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Mark W. Buktenica for the degree of Master of Science in Fisheries Science presented on May 23, 1988.

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Gary L. Larson

Crater Lake, originally barren of fish, was stocked on an irregular basis from 1888 through 1941 with several species of salmonids. Two species occur in the lake today--kokanee salmon (Oncorhynchus nerka) and rainbow trout (Salmo gairdneri). This study was initiated in the summer of 1986 to evaluate the ecology of adult fish in terms of length, weight, age, growth, morphology, food habits, and distribution in Crater Lake relative to the lake's limnological characteristics. Fish were captured with gill nets, by angling, and with a modified downrigger. Age determinations from scale analysis, supported by modal progressions in length frequency histograms indicated that kokanee salmon age composition was heavily dominated, in number, by the 1984 year class. Spawning by members of this cohort was recorded in January 1988. Both species exhibited growth rates comparable to other northwest populations in

oligotrophic lakes. Food resources were partitioned in that kokanee salmon generally fed on small-bodied taxa (mean weight 1.2 mg) from the midwater column and from the lake bottom, rainbow trout fed on large-bodied taxa (mean weight 9.8 mg) from the lake surface and the lake bottom. Distribution and diel migrations of fish were assessed with hydroacoustic techniques during the first week in September 1987. Fish underwent diel migrations within and between the nearshore (0 m to 100 m contour) and offshore (100 m to 589 m contour) zones of the lake. Based on capture records, it appeared that kokanee were primarily offshore and in deep water during the day, and then they moved shoreward into shallower water at night. Rainbow trout appeared to remain nearshore, in shallower water during the day than at night. The maximum depth for an acoustic target was 98.5 m. The maximum depth of capture for kokanee in Crater Lake was 86.25 m.

ECOLOGY OF KOKANEE SALMON AND RAINBOW TROUT IN CRATER LAKE, A DEEP ULTRAOLIGOTROPHIC CALDERA LAKE (OREGON)

by

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INTRODUCTION

Crater Lake covers the floor of the Mt. Mazama caldera that formed about 6,800 years ago (Bacon, 1983). It is a closed lake system in that the surface inlets originate inside of the caldera and there is no surface outlet. Though originally barren of fish, several species of salmonids were stocked on an irregular basis from 1888 through 1941 (Table 1). The species included rainbow trout (*Salmo gairdneri*), brown trout (*Salmo trutta*), cutthroat trout (*Salmo clarki*), steelhead trout (*Salmo gairdneri*), and coho or "silverside" salmon (*Oncorhynchus kisutch*). However, Wallis and Bond (1950) identified six kokanee salmon (*Oncorhynchus nerka*) that had been collected in 1939 and 1947 and presumed to be coho salmon. Since there is no stocking record of kokanee in Crater Lake, it is unclear if early fisheries investigations collected one or both of the Pacific salmon species. No coho salmon have been identified from Crater Lake since 1950. Today only two fish species are known to inhabit the lake, kokanee salmon and rainbow trout.

Fisheries investigations of Crater Lake date back to 1896 (Table 2). Most were conducted during the stocking era. Many of these studies were restricted by small sample sizes and were of short duration (e.g., one day) because the investigations were dependent on samples from fishermen's creels. Among the more comprehensive works were Hasler and Farner's (1942) study of food habits and growth of fish and Brode's (1938) general study of flora and fauna of Crater Lake. Although these studies provide a historic data base for future studies, it is clear that very little is known about the roles of fish within the structure and organization of the Crater Lake ecosystem.

Optical and phytoplankton studies conducted from 1978 to 1981 raised concern that the process of eutrophication had been

Table 1. Recorded Fish Liberations in Crater Lake, Oregon.

YEAR	RAINBOW TROUT	BROWN TROUT	SILVERSIDE SALMON	CUTTHROAT TROUT	STEELHEAD TROUT
1888	37	-	-	-	-
1910	50,000	-	-	-	-
1914	2,000	15,000	-	-	20,000
1922	25,000	-	3,500	-	-
1923	-	-	-	14,000	11,000
1924	24,000	-	-	-	-
1925	-	-	22,500	-	-
1926	-	-	-	-	-
1927	46,800	-	-	-	-
1928	64,000	-	-	-	-
1929	-	-	-	-	-
1930	3,000	-	7,500	-	-
1931	-	-	-	-	98,000
1932	156,000	-	-	-	163,000
1933	-	-	200,000	-	150,000
1934	-	-	54,000	-	-
1935	-	-	100,000	-	20,000
1936	-	-	25,000	-	25,000
1937	100,000	-	50,000	-	-
1938	-	-	-	-	-
1939	100,000	-	50,000	-	-
1940	85,820	-	-	-	-
1941	20,000	-	-	-	-

Table 2. Fisheries Investigations on Crater Lake, Oregon.

YEAR(S) OF STUDY	PRIMARY TOPIC	SAMPLE SIZE RAINBOW TROUT	 "SILVERSIDES"	 KOKANEE	 UNSPECIFIED	REFERENCES
1896	Fitness of Crater Lake as Fish Habitat	--	--	--	--	Evermann(1897)
1933	Food Habits of Oregon Trout	1	0	0	0	Dimick and Mote (1934)
1933	Food Habits	0	0	0	70	Hubbard (1934) (Unpublished Manuscript)
1934	Food Habits	4	46	0	0	Brode (1935)
1934-1936	Floral and Faunal Survey Food Habits	0	214	0	0	Brode (1938)
1937	Creel Census Age and Growth	-- 124	-- 151	-- 0	-- 0	Hasler (1938)
1937-1940	Creel Census Age and Growth Food Habits (1940 Only)	-- 0 0	-- 0 0	-- 0 0	-- 749 79	Hasler and Farner (1942)
1939, 1947	Identification of Kokanee Salmon in Crater Lake, Oregon	0	6	0	0	Wallis and Bond (1950)
1952-1953	Food Habits	6	4	0	0	Baird (1956)
1953-1956	Food Habits	117	44	0	0	Patten and Thompson (1957) (Unpublished Manuscript)
1966	Age and Size	0	0	0	179	Kibby (1966) (Unpublished Manuscript)
1982	Gill net Capture Feasibility	34	5	0	0	Fortune and Toman (1982) (Unpublished Manuscript)
1985	Hydroacoustics Feasibility	--	--	--	--	Thorne and Marino (1985) (Unpublished Manuscript)

accelerated in Crater Lake (Larson, 1984). This concern led to a comprehensive ten-year limnological investigation of Crater Lake of which this study is a part. The goals of this limnological investigation are (1) to develop a reliable limnological data base for the lake for future comparison; (2) to develop a better understanding of physical, chemical, and biological characteristics and processes of the lake; and (3) to establish a long-term monitoring program to examine the characteristics of the lake through time. The main objective is to stress ecological relationships among trophic levels and environmental conditions to bring a more holistic approach to the baseline data in order to evaluate the hypothesis that the lake has changed (Larson, 1987).

The principal goal of this thesis is to develop a better understanding of the ecological roles of fish in Crater Lake. The primary objectives toward attaining this goal are as follows:

Objective 1. Document and compare the ecology of adult fish in terms of length, weight, age, growth, morphology, food habits and distribution in Crater Lake.

Objective 2. Evaluate the ecology of each species relative to the limnological characteristics of Crater Lake.

Development of a thorough understanding of the ecological role of fish in Crater Lake would require a study of the ecology of the fish throughout their life histories. Because of limitations imposed by the nature and accessibility of Crater Lake, and limitations inherent in sampling equipment, this study will necessarily focus on the ecology of adult kokanee salmon and rainbow trout. None the less, this study will serve as a strong foundation on which to build future programs.

STUDY AREA

Crater Lake is an ultraoligotrophic, caldera lake, located at 1,882 meters in elevation (Nelson, 1967) on the backbone of the Cascade Mountains in southwestern Oregon. The lake is widely known for its exceptional water clarity. Crater Lake is the eighth deepest lake in the world and is one of the clearest freshwater lakes (Hutchinson, 1957).

Crater Lake, with its distinctive regime of environmental conditions, provides an unusual habitat for its biota. The caldera walls are composed of rock cliffs and precipitously steep talus slopes rising 250 to 600 meters above the lake surface and continuing at slightly reduced slopes below the water line where they eventually flatten out into three main basins at 450 meters, 550 meters, and 589 meters in depth. The littoral zone is comprised of a very narrow band around the 48 km^2 lake that widens slightly around Wizard Island where nearly one third (by surface area) of the littoral region exists.

A shallow epilimnion typically forms to a depth of 5 to 20 m from late July to September; a well defined thermocline may not develop until September as occurred in 1986 (Larson, 1987). The water column is well oxygenated displaying a slight decrease in dissolved oxygen (D.O.) in the surface strata with increasing temperature, and a slight decrease in D.O. at 550 m. Total Alkalinity is generally uniform with depth ranging from 25 to 27 mg/l $CaCO_3$. Conductivity ranges from 112 to 120 micromhos/cm and increases slightly with depth.

The photic zone extends to great depths as evidenced in part by Secchi disc transparency readings approaching 40 meters (37.2 m, July 1985) and 1% incident surface light intensities extending 80 to 100 m in depth (Larson, 1986). It is further evidenced by the unusually deep depth distributions of the lake's flora and fauna. During summer months the chlorophyll maxima typically occur between

100 m and 140 m (Larson, 1986). Zooplankton abundance was greatest between 40 m and 120 m in depth and was dominated in abundance by rotifers in 1986 and 1987 (Karnaugh, 1988). The freshwater mosses, Fontinalis and Drepanocladus, have been found growing in thick mats at 120 meters, the deepest reported occurrences in the world (Hasler, 1938).

MATERIALS AND METHODS

Capture Methods

Fish were collected from early June through September at weekly intervals in 1986 and 1987. In addition, fish were collected once in April 1987, October 1987, and January 1988. Horizontal gill nets were set overnight on the limited shelf-like areas around Crater Lake down to 20 meters to capture fish near the shore (Figure 1). Both floating and sinking multifilament nets measuring 38 m x 3 m were used. Mesh sizes ranged from 19 mm (3 1/4 in.) to 51 mm (2 in.) square mesh, in five 7.6 m panels.

Vertical gill nets were designed and deployed from the lake surface to depths of 86 meters (275 feet). Two monofilament panels 3 m x 86 m, one of 38 mm square mesh and one of 32 mm square mesh (the most successful mesh sizes in capturing kokanee near the shore), were made and tested in 1986. No fish were captured. Larger panels were impractical to deploy from the research vessels. Vertical gill nets were not used in 1987.

A sportsmen's downrigger (fine cable on a hand-winch) was modified to troll for fish in the offshore areas (from the 100 m to the 589 m contour). An artificial lure or a lure and flasher (for attraction) was attached to the cable at five-meter intervals to 100 meters (Figure 2). A similar lure was trolled behind the boat to fish the near surface depths. Angling with rod and reel was employed along the shoreline with artificial lures.

