	—	1.41	—	.15	.35	.23
Tipulidae	1.02	11.75	.02	15.15	2.59	1.01	3.04	2.89	16.19	.25	.10	1.11	.56	2.64
Gastropoda:														
Physidae	—	—	—	—	—	—	—	1.88	—	—	—	—	—	.13
Fish larvae	.65	—	—	—	—	—	.14	—	5.92	—	1.15	—	—	.95
Aquatic food total	90.14	64.49	48.68	46.21	37.74	96.88	74.70	92.70	91.53	68.22	71.79	57.79	95.60	73.24
Annelida	—	—	—	19.29	—	—	.90	—	—	—	—	—	—	—
Arachnida	.91	1.27	1.93	—	—	.26	.63	—	.75	1.47	.98	.91	—	.80
Coleoptera	2.91	5.15	3.19	.47	19.16	.19	4.82	5.30	3.83	4.29	5.27	12.07	2.64	7.05
Dermoptera	—	—	1.04	—	.98	—	.27	—	.17	.23	.06	.87	—	.35
Diptera	1.18	5.94	9.21	18.37	13.48	1.16	5.39	.88	1.36	6.58	5.82	7.15	—	4.98
Hemiptera	.93	.88	11.64	2.33	2.35	.47	2.17	1.12	.44	6.63	6.44	3.21	1.76	3.67
Homoptera	3.77	13.93	10.33	10.96	14.59	.34	6.45	—	.95	1.46	2.00	14.01	—	5.49
Hymenoptera	.16	2.89	13.98	2.37	11.70	.70	4.09	—	.97	8.93	7.64	3.99	—	4.15
Lepidoptera	—	5.45	—	—	—	—	.58	—	—	2.19	—	—	—	.27
Terrestrial food total	9.86	35.51	51.32	53.79	62.26	3.12	25.30	7.30	8.47	31.78	28.21	42.21	4.40	26.76

identical for the two species. Terrestrial prey were most important in the diurnal diet of steelhead (28.2-42.4%) whereas nocturnal feeding was almost exclusively on autochthonous prey (92.7-95.6%). Like coho salmon, peak consumption of terrestrial invertebrates by steelhead occurred from 1600 to 2000 h while peak consumption of aquatic prey was from 2000 to 2400 h. Baetid, caenid, and leptophlebiid mayfly nymphs along with immature and adult chironomids were the

only aquatic prey taxa which were well represented in the diet of steelhead during each 4-h interval (Table 2).

The two species exhibited diel differences in feeding intensity (Figure 1). Coho salmon fry fed heaviest from 2000 to 2400 h, while peak feeding of steelhead trout fry occurred from 1600 to 2000 h. (The feeding intensity of steelhead fry also increased substantially from 1200 to 1600 h.) In general, the greatest variation in the amount of

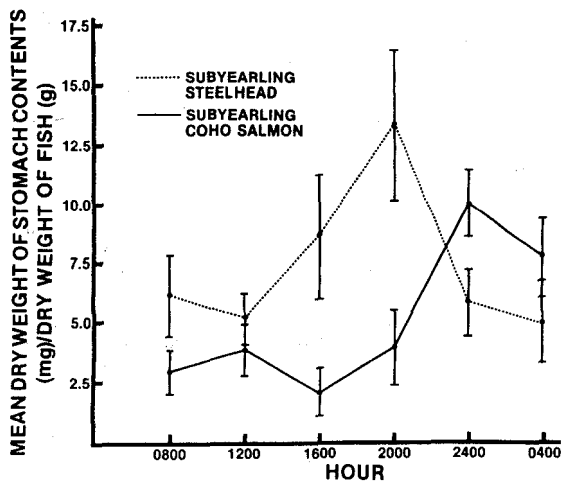


FIGURE 1.—Relative food contents (with 95% confidence limits) of subyearling coho salmon and steelhead at 4-h intervals, 13-14 July 1979, in Orwell Brook, NY.

food consumed among individual fish occurred during peak feeding periods in both species. Coho salmon appear to be primarily nocturnal feeders since their stomachs during periods of low light intensity (2000-0800 h) were much fuller ($\bar{x} = 6.87$ mg stomach contents/g fish) than during daylight periods (0800-2000 h) ($\bar{x} = 3.23$ mg stomach contents/g fish). Conversely, steelhead are predominately diurnal feeders. Their stomachs during the day ($\bar{x} = 9.03$ mg stomach contents/g fish) were considerably fuller than at night ($\bar{x} = 5.60$ mg stomach contents/g fish).