Field Measurements

Fork length and total length were measured to the nearest millimeter on an 0.6 m measuring board. Whole fish weights were determined on a Homs top-loading temperature compensated spring dial scale (1000 gm in 2 gm increments) to the nearest gram. Scales for ageing were taken, by scraping with the blunt edge of a scalpel blade, just below the posterior margin of the dorsal fin and above

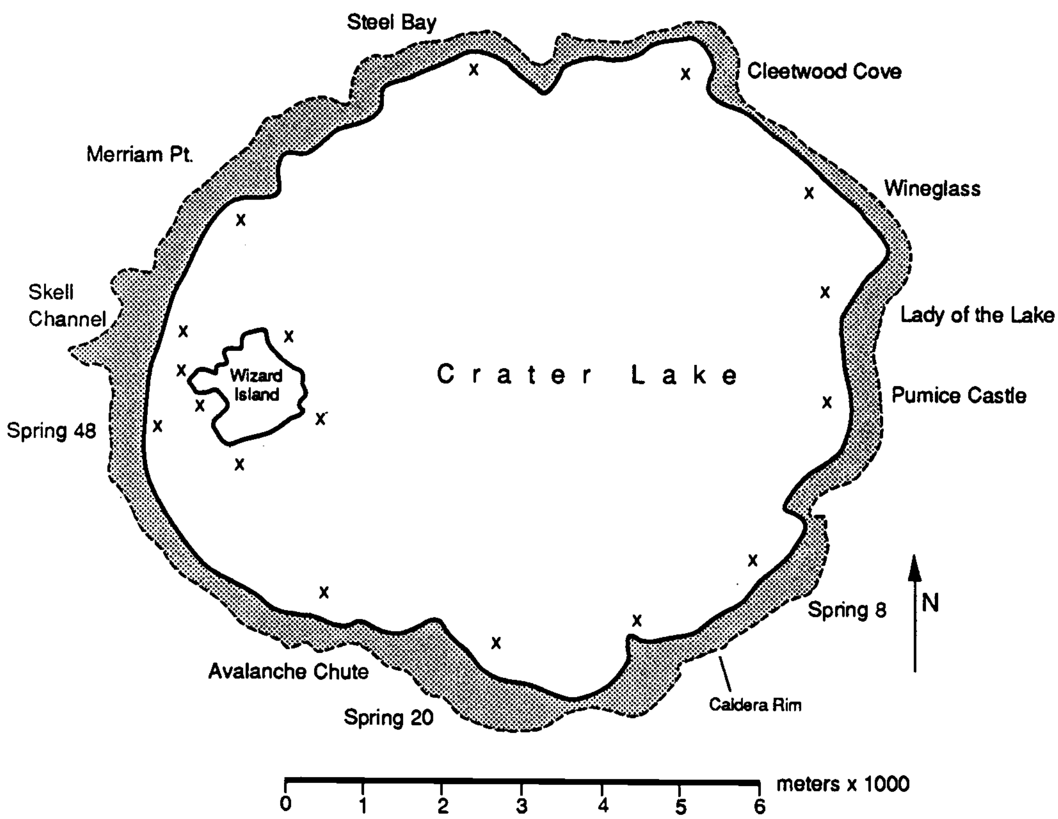


Figure 1. Location of Horizontal Gill Net Sets (X) on Crater Lake, Oregon.

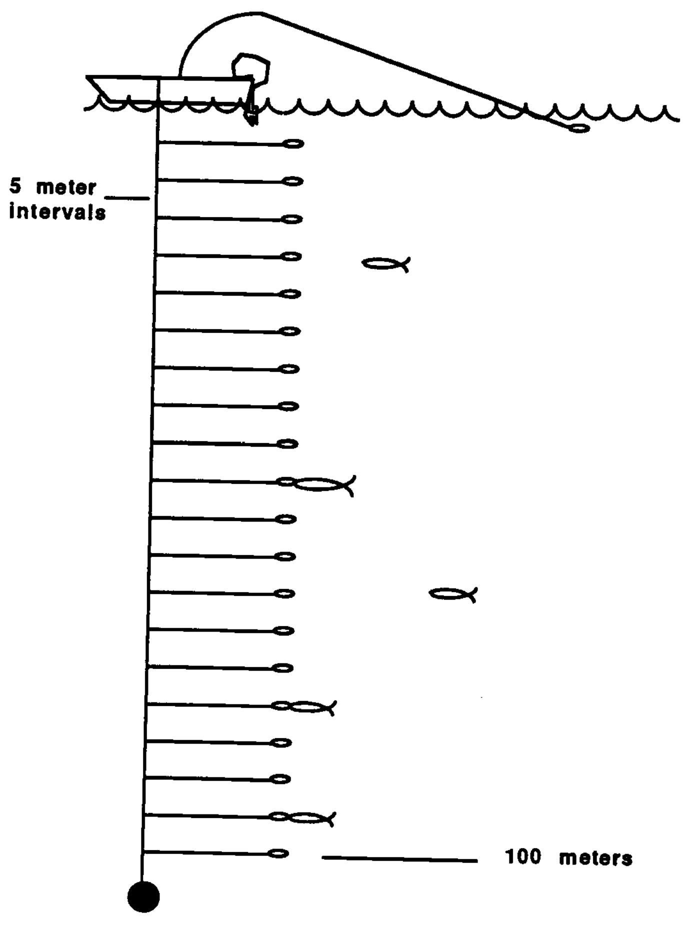


Figure 2. Diagram Depicting the Downrigger Capture Method with Lures at 1 m below the surface and at 5 m Intervals to 100 m.

the lateral line (Jearld, 1983). After the body cavity was slit ventrally, the fish were sexed (ripening ova were removed, preserved and archived) and the specimens were preserved in 10% formalin.

Meristics and Morphometrics

All fish collected were stratified by length class, and a subsample of ten fish was chosen randomly out of each length class for rainbow trout, kokanee captured in the nearshore area, and kokanee captured in the offshore area. Mouth width was estimated as the greatest ventral distance across the mouth opening. Gill raker measurements and counts were taken on the first left gill arch, under magnification. Gill raker counts included all projections lying in a near linear series along the arch (Nelson, 1968b). Gill raker length was measured, using pointed dial calipers (.05 mm dial graduations), as the distance from the tip to the ventral margin of the base of the longest anterior gill raker (Kliewer, 1970). Gill raker spacing was measured as the distance from center to center, from the origin of the base of the longest anterior gill raker to the same location on the gill raker ventral to it. Analysis of variance was used to statistically analyze the meristic data.

Age

Six scales from each fish were cleaned and mounted between two microscope slides. The mounted scales were viewed through a microfiche projector for age determination. Distances between the scale focus, annuli, and the scale margin were taken on a subsample of scales utilizing a BioSonics Optical Pattern Recognition System (OPRS). The OPRS consists of a microscope, a video camera and monitor, a real-time video frame grabber, a digitizing tablet, and a microcomputer and software. Individual circuli distances and optical images were stored on floppy disk and archived. Length frequency analysis and modal-progression analysis (e.g. following the relative abundance of a dominant year class from year to year) were used as age validation techniques (Jearld, 1983).

The internationally accepted convention for aging fish is to designate January 1 as the birth date of fish in the Northern Hemisphere, whether or not the annular ring or slow growth zone is complete by this date (Jearld, 1983). No scales have been analyzed from fish captured between October and April at Crater Lake due to the inaccessability of the lake in the winter; therefore, the terminal edge of the annular ring was used to designate age class instead of scale development on January 1. Fish in their first year of life, before completion of the first annular ring were designated as members of the age-0 group. Fish captured after the completion of the first annular ring but prior to completion of the second annular ring were designated as members of the age-I+ group. The same convention was used to designate members of subsequent age groups (e.g., II+, III+, IV+, . . . VII+).

Growth

Growth of Crater Lake fish was assessed from the length-weight relationships, by length at age, and by back-calculated length at age. Length at age averages the length at capture over the sampling season for a given age class. Back-calculated length at age calculates the length at time of annular ring formation. Values from the two methods are expected to differ; however, both methods can be useful in comparing growth of Crater Lake fish with other lake populations and with historic Crater Lake fish data.

Food Habits

Whole fish were originally fixed in 10% formalin, primarily to harden fragile stomach contents (e.g. zooplankton) and later transferred to ethanol. After the stomachs were removed, the contents from each stomach were flushed (from the esophagus to the pyloric sphincter) and stored in 70% ethanol in individual containers for later enumeration.

Samples were sorted with the aid of a binocular dissecting microscope 6x to 50x. Remains of all taxa were identified and enumerated when either an intact individual was present or when an intact and readily identifiable body part was present: midge larvae--head capsule; caddis pupae and adults--thorax or genitalia; Hymenoptera--thorax or head capsule (Bob Wisseman, Oregon State University, Department of Entomology). Samples were identified to a finer taxonomic resolution for mean weights and ecological classification (Table 3) and grouped into taxonomic categories (e.g., order) for primary data analysis. Zooplankton samples were diluted to an acceptable concentration and two 1-ml subsamples were counted. Remains were enumerated when either whole specimens were intact or individual eyespots were intact. Samples were counted in a rectangular counting chamber with longitudinal divisions under a binocular dissecting microscope (40x). Subsample counts were multiplied by their corresponding dilution factors to obtain the total zooplankton count for each stomach sample.

Replicate sets of one to one hundred individuals of the least digested individuals of each taxa were sorted for weight measurements. Estimated weights were applied to many taxa (when good specimens were not available); the estimated weights are based on equivalent sized specimens (ethanol preserved) in various data sets available through R.W. Wisseman and N.H. Anderson (Oregon State University, Department of Entomology). Samples were dried at 60^{o} Celsius to constant weight and placed in a dessicator to cool to room temperature. Dry weights were measured on a Mettler H16 (accuracy 0.05 mg) and a Cahn 4100 Electrobalance (accuracy 0.005 mg). All weights are uncorrected for partial digestion and preservation in formalin and ethanol.

Food habits analysis included frequency of occurrence, percent composition by number, percent composition by weight, percent composition by vertical distribution (by weight), percent composition by aquatic or terrestrial origin (by weight), and mean

Table 3. Life Stage, Mean Weight, and Percent Composition by Aquatic Versus Terrestrial Production (by Weight) and by Vertical Distribution in the Water Column (by Weight) for each Prey Taxa Found in Kokanee Salmon and Rainbow Trout Stomach Samples, Crater Lake, Oregon.

Taxa	Life Stage[a]	Mean Weight (milligrams)[b]	Percent Composition by Aquatic vs. Terrestrial Production (by weight)[c]	Percent Composition by Vertical Distribution in the Water Column (by weight)[d]	Comments
EPHEMEROPTERA					
Baetidae					
Callibaetis sp.	L	2.45	A	B	·mostly pre-emergent larvae
ODONATA					
Anisoptera	A	(70.0)	T	S	·all adults
Zygoptera	A	(12.0)	T	S	·all adults
ORTHOPTERA	A	100.0	T	S	
PLECOPTERA					
Chloroperlidae	L	(4.0)	A	B	
	A	(4.0)	A	S	
Sweltsa sp.	A	--	A	S	
Triznaka pintada	A	--	A	S	
PSOCOPTERA	A	0.18	T	S	·all adult bark lice
HEMIPTERA					
Aquatic					
Corixidae	A	3.31	A	B	·all adults
Notonectidae					
Notonecta sp.	A	10.0	A	B	·all adults
Terrestrial					·no dominant taxa
Miscellaneous large	A	37.97	T	S	
Miscellaneous small	A	0.82	T	S	
Pentatomidae	A	16.11	T	S	
HOMOPTERA					
Cicadellidae	A	0.32	T	S	·common
Membracidae	A	5.82	T	S	·rare
Cicadidae	A	104.5	T	S	·rare
Aphidae	A	0.09	T	S	·common, all winged adults

Table 3 (continued)

Taxa	Life Stage[a]	Mean Weight (milligrams)[b]	Percent Composition by Aquatic vs. Terrestrial Production (by weight)[c]	Percent Composition by Vertical Distribution in the Water Column (by weight)[d]	Comments
NEUROPTERA					
Hemerobiidae	A	0.805	T	S	·all adults
Sialidae					
<u>Sialis</u> <u>rotunda</u>	L	6.31	A	B	
	A	(8.0)	A	S	
COLEOPTERA					
Aquatic					
Dytiscidae	L	(5.0)	A	B	
	A	9.06	A	B	
Hydrophilidae	A	0.75	A	B	·rare
Terrestrial					
Miscellaneous large	A	15.04	T	S	·mostly arboreal
medium	A	2.99	T	S	taxa, fewer
small	A	0.24	T	S	·ground & shore-line taxa
Buprestidae	A	--	T	S	
Elateridae	A	--	T	S	
Scolytidae	A	--	T	S	
Staphylinidae	A	--	T	S	
TRICHOPTERA					
Rhyacophilidae					·case dwellers weighted with outcases
<u>Rhyacophila</u> <u>sp</u>.	L	(5.0)	A	B	·rare, stream dweller
Hydroptilidae					
<u>Hydroptila</u> <u>sp</u>.	L	(0.25)	A	B	·all 5th instars
	P	(0.20)	A	C	in cases
	A	(0.15)	A	S	
Polycentropodidae					
<u>Polycentropus</u> <u>variegatus</u>	L	2.75	A	B	
	P	2.51	A	C	
	A	2.29	A	S	
Limnephilidae					
<u>Clistoronia</u> <u>magnifica</u>	L	(20.0)	A	B	·all 5th instars
	P	(32.0)	A	C	in organic cases
	A	(29.2)	A	S	
<u>Dicosmoecus</u> <u>atripes</u>	L	(75.0)	A	B	·5th instars in
	P	(36.4)	A	C	mineral cases

Table 3 (continued)

Taxa	Life Stage[a]	Mean Weight (milligrams)[b]	Percent Composition by Aquatic vs. Terrestrial Production (by weight)[c]	Percent Composition by Vertical Distribution in the Water Column (by weight)[d]	Comments
TRICHOPTERA (continued)					
Ecclisomyia conspersa	L	6.26	A	B	·range of instars
	P	4.01	A	C	
	A	(3.0)	A	S	
Imania sp.	L	(2.0)	A	B	·rare, stream taxa
Neophylax sp.	L	(3.0)	A	B	·rare, stream taxa
Psychoglypha sp.	L	(10.0)	A	B	·rare, stream taxa
Limnephilus sp.	A	(4.0)	A	S	·adults only
L. acula	A	--	A	S	
L. fagus	A	--	A	S	
L. spinatus	A	--	A	S	
LEPIDOPTERA	A	44.48	T	S	·all adults
DIPTERA					
Brachycera large	A	4.04	T	S	·miscellaneous terrestrial taxa
medium	A	1.35	T	S	
small	A	0.63	T	S	
Nematocera					
Miscellaneous	A	0.298	T	S	
Tipulidae	L	2.0	A	B	
	A	4.90	A	S	
Chironomidae	L	0.26	A	B	
	P	0.25	A	C	
Tanypodinae					
Procladius sp.	L	--	A	B	
Zavrelimyia sp.	L	--	A	B	
Diamesinae					
Diamesa sp.	L	--	A	B	
Pseudodiamesa sp.	L	--	A	B	
Orthocladiinae					
Cricotopus sp.	L	--	A	B	
Orthocladius sp.	L	--	A	B	
Parametriocnemus sp.					·common taxa found in kokanee stomachs
Chironominae					
Phaenopsectra sp.	L	--	A	B	

Table 3 (continued)

		Life Stage[a]	Mean Weight (milligrams)[b]	Percent Composition by Aquatic vs. Terrestrial Production (by weight)[c]	Percent Composition by Vertical Distribution in the Water Column (by weight)[d]	Comments
HYMENOPTERA						
Ichneumonoidea						
Miscellaneous parasitroids	large	A	12.55	T	S	
	medium	A	1.50	T	S	
	small	A	0.238	T	S	
Formicidae	large	A	37.0	T	S	
	medium	A	9.59	T	S	
	small	A	0.76	T	S	
CLADOCERA						
Daphia pulicaria		--	0.0019	A	C	
AMPHIPODA						
Talitridae						
Hyalella azteca		--	0.57	A	B	
DECAPODA						
Astacidae						
Pacifasticus Teniusculus		--	596.0	A	B	
GASTROPODA		--	4.72	A	B	•weights include shell
Planorbidae						
Vorticifex effusa		--	--	A	B	•common
Lymnaeidae						
ARACHNIDA						
Miscellaneous	large	--	7.25	T	S	
	medium	--	2.08	T	S	
	small	--	0.29	T	S	
Acari		--	(0.01)	A	B	

[a]Life Stage: L = larvae, P = pupae, A = adult

[b]Mean weights of food items from replicate sets of one to one hundred individuals of the least digested individuals of each taxa.
( ) denotes estimated weights based on equivalent sized specimens (ethanol preserved) in data sets available through R.W. Wisseman and N.H. Anderson, Oregon State University, Department of Entomology.

[c]Aquatic vs Terrestrial production: A = aquatic, T = terrestrial

[d]Vertical Distribution: S = water surface, C = mid-water column, B = benthos.
-- denotes data not available.
Species identifications by R.W. Wisseman, Oregon State University, Department of Entomology

weight of food items. Frequency of occurrence describes the uniformity with which a group of fish select their diet (Bowen, 1983). Percent composition by number and percent composition by weight provides some information on the relative importance of individual food types to the nutrition of fish (Hynes, 1950; Bowen, 1983).

Food types also were classified by vertical distribution in the water column and by aquatic or terrestrial origin. For example, chironomid larvae were assumed to have been taken from the benthos and their biomass derived in the lake, Daphnia were assumed to have been taken from the midwater column and their biomass also derived in the lake, and Lepidoptera adults were assumed to be taken at the surface and their biomass derived in the terrestrial environment. Since most aquatic adult insects (e.g., Trichoptera and Ephemeroptera) do not feed, their biomass was assumed to be derived in the lake or in the caldera springs (Bob Wisseman, Oregon State University, Department of Entomology). Odonata adults, which feed extensively as adults and may migrate great distances, were classified as terrestrial. All percent composition values were calculated for each stomach sample, means were calculated for fish groups of interest (e.g., by species, year, age, etc.).

Distribution

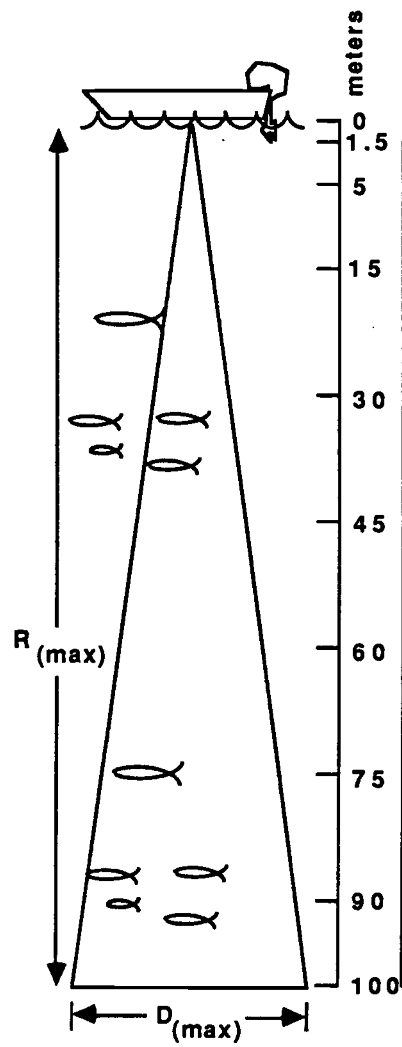
Fish distributions were evaluated by hydroacoustic and fish capture techniques. The use of hydroacoustics for the assessment of fish distribution and behavior has been covered extensively in the literature (e.g., Forbes and Nakken, 1972; Burczynski, 1979; and Thorne, 1983). The equipment operates in principle as follows. A transmitter produces an electrical pulse that is converted to an underwater acoustic signal or sound wave by a transducer. The sound wave travels through the water until it hits a target (a fish) or the lake bottom and is then reflected back to the transducer as an "echo." The transducer receives the echo and transforms it back into electrical energy. The receiver-amplifier modifies the signal and relays it to a display device. Commercial fish finders and depth sounders operate on these same principles. The primary difference in a scientific echo sounder is stability in receiver sensitivity and range corrections based on quantitative physical principles relative to absorption and attenuation of sound waves as they move through water (Thorne, 1983).

A BioSonics model 101 420 KHz scientific sounder with a 15^{0} transducer was used. The output was recorded on an EPC model 1600S paper chart recorder with a model 165 BioSonics chart recorder interface, and monitored on a Hewlett Packard model 1703A storage oscilloscope. The system operated off 110 volt AC current supplied by an on-board model EX (extra quiet) 650 Honda generator.

Acoustic data must first be standardized to account for the near conical shape of the ensonified beam before the vertical depth distribution can be calculated. Since the volume of the beam increases proportionally with depth, each fish detection must be multiplied by a geometric weighting factor that decreases with depth (Dawson, et al., 1985). The transformed or weighted data then are assumed to represent the hypothetical detection results if the ensonified area were a cylinder equal in diameter to the base of the cone at maximum range. An example of how weighted fish detections were determined is shown in Figure 3. At range R the weighting factor W(R) is the ratio of the diameter of the beam at maximum range D(max) to the diameter of the beam at the detection range D(R):

$$W(R) = \frac{D(max)}{D(R)} = \frac{D(max)}{2\ R\ \tan\ (\theta/2)}$$

A nominal beam width (θ) of 17^{0} was used in the calculations. The nominal beam angle was determined from a beam pattern plot obtained at the time of system calibration. The nominal beam angle is defined as the full angle at which the transmitted acoustic intensity is one-half (3 dB less) of the on-axis acoustic intensity (Dawson, et al., 1985).