We estimated the daily meal (amount of food consumed per day) and the daily ration (amount of food consumed per day expressed as a percentage of the fish's body weight) for subyearling coho salmon and steelhead in Orwell Brook. The daily meal of coho salmon was estimated as 10.6 mg and the daily ration was 1.7% of their dry body weight. For steelhead the daily meal was estimated as 7.8 mg and the daily ration as 2.8%.

To investigate the hypothesis that the diet of coho salmon fry was more variable than that of steelhead fry over a 24-h period the overlap formula was used to compare diet similarity for each species between each 4-h sampling interval. When employing this formula, $C_\lambda \geq 0.60$ is assumed significant (Zaret and Rand 1971). Using this criterion, all possible combinations for steelhead are significant (Table 3). Only 4 of the 15 comparisons for coho salmon are significant while

TABLE 3.—Diet similarity values (C_λ) for subyearling coho salmon and steelhead between sampling periods spaced 4 h apart, 0800 h 13 July to 0400 h 14 July 1979.

		Steelhead					
		0800	1200	1600	2000	2400	0400
Coho salmon	0800		0.82	0.65	0.67	0.80	0.86
	1200	0.41		0.89	0.72	0.78	0.84
	1600	0.72	0.47		0.69	0.72	0.71
	2000	0.47	0.60	0.56		0.73	0.76
	2400	0.50	0.12	0.20	0.10		0.94
	0400	0.64	0.24	0.38	0.26	0.73	

their mean C_λ , 0.43, is much lower than that of steelhead, 0.77 (Table 4).

The diet of coho salmon and steelhead during similar 4-h intervals differed. The greatest overlap occurred between 2400 and 0400 h and the lowest from 1200 to 1600 h (Table 1). Overall, the mean diel overlap in diet between coho salmon and steelhead was significant ($C_\lambda = 0.67$).

Discussion

The results of this study support the hypothesis that the diet composition of subyearling coho salmon is more variable over a 24-h period than that of sympatric subyearling steelhead. The C_λ 's for each species between different 4-h intervals (Table 4) indicate that the diet composition of coho salmon was variable, whereas that of steelhead was fairly uniform over the 24-h study period. In fact, the data show that at no time did the diet of steelhead fry (mainly aquatic invertebrates) differ substantially from diets at other 4-h intervals (e.g., all C_λ 's were significant). The low similarity in the diel diet of coho salmon, as postulated, was due to the predominance of terrestrial prey in their daytime diet and predominance of aquatic prey in their nocturnal diet as C_λ 's between daytime (0800-2000 h) and nocturnal (2000-0800 h) periods for coho salmon were generally the lowest ($\bar{x} = 0.32$). Unfortunately, samples of the invertebrate drift were not taken at 4-h intervals concurrent with these fish collections. We suspect, however, that the variability in the diet of coho salmon was due to diel fluctuations in the composition of the drift, which are well documented in streams (Hynes 1970). In many streams during the summer, terrestrial invertebrates dominate the diurnal drift (Hinckley and Kennedy 1972; Johnson and Ringler 1980) while aquatic invertebrates dominate the nocturnal drift (Hynes 1970; Hinckley and Kennedy 1972). Since the diet of coho salmon fry in Orwell Brook has been shown to be significantly associated with the composition

of the drift, it is apparent why the diet composition, in synchrony with the drift, varies over a 24-h period.