Average Weighting Factor	Number of Fish Detections	Weighted Fish Detections	Vertical Distribution Percentage
42.0	1	42	12
8.75	13	114	33
4.99	34	170	49
2.72	5	14	4
2.10	1	2	1
1.90	2	4	1
1.12	0	0	0
1.00	0	0	0
Totals	56	345	100

Figure 3. An Example of How the Weighted Fish Detections Were Determined from Raw Hydroacoustic Data Collected at Crater Lake, Oregon. At Range R the Weighting Factor W(R) is the Ratio of The Diameter of the Beam at Maximum Range D(max) to the Diameter of the Beam at the Detection Range D(R):

$$W(R) = \frac{D(max)}{D(R)} = \frac{D(max)}{2\ R\ \tan\ (\theta/2)}$$

Where $\theta = 17^{o}$, and D(max) = 100 m.
After Dawson et al. (1985).

RESULTS

Capture

Horizontal gill nets were the most efficient capture method (Table 4). The downrigger and angling methods were valuable in that they provided samples from the offshore zone and at times of the day when the gill nets were not effective. Sampling methods targeted adult fish. No age-0+ fish of either species were captured. Age I+ rainbow trout were caught on hook and line and by gill nets. No age-I+ kokanee salmon were captured.

Meristics and Morphometrics

There was clearly a difference in gill raker number, gill raker length, and gill raker space between kokanee salmon and rainbow trout; the ranges of these characteristics for the two species did not overlap, and the standard deviations were small (Table 5). Kokanee had significantly narrower mouths than did rainbow trout, though the difference was not as great as for the other characteristics (Table 6). Gill raker length, gill raker space, and mouth width measurements are presented as a percentage of fork length to account for the linear increase in each characteristic with an increase in fork length (Appendix I).

Gill raker space and mouth width were significantly different for offshore-captured kokanee and nearshore-captured kokanee (Table 6). Offshore-captured kokanee had narrower gill raker space and narrower mouth widths than did nearshore-captured kokanee. There was no statistical evidence that gill raker number and gill raker length were different between the two groups of kokanee.

The same fish were used to obtain all of the meristic measurements. It is unlikely that the number of gill rakers, gill raker length, gill raker space, and mouth width are independent of one another. Therefore, the p-value (the probability value from the statistical test) of one character likely has some relationship with

Table 4. Fish Captures for Crater Lake Kokanee Salmon and Rainbow Trout by Sampling Method and by Year.

		SAMPLING METHOD			
SPECIES	YEAR	HORIZ. GILL NET	ANGLING	DOWNRIGGER	TOTAL
Kokanee	1986	55	22	27	104
Salmon	1987	171	4	4	179
Rainbow	1986	23	37	0	60
Trout	1987	50	21	0	71
Totals		299	84	31	414

Table 5. Meristic and Morphometric Summary Statistics for Kokanee Salmon and Rainbow Trout, and for Offshore-Captured and Nearshore-Captured Kokanee, from Crater Lake, Oregon.

	GILL RAKER NUMBER		GILL RAKER LENGTH*		GILL RAKER SPACE*		MOUTH WIDTH*		Sample
	Range	Mean+/-STD	Range	Mean+/-STD	Range	Mean+/-STD	Range	Mean+/-STD	Size
Kokanee Salmon	31-36	32.97+/-1.25	2.27-3.54	2.89+/-0.30	0.38-0.59	0.46+/-0.05	4.71-7.24	6.05+/-0.61	59
Rainbow Trout	18-21	19.56+/-1.01	1.51-2.26	1.82+/-0.19	0.60-1.08	0.81+/-0.12	5.34-8.21	6.85+/-0.74	32
Offshore Kokanee	31-35	32.73+/-1.40	2.46-3.34	2.98+/-0.24	0.39-0.52	0.45+/-0.03	5.08-6.74	5.82+/-0.49	26
Nearshore Kokanee	31-36	33.15+/-1.09	2.27-3.54	2.82+/-0.33	0.38-0.59	0.48+/-0.05	4.71-7.24	6.23+/-0.63	33

*Values for Gill raker Length, Gill raker Space, and Mouth Width are Presented as Percent Fork Length.

Table 6. Results of Statistical Analysis (ANOVA) for Gill Raker Number, and for Normalized Gill Raker Length, Gill Raker Space, and Mouth Width for Kokanee Salmon and Rainbow Trout from Crater Lake, Oregon. Level of Significance 0.05.

COMPARISON	P	CONCLUSION
Rainbow Trout vs. Kokanee Salmon		
Gill Raker Number	P<0.001	Kokanee > Rainbow
Gill Raker Length	P<0.001	Kokanee > Rainbow
Gill Raker Space	P<0.001	Kokanee < Rainbow
Mouth Width	P<0.001	Kokanee < Rainbow
Offshore-Captured Kokanee vs. Nearshore-Captured Kokanee		
Gill Raker Number	P=0.20	Offshore = Nearshore
Gill Raker Length	P=0.05	Offshore ? Nearshore
Gill Raker Space	P=0.022	Offshore < Nearshore
Mouth Width	P=0.0088	Offshore < Nearshore

the p-value of another character. Extremely high or extremely low p-values are accepted as meaningful, p-values between 0.08 and 0.03 should be interpreted with caution (Lisa Ganio, Oregon State University, Department of Statistics, personal communication).

Age

Patterns of circuli deposition were apparent for kokanee salmon and rainbow trout. A great deal of variation in scale size and shape occurred, particularly in the kokanee, even among scales taken within a small area on the same fish. All of the kokanee scales exhibited a weak but persistent annular check or node near the focus. The second, third, and fourth annuli (when they occurred) were well developed. The spacing of the circuli and distance between the annuli suggested good growth throughout their life history. Inconsistent with this was the fact that many scales exhibited signs of reabsorption or abrasion, particularly along the dorsal and ventral margins. The occurrence of regenerated scales was common. As the kokanee matured in fall of 1987 and early winter of 1988 their scales were reabsorbed.

Rainbow trout scales were easier to interpret, exhibiting less variation in size and shape than kokanee scales. The first annuli occurred very close to the focus and were well defined in most cases as were subsequent annuli. Reabsorption and abrasion was not uncommon, generally occurring most in IV+ or older fish, possibly representing a spawning check.

Age frequency histograms suggest one dominant year class for kokanee (Figure 4). Length frequency histograms strongly support this trend (Figure 5). For rainbow trout, however, no clear patterns are readily apparent for age frequency (Figure 4) and length frequency (Figure 6). The II+ and III+ fish did appear to be the most abundant age class in 1986 and 1987 respectively (Figure 4). These results indicate a far more complex population structure for rainbow trout than that for kokanee salmon.

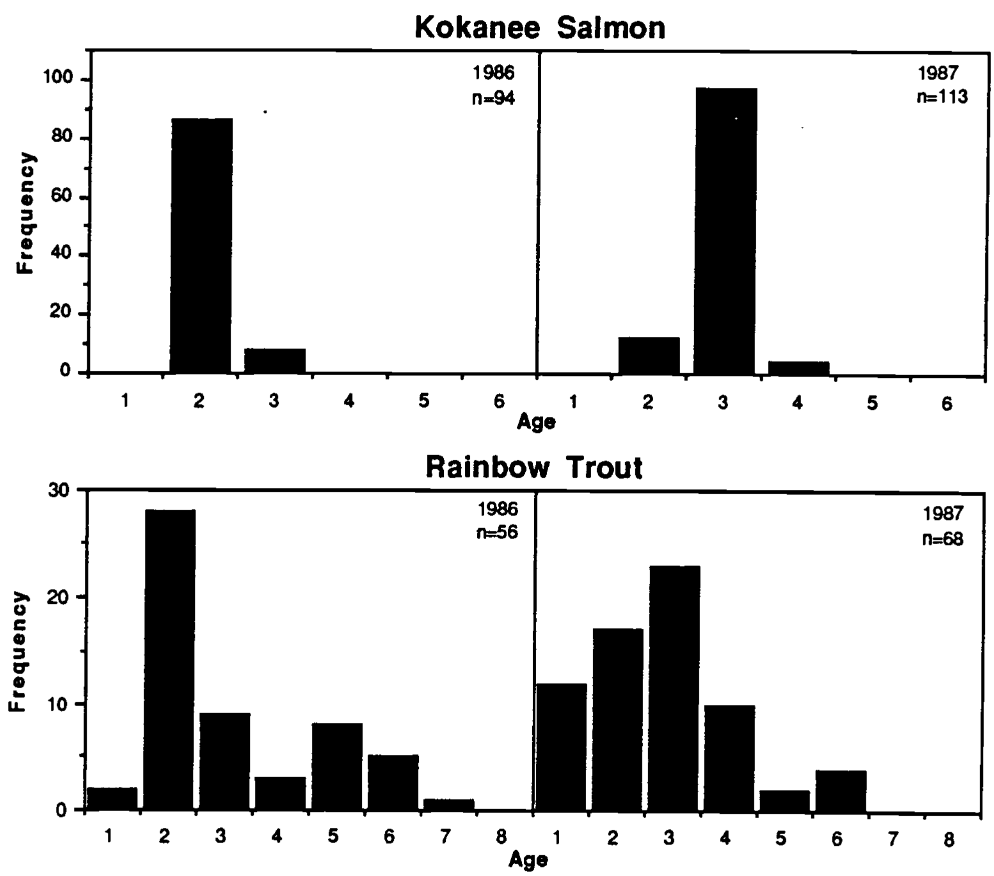


Figure 4. Age Frequency Histograms for Kokanee Salmon and Rainbow Trout Captured in 1986 and 1987, from Crater Lake, Oregon. Note the Different Scales on the Y Axes.

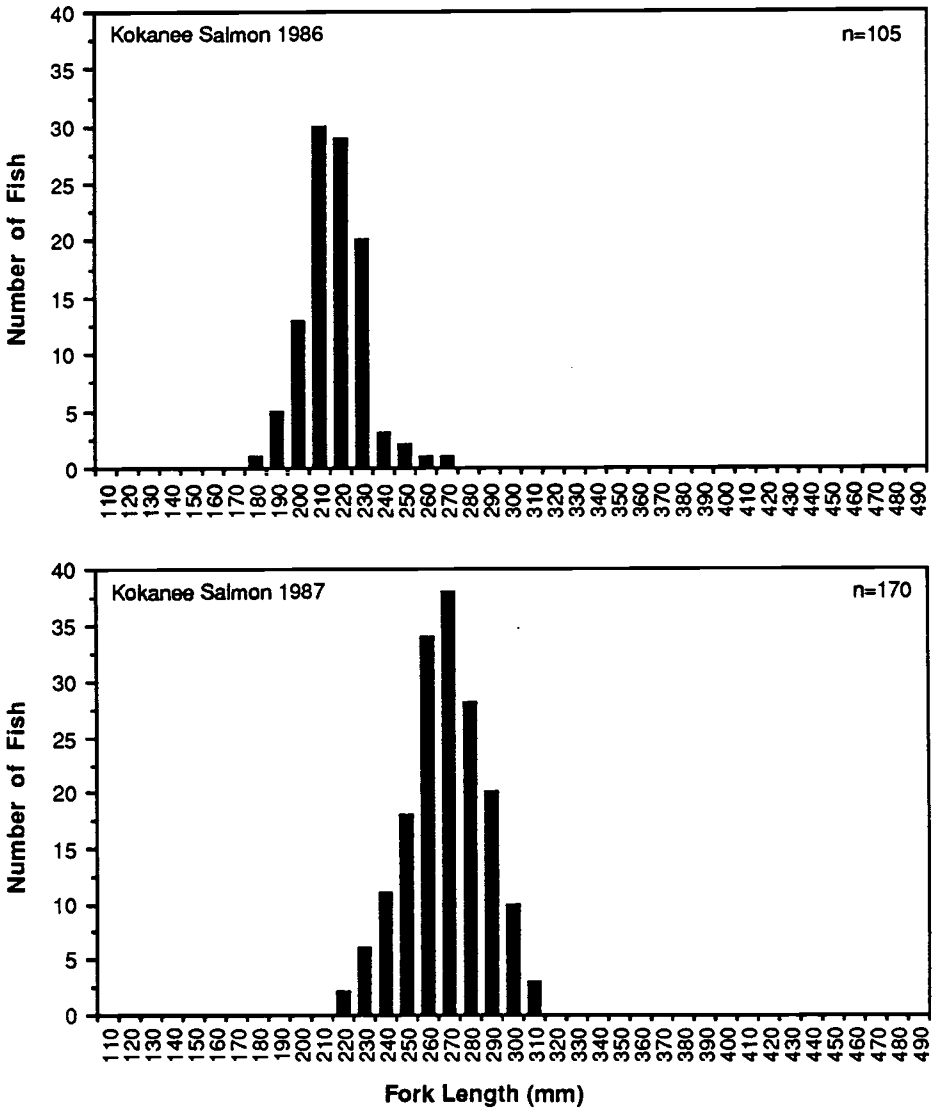


Figure 5. Length Frequency Histograms for Kokanee Salmon Captured in 1986 and 1987, from Crater Lake, Oregon.

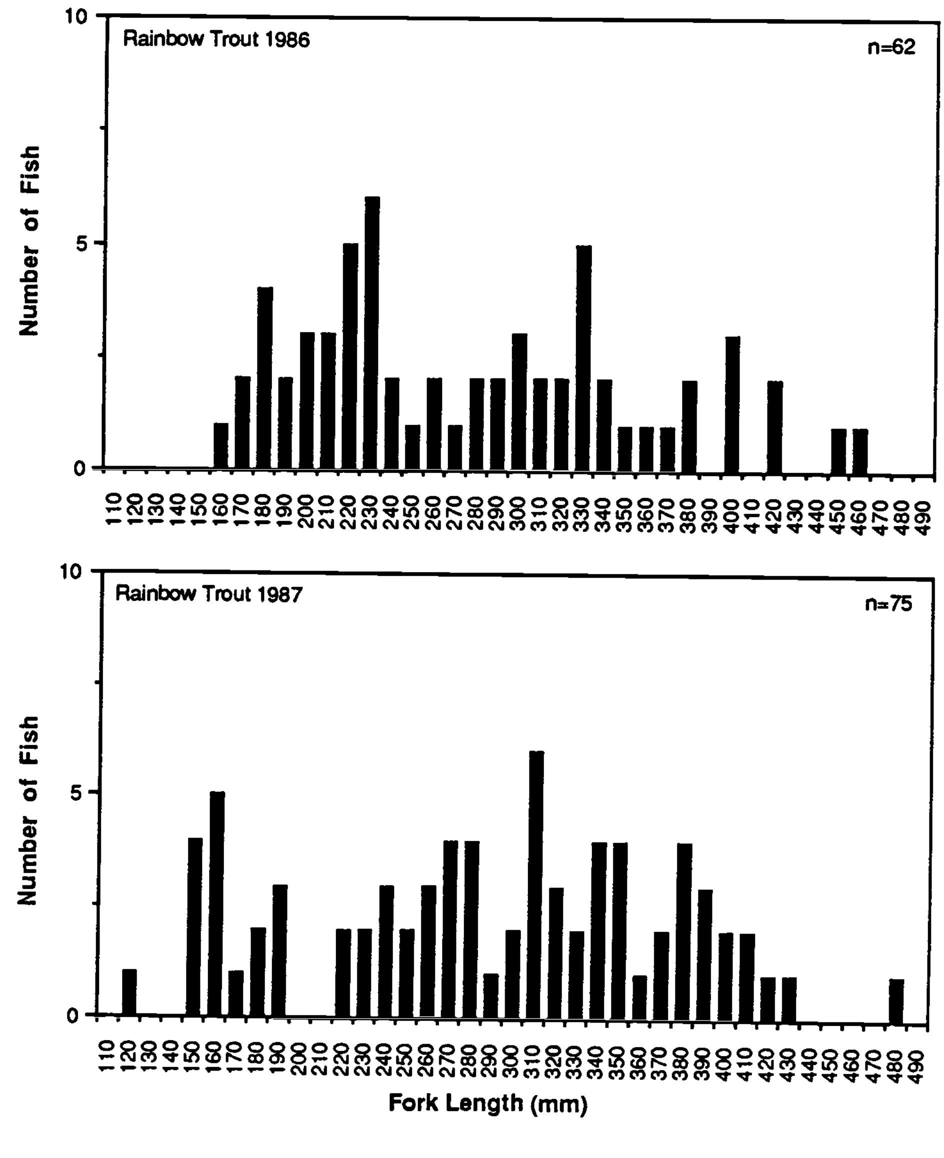


Figure 6. Length Frequency Histograms for Rainbow Trout Captured in 1986 and 1987, from Crater Lake, Oregon.

Growth

Plots of raw and log transformed data on fork length and weight for kokanee salmon and rainbow trout are shown in Figure 7. Regression lines were fit for the log-transformed data. Analysis of covariance was used to test the hypothesis that kokanee salmon and rainbow trout have the same length-weight relationship. The hypothesis was rejected with a p value $<.001$ (significant at the .001 level), and this result indicated that rainbow trout were heavier than kokanee for a given body length.

Fork length at age (Figure 8) and back-calculated fork length at age (Tables 7, 8, and 9) were calculated for both species. Both methods indicated that the growth for kokanee was comparable to the growth for kokanee in other oligotrophic systems (e.g., Odell Lake, Lindsay and Lewis, 1978). Rainbow trout grew rapidly in a near linear fashion until age IV when there was the tendency for the annual increments to diminish (Figure 8, Tables 8 and 9). For rainbow trout, data from 1986 and 1987 were combined for growth estimates by length at age to obtain larger sample sizes for each age class; this required the assumption that the lake environment was in a steady-state equalibrium. However, there was no reason to believe that Crater Lake was in a steady state. Since the 1986 kokanee were nearly all age II and the 1987 kokanee were nearly all age III, data from the two years were necessarily combined for kokanee salmon lengths at age and back-calculated lengths at age. Age data and length frequency data strongly suggested that one dominant year class of kokanee existed in Crater Lake; therefore, the basic assumptions of the models were not violated for kokanee salmon.

Food Habits

Food habits parameters were evaluated by fish species, by year, by fish age and length, by offshore versus nearshore capture, and by capture method.

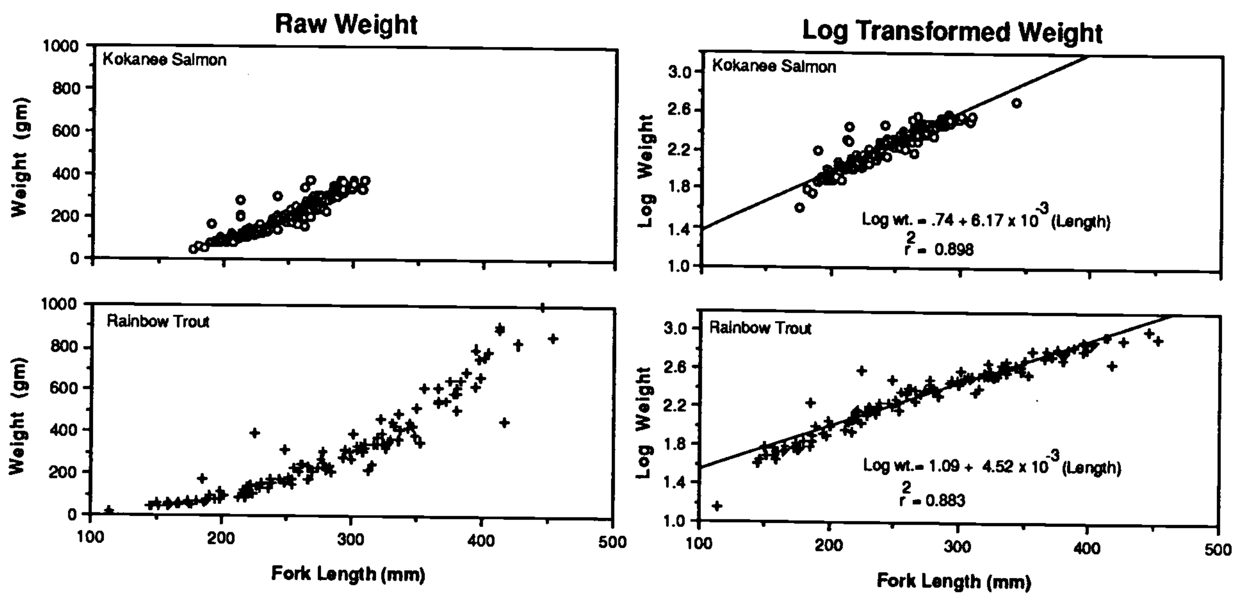


Figure 7. Plots of Raw and Log-Transformed Data on Fork Length and Weight for Kokanee Salmon and Rainbow Trout from Crater Lake, Oregon.