Mason (1966) demonstrated nocturnal feeding activity of coho salmon fry. He attributed the night feeding habits of coho salmon to high retinal cone sensitivity, believing that it aided them in utilizing the increased drift of aquatic invertebrates during periods of low light intensity. Jenkins³ observed that rainbow trout fed most actively at midday and that the diet at this time was composed mainly of terrestrial invertebrates which predominated in the drift. However, these fish were overyearlings, so a direct comparison with this study (fry) cannot be made since as salmonids grow older (and larger), not only do they occupy different habitats (Saunders and Smith 1962) but they also utilize different prey species (Kallenberg 1958), in addition to eating larger prey when available (Allen 1969). Tippets and Moyle (1978), however, did demonstrate that during the summer, rainbow trout fry fed predominantly on drifting invertebrates during the day in the McCloud River, Calif. In Orwell Brook in 1977, the diurnal diet of steelhead fry during the summer was found to be more closely associated with the composition of the bottom fauna rather than with the composition of the drift (Johnson and Ringler 1980). These differences in the feeding of steelhead may be due to social interaction between coho salmon and steelhead fry in Orwell Brook. In sympatry, during the summer, coho salmon occupy pools while steelhead utilize riffles (Hartman 1965; Allee 1974). In allopatry, although steelhead fry occupy both habitats, they prefer pools (Hartman 1965). If riffle versus pool occupancy influences the prey selection of coho salmon and steelhead as suggested by Johnson and Ringler (1980), the diets of steelhead fry in allopatric (predominately pools) and sympatric (predominantly riffles) situations with coho salmon may be expected to differ.

Although subyearling coho salmon actually consumed more food (10.6 mg daily meal) than subyearling steelhead (7.8 mg), because coho salmon were much heavier (Table 1), their daily ration was substantially less than steelhead (1.7 and 2.8% daily rations). Elliott and Persson (1978) suggested that, when using their formula to esti-

mate daily food consumption, sampling intervals should be 3 h or less; larger intervals may result in inaccurate estimates. Since our sampling interval was 4 h and rates of gastric evacuation were determined from the literature (i.e., rainbow trout fry fed oligochaetes, Windell et al. 1976) using mean water temperatures (16°-21° C) for each 4-h interval, our results are, at best, rough estimates of the daily meal and daily ration of subyearling coho salmon and steelhead. However, our estimates are well within the range of juvenile sockeye salmon, *Oncorhynchus nerka*, in a lacustrine environment in Washington (Doble and Eggers 1978).

Johnson and Ringler (1980) found that the diurnal diet (0900-1500 h) of coho salmon and steelhead fry did not overlap substantially (i.e., $C_{\lambda} \geq 0.60$) from June through September in Orwell Brook during 1977. Interestingly, the only time that the diet of these two species did not overlap significantly in this study was during approximately the same period, 0800-1600 h (Table 1). The highest degree of overlap in the diets of coho salmon and steelhead occurred from 2000 to 0400 h when both species were feeding mainly on aquatic invertebrates. Inspection of diet overlap during twilight feeding periods (0400-0800 and 1600-2000 h) indicates significant overlap ($\bar{x} = 0.67$), which is distinctly intermediate between diurnal ($\bar{x} = 0.48$) and nocturnal ($\bar{x} = 0.87$) periods. The large diel fluctuations in diet similarity between these two species indicate that diel studies are necessary when examining aspects of their trophic ecology, at least when the species occur sympatrically. Daytime food studies could lead to the erroneous speculations that the diet of sympatric juvenile coho salmon and steelhead is not similar and that terrestrial invertebrates (at least during certain periods of the year) are the major component in the diet of coho salmon. Conversely, examination of the stomachs contents during nocturnal and crepuscular periods would indicate a great deal of similarity in diet and would not reflect the importance of allochthonous material in the daytime diet of coho salmon.

Acknowledgments

We thank N. Ringler and R. Sloan for their helpful comments on the manuscript. We also thank A. Crawford who typed the manuscript and G. Furman who prepared the figure.

³Jenkins, T. M., Jr. 1970. Behavior-ecology. In Progress in sport fishery research, p. 138-141. U.S. Fish Wildl. Serv., Bur. Sport Fish Wildl.