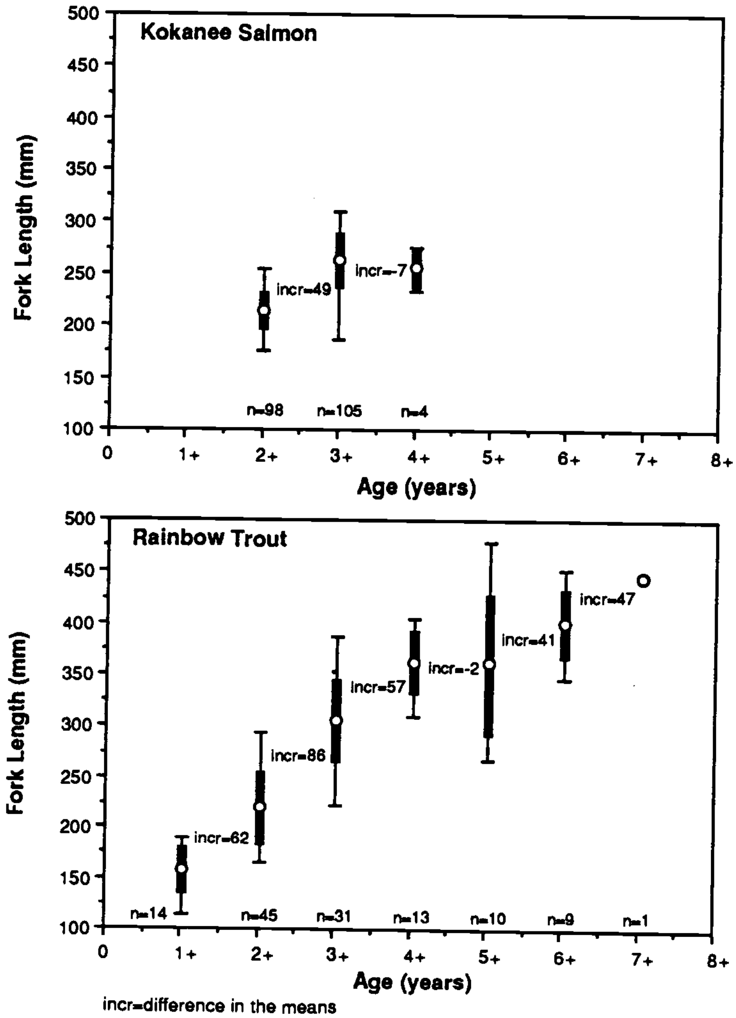


Figure 8. Mean Fork Length, Mean Length Increments Between Age Classes (incr), Standard Deviation (Bar), Range (T-Bar) and Sample Size (n) at Age for Kokanee Salmon and Rainbow Trout, Crater Lake, Oregon.

Table 7. Mean Back-Calculated Fork Length (mm) at Time of Annular Ring Formation for Kokanee Salmon from Crater Lake, Oregon.

		LENGTH AT CAPTURE (mm)		ANNULUS		
AGE GROUP	N	RANGE	MEAN+/-STD	1	2	3
I	0	---------	---------------	------		
II	32	181-256	212.84+/-16.00	122.93	203.58	
III	17	196-298	263.47+/-27.47	122.71	194.34	252.85
			N:	49	49	17
			MEAN:	117.82	198.96	252.85
			ANNUAL INCREMENT:	117.82	81.14	53.89

Table 8. Mean Back-Calculated Fork Length (mm) at Time of Annular Ring Formation for Rainbow Trout Captured in 1986, from Crater Lake, Oregon.

		LENGTH AT CAPTURE (mm)		ANNULUS					
AGE GROUP	N	RANGE	MEAN+/-STD	1	2	3	4	5	6
I	0	-------	--------------	-----					
II	10	174-293	215.50+/-35.48	80.62	171.63				
III	0	-------	--------------	-----	------	------			
IV	1	353-353	353.00+/-0.00	80.41	150.20	195.24	281.71		
V	4	267-413	333.25+/-63.13	73.71	143.59	202.21	272.77	316.65	
VI	4	378-453	410.75+/-27.27	76.76	136.76	201.65	272.56	324.77	371.87
			N:	19	19	9	9	8	4
			MEAN:	77.89	150.55	199.7	275.68	320.71	371.87
			ANNUAL INCREMENT:	77.89	72.66	49.15	75.98	45.03	41.16

Table 9. Mean Back-Calculated Fork Length (mm) at Time of Annular Ring Formation for Rainbow Trout Captured in 1987, from Crater Lake, Oregon.

	LENGTH AT CAPTURE (mm)			ANNULUS					
AGE GROUP	N	RANGE	MEAN+/-STD	1	2	3	4	5	6
I	0	114-159	147.88+/-13.83	91.81					
II	4	177.270	238.50+/-36.64	69.03	156.93				
III	5	251-322	284.60+/-25.19	71.88	157.64	241.83			
IV	5	366-404	380.40+/-12.92	66.81	140.43	231.99	351.79		
V	2	375.479	427.00+/-52.00	72.00	163.51	276.64	351.09	386.14	
VI	4	395-426	405.00+/-12.39	69.72	150.91	208.81	263.15	319.71	379.84
			N:	28	20	16	10	6	4
			MEAN:	73.54	153.88	239.82	322.01	352.93	379.84
			ANNUAL INCREMENT:	73.54	80.34	85.93	82.19	30.92	26.91

Species: Kokanee salmon primarily fed on four food groups (Figure 9): Chironomidae, Trichoptera, Amphipoda, and Cladocera. Chironomid larvae and chironomid pupae were very important food resources for kokanee, each occurred in over 70% of the stomachs examined. Chironomid larvae and pupae together accounted for 53% of composition by number and 51% composition by weight. Trichoptera and Amphipoda occurred in over 40% of the kokanee stomachs; however, they were of lesser importance in terms of percent composition by number (6% and 8%) and percent composition by weight (13% and 9%). Cladocerans were almost exclusively represented by *Daphnia pulicaria*. *Bosmina longirostris* occurred in one stomach sample along with the *Daphnia*. *Daphnia* occurred in 37% of the kokanee sampled. Due to partial digestion and fragmentation *Daphnia* were only countable in 63 out of 99 stomachs. Therefore, *Daphnia* are under-represented in both percent composition by number (21%) and percent composition by weight (15%).

Rainbow trout fed heavily on Trichoptera, Hymenoptera, Chironomidae pupae, terrestrial Coleoptera, Diptera, aquatic Coleoptera, Ephemeroptera ($\geq$ 30% occurrence), Gastropoda and terrestrial Hemiptera ($\geq$ 25% occurrence) (Figure 9). Trichoptera were the dominant food type by number (22%) and by weight (25%). Chironomid pupae, aquatic Coleoptera, and Hymenoptera each made up just over 10% composition by number. Trichoptera (25%) and Hymenoptera (14%) were the only orders that represented more than 10% composition by weight, the remaining 61% composition by weight was accounted for by 17 additional food types.

Rainbow trout were more likely to have a large variety of prey species in a single stomach sample than were kokanee, though many stomachs were full of primarily one food type (e.g., Amphipods or Gastropods). Kokanee stomach samples were strongly characterized by having a few food types per stomach. One or two food types typically dominated a sample, many stomachs were stratified with layers of chironomid larvae and chironomid pupae. These well-defined strata may suggest alternating feeding periods in different locations.

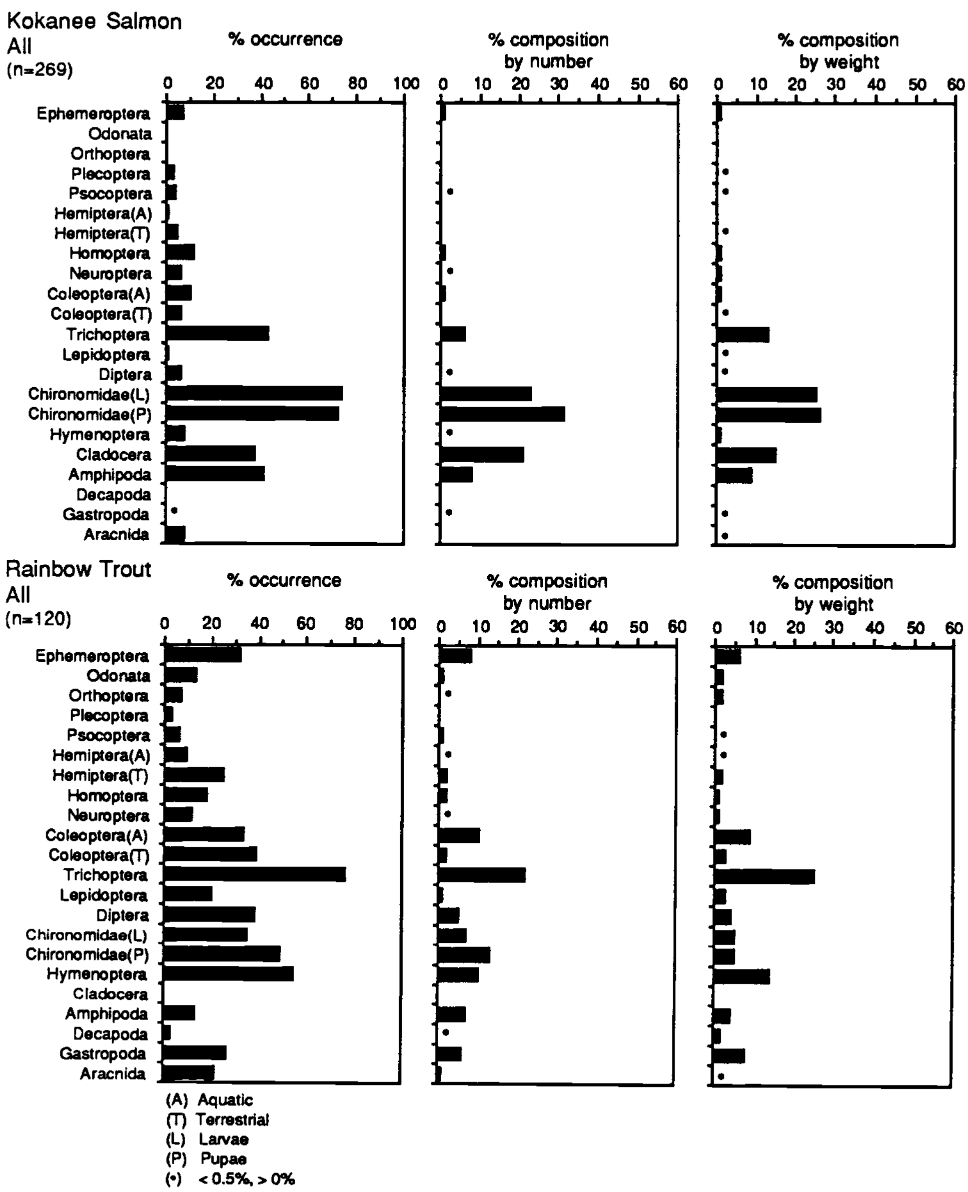


Figure 9. Percent Occurrence, Percent Composition by Number, and Percent Composition by Weight, of food types, for Kokanee Salmon and Rainbow Trout from Crater Lake, Oregon.

Kokanee as a group fed almost solely on aquatic food types (Table 10). The low percentage of terrestrial food types corresponds with a low percentage (by weight) of food types that were presumably taken on the lake surface (5%). Fifty-four percent of their diet was assumed to be taken from the midwater column, while 41% were taken from the benthos. The mean weight of the individual prey in the kokanee stomach samples was 1.27 milligrams.

Rainbow trout also fed heavily on aquatic food items (69%), but more food items from terrestrial origin (31%) were eaten (Table 10). Thirty-seven percent of their diet was assumed to be taken from the water surface, 11% from the midwater column and 52% from the benthos. The mean weight of individual prey in the rainbow trout stomach samples was 9.82 milligrams.

Year: While the same food types remained important for kokanee in 1986 and 1987, the relative importance of these food types shifted in terms of percent composition by number and weight (Figure 10). Chironomid larvae increased in importance, while chironomid pupae decreased. *Daphnia* accounted for less than 10% of the diet by number and by weight in 1986; in 1987 they accounted for 29% by number and 22% by weight. In 1987, *Daphnia* were quantifiable in 49 out of the 79 stomachs in which they occurred. The shift from chironomid pupae to chironomid larvae is likely responsible for the decrease in the percentage of biomass taken from the midwater column and the increase in biomass taken from the benthos noted in 1987 (Table 11). The reduction in mean weight of food items is probably associated with the increased occurrence of *Daphnia* in the stomachs.

Food habits for rainbow trout did not change radically between 1986 and 1987 (Figure 11). A wide variety of prey species were taken in both years. Only Ephemeroptera and Trichoptera increased greatly in percent composition by number or by weight. Aquatic Coleoptera, Diptera, and chironomid larvae decreased in occurrence and abundance in stomach samples from 1986 to 1987.

Table 10. Sample Size, Mean Weight, Percent Composition by Aquatic Versus Terrestrial Origin (by Weight) and by Vertical Distribution in the Water Column (by Weight) of Food Items for Kokanee Salmon and Rainbow Trout from Crater Lake, Oregon.

SUMMARY DATA FOR:	SAMPLE SIZE	MEAN WEIGHT OF FOOD ITEMS	PERCENT COMPOSITION BY VERTICAL OISTRIBUTION			PERCENT COMPOSITION BY AQUATIC VS. TERRESTRIAL ORIGIN	
	(N)	(MILLIGRAMS)	SURFACE	COLUMN	BENTHOS	AQUATIC	TERRESTRIAL
All Kokanee Salmon	269	1.27	5	54	41	98	2
All Rainbow Trout	120	9.82	37	11	52	69	31

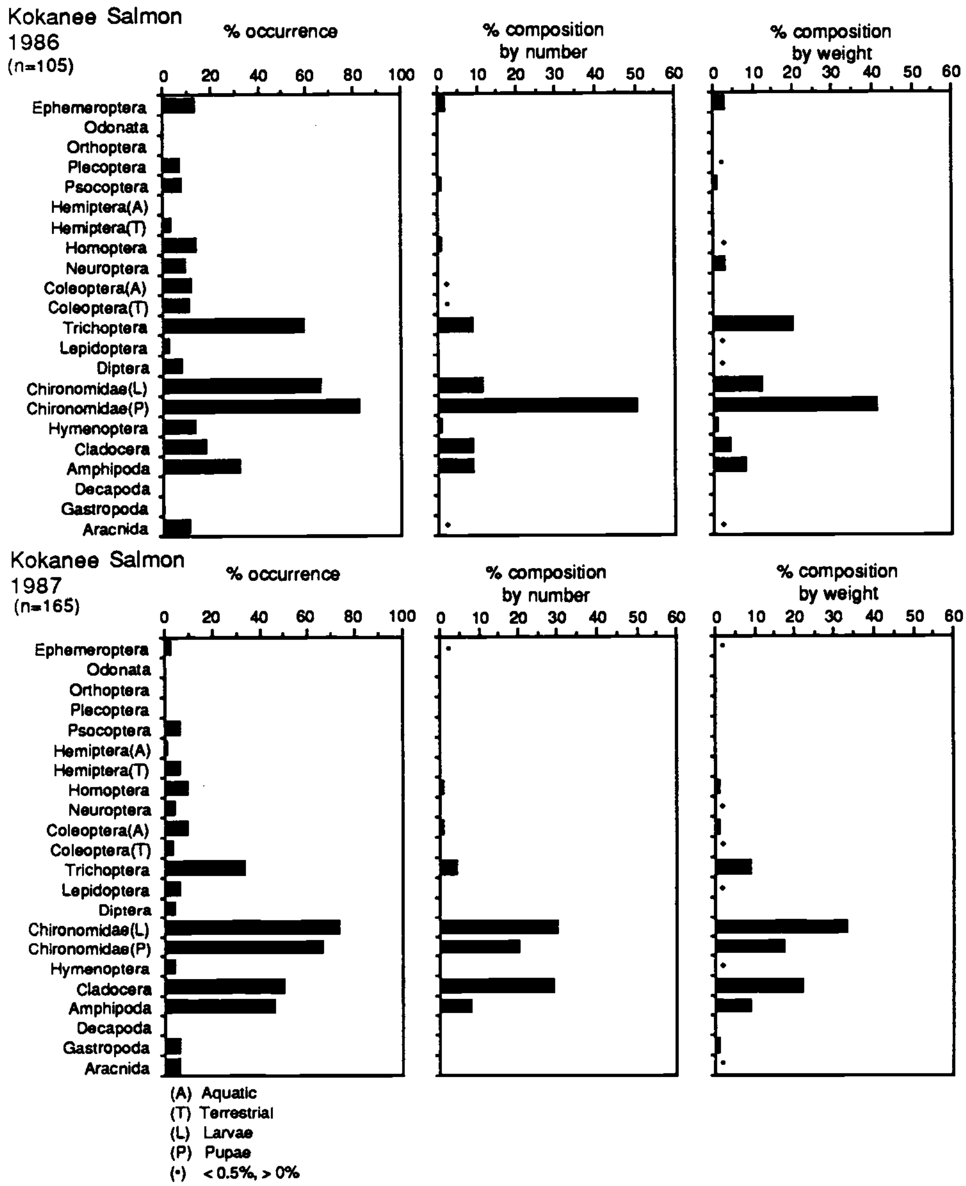


Figure 10. Percent Occurrence, Percent Composition by Number and Percent Composition by Weight, of food types, for Kokanee Salmon from Crater Lake, Oregon, by Year.

Table 11. Sample Size, Mean Weight, Percent Composition by Aquatic Versus Terrestrial Origin (by Weight), and by Vertical Distribution in the Water Column (by Weight) of Food Items for Kokanee Salmon and Rainbow Trout from Crater Lake, Oregon, by Year.

SUMMARY DATA FOR:	SAMPLE SIZE	MEAN WEIGHT OF FOOD ITEMS	PERCENT COMPOSITION BY VERTICAL DISTRIBUTION			PERCENT COMPOSITION BY AQUATIC VS. TERRESTRIAL ORIGIN	
	(N)	(MILLIGRAMS)	SURFACE	COLUMN	BENTHOS	AQUATIC	TERRESTRIAL
Kokanee Salmon, 1986	105	1.69	7	6	29	97	3
Kokanee Salmon, 1987	165	1.01	3	48	49	99	1
Rainbow Trout, 1986	59	10.36	40	12	48	68	32
Rainbow Trout, 1987	61	9.28	33	12	55	70	30

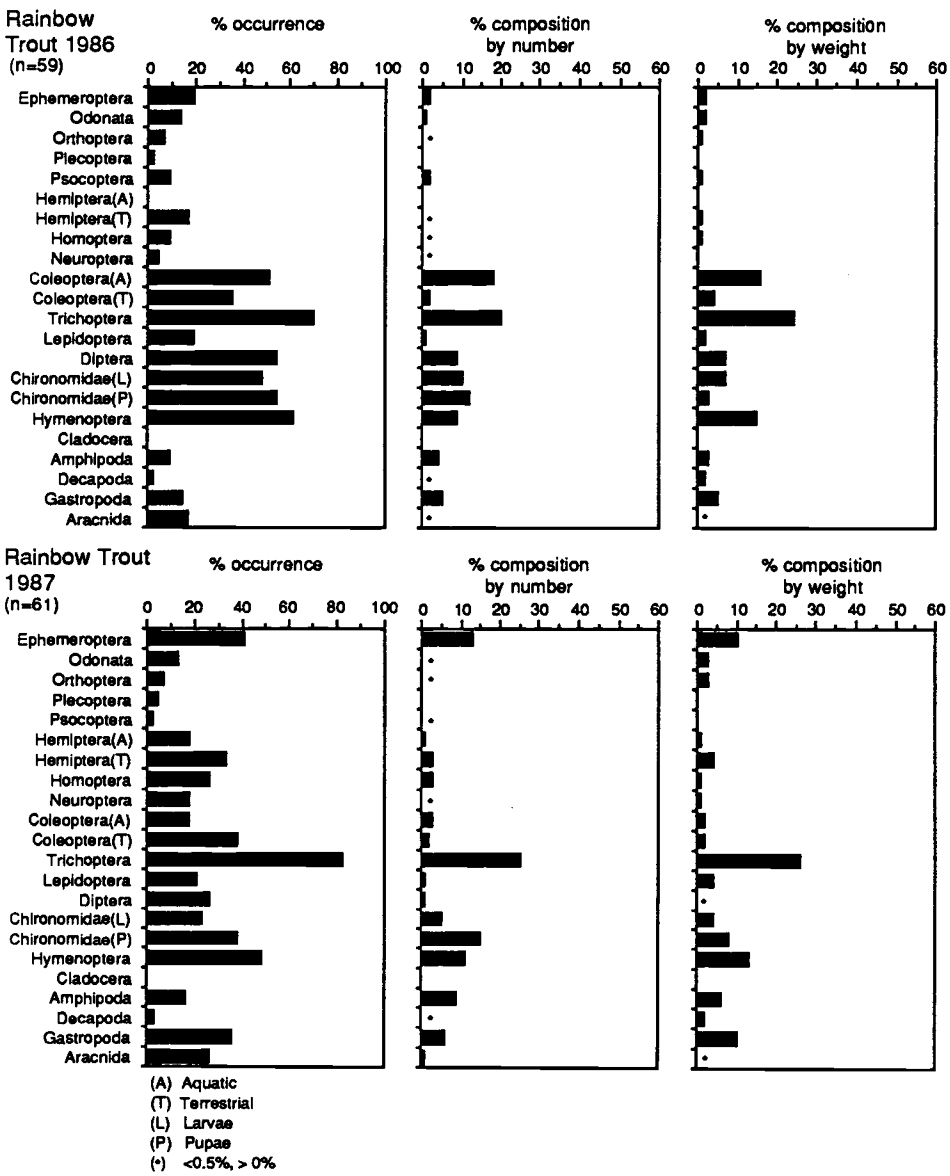


Figure 11. Percent Occurrence, Percent Composition by Number and Percent Composition by Weight, of Food Items, for Rainbow Trout from Crater Lake, Oregon, by Year.

Age and Length: As expected, the same food habit trends between years for kokanee salmon occurred between age classes, and between length classes as these characteristics closely correspond with the year of capture (Appendix II).