Literature Cited

- ALLEE, B. J.
1974. Spatial requirements and behavioral interactions of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). Ph.D. Thesis, Univ. Washington, Seattle, 160 p.
- ALLEN, K. R.
1969. Limitations on production in salmonid populations in streams. In T. G. Northcote (editor), Symposium on salmon and trout in streams, p. 3-18. H. R. MacMillan Lectures in Fisheries, Univ. B.C., Vancouver.
- DOBLE, B. D., AND D. M. EGGERS.
1978. Diel feeding chronology, rate of gastric evacuation, daily ration, and prey selectivity in Lake Washington juvenile sockeye salmon (*Oncorhynchus nerka*). Trans. Am. Fish. Soc. 107:36-45.
- ELLIOTT, J. M., AND L. PERSSON.
1978. The estimation of daily rates of food consumption for fish. J. Anim. Ecol. 47:977-991.
- HARTMAN, G. F.
1965. The role of behavior in the ecology and interaction of underyearling coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 22:1035-1081.
- HINCKLEY, T. M., AND H. D. KENNEDY.
1972. Fluctuations of aquatic and terrestrial invertebrates in drift samples from Convict Creek, California. Northwest Sci. 46:270-276.
- HORN, H. S.
1966. Measurement of "overlap" in comparative ecological studies. Am. Nat. 100:419-424.
- HYNES, H. B. N.
1970. The ecology of running waters. Univ. Toronto Press, Toronto, 555 p.
- JOHNSON, J. H.
1980. Production and growth of subyearling coho salmon, *Oncorhynchus kisutch*, chinook salmon, *Oncorhynchus tshawytscha*, and steelhead, *Salmo gairdneri*, in Orwell Brook, tributary of Salmon River, New York. Fish. Bull., U.S. 78:549-554.
- JOHNSON, J. H., AND N. H. RINGLER.
1980. Diets of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*) relative to prey availability. Can. J. Zool. 58:553-558.
- KALLENBERG, H.
1958. Observations in a stream tank of territoriality and competition in juvenile salmon and trout (*Salmo salar* L. and *S. trutta* L.). Inst. Freshwater Res. Drottningholm Rep. 39:55-98.
- MASON, J. C.
1966. Behavioral ecology of juvenile coho silver salmon (*O. kisutch*) in stream aquaria with particular reference to competition and aggressive behavior. Ph.D. Thesis, Oregon State Univ., Corvallis, 195 p.
- MILNE, D. J.
1948. The growth, morphology and relationship of the species of Pacific salmon and the steelhead trout. Ph.D. Thesis, McGill Univ., Montreal, 101 p.
- MORISITA, M.
1959. Measuring of interspecific association and similarity between communities. Mem. Fac. Sci. Kyushu Univ., Ser. E (Biol.), 3:65-80.
- NILSSON, N. A.
1967. Interactive segregation between fish species. In S. D. Gerking (editor), The biological basis of freshwater fish production, p. 295-313. Blackwell Sci. Publ., Oxf.
- PARKER, R. R.
1963. Effects of Formalin on length and weight of fishes. J. Fish. Res. Board Can. 20:1441-1455.
- SAUNDERS, J. W., AND M. W. SMITH.
1962. Physical alteration of stream habitat to improve brook trout production. Trans. Am. Fish. Soc. 91:185-188.
- TIPPETS, W. E., AND P. B. MOYLE.
1978. Epibenthic feeding by rainbow trout (*Salmo gairdneri*) in the McCloud River, California. J. Anim. Ecol. 47:549-559.
- WINDELL, J. T., J. F. KITCHELL, D. O. NORRIS, J. S. NORRIS, AND J. W. FOLTZ.
1976. Temperature and rate of gastric evacuation by rainbow trout, *Salmo gairdneri*. Trans. Am. Fish. Soc. 105:712-717.
- ZARET, T. M., AND A. S. RAND.
1971. Competition in tropical stream fishes: support for the competitive exclusion principle. Ecology 52:336-342.

JAMES H. JOHNSON

New York State Department of Environmental Conservation
50 Wolf Road, Albany, N.Y.
Present address: Nez Perce Tribe of Idaho
P.O. Box 365, Lapwai, ID 83540

EMILY Z. JOHNSON

Department of Environmental and Forest Biology
State University of New York College of
Environmental Science and Forestry
Syracuse, NY 13210

THE OCCURRENCE OF *CIROLANA BOREALIS* (ISOPODA) IN THE HEARTS OF SHARKS FROM ATLANTIC COASTAL WATERS OF FLORIDA

Extensive depredation of catch triggered the closing of the only large commercial shark fishery on the Florida east coast (at Cape Canaveral) in October 1978. Shark catches had been affected throughout a 403 km stretch of nearshore waters from St. Augustine to Fort Pierce, Fla., from between 29 and 56 km offshore, at depths of 20-43 m. The organism responsible was a marine isopod, *Cirolana borealis* (Bowman¹).

The presence of isopods (thought to be worms by the fishermen) in the heart of a shark was discovered in October 1977, when the pericardial

¹Thomas E. Bowman, Curator, Crustacea, Department of Invertebrate Zoology, National Museum of Natural History, Washington, DC 20560, pers. commun. September 1978.