Because of the small sample sizes for rainbow trout in different age classes, the results were interpreted with caution, but some trends may be noted. Age I+ trout fed heavily on small benthic organisms, primarily chironomid larvae, Trichoptera, and small gastropods. Twenty-three percent of their food items (by weight) were assumed to be taken on the water surface (Table 12). This value may be biased due to the occurrence of one Odonata. The surface and benthic component were important for all ages. The column organisms were most important for age II+, age III+, and age IV+ trout. The most notable difference between age and length classes was the increase in mean weight of food items with rainbow trout size and age.

Kokanee in length classes 1 and 2 fed more uniformly than did rainbow trout on chironomids, cladocerans, and Amphipods (Figure 12 and Figure 13). Rainbow trout fed more uniformly on Odonata, Orthoptera, terrestrial Hemiptera, Homoptera, Coleoptera, Trichoptera, Lepidoptera, Diptera, Hymenoptera, Gastropoda, and Aracnida. Both species fed heavily on Ephemeroptera and Trichoptera. The importance of food type as indicated by percent composition by number and percent composition by weight further separated the salmon and the trout by length. Kokanee relied heavily on chironomids and cladocerans. Rainbow trout utilized aquatic Coleoptera, Diptera, and Hymenoptera. Both groups fed on Trichoptera and Amphipoda.

Capture Method and Location: Rigorous evaluations of food habits by method of fish capture require that variables such as time (e.g., day versus night), location (e.g., nearshore versus offshore), and sample size remain consistent for all capture methods. This was not possible here, so it is difficult to separate the effects of these variables from the effects of capture methods.

Table 12. Sample Size, Mean Weight, Percent Composition by Aquatic Versus Terrestrial Origin (by Weight), and by Vertical distribution in the Water Column (by Weight) of Food Items for Rainbow Trout from Crater Lake, Oregon, by Age.

SUMMARY DATA FOR:	SAMPLE SIZE	MEAN WEIGHT OF FOOD ITEMS	PERCENT COMPOSITION BY VERTICAL DISTRIBUTION			PERCENT COMPOSITION BY AQUATIC VS. TERRESTRIAL ORIGIN	
RAINBOW TROUT	(N)	(MILLIGRAMS)	SURFACE	COLUMN	BENTHOS	AQUATIC	TERRESTRIAL
By Age							
Age 1	12	4.22	23	6	71	81	19
Age 2	40	6.46	44	9	47	62	38
Age 3	23	8.01	35	23	42	68	32
Age 4	10	10.41	36	17	47	68	32
Age 5	9	17.54	37	0	63	63	37
Age 6	6	18.22	34	1	65	78	22

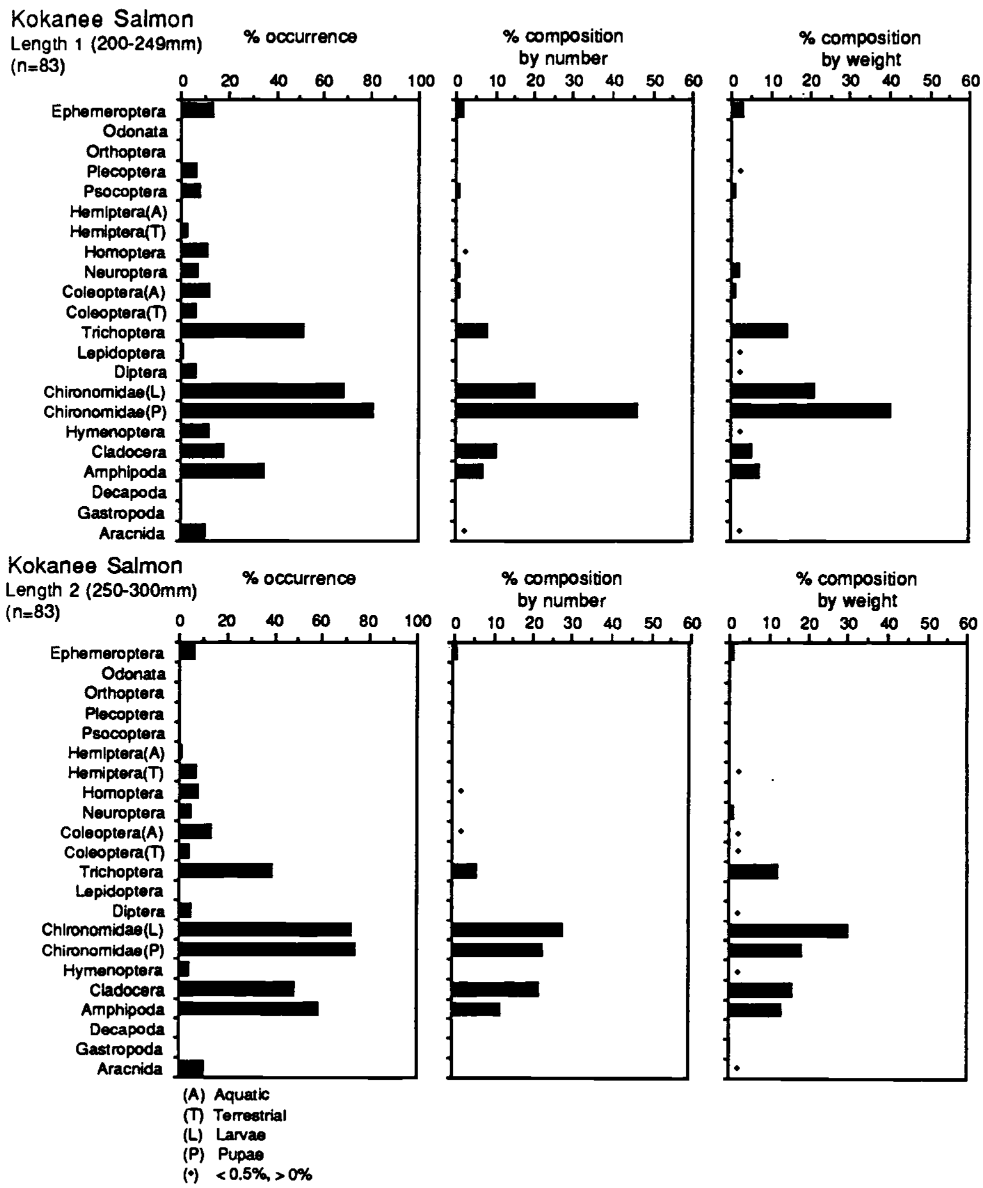


Figure 12. Percent Occurrence, Percent Composition by Number, and Percent Composition by Weight, of Food Types, for Kokanee Salmon from Crater Lake, Oregon, by Length.

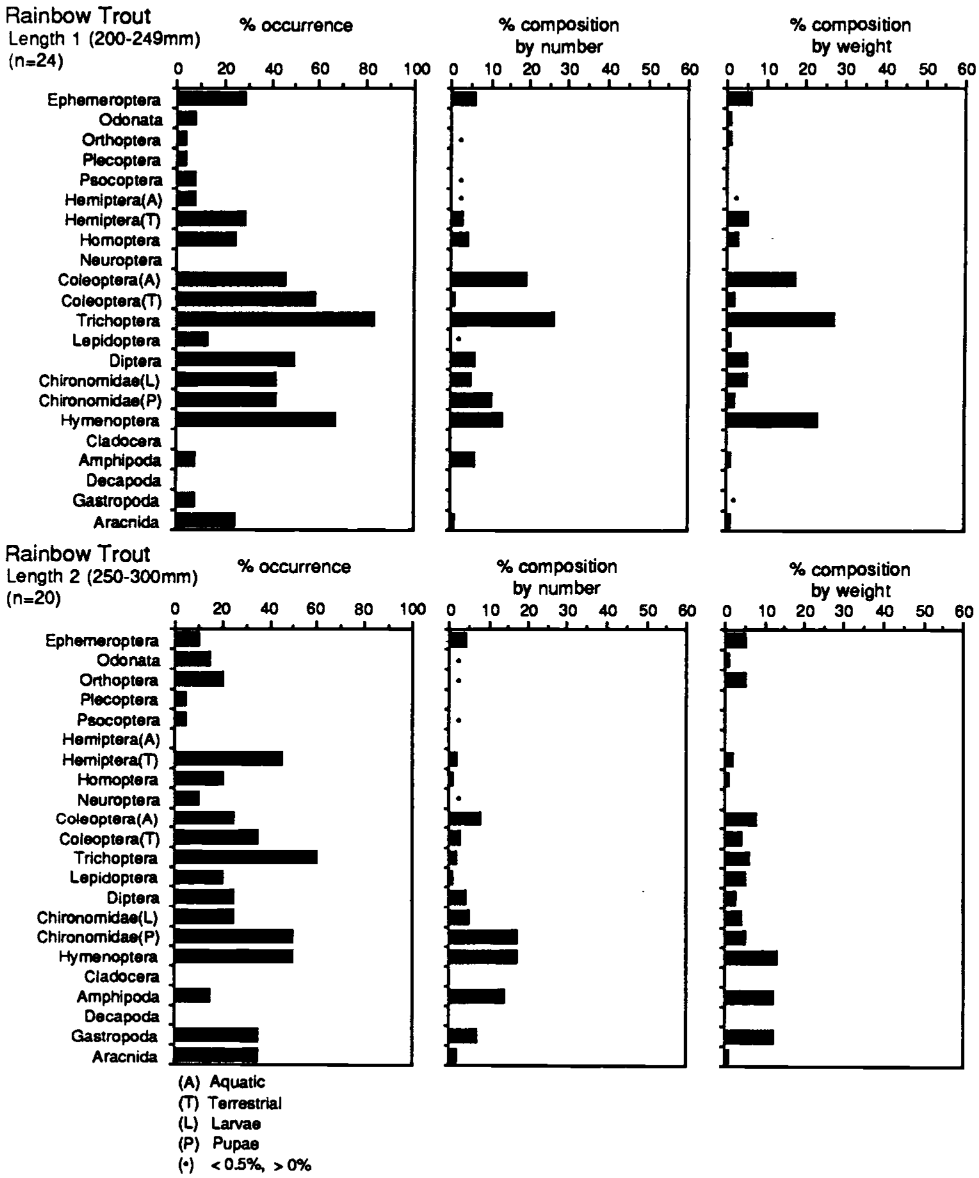


Figure 13. Percent Occurrence, Percent Composition by Number, and Percent Composition by Weight, of Food Types, for Rainbow Trout from Crater Lake, Oregon, by Length.

For example, angling occurred along the shoreline during the day and in the evening. Gill nets were set overnight in the nearshore zone. The downrigger was employed in the offshore zone of the lake during the day.

Kokanee captured in the offshore area on the downrigger had a higher percent occurrence of small terrestrial insects (e.g. Psocoptera, Homoptera, Coleoptera, Hymenoptera, and Aracnida) than did angled and gill netted kokanee even though many of these fish were taken from great depth (Appendix II). Cladocerans occurred in a higher percentage of the kokanee captured nearshore in gill nets (44%) than they did in kokanee angled nearshore (15%) or in kokanee captured offshore (33%). However, cladocerans were more important by number and by weight to offshore-captured kokanee than to nearshore-captured kokanee.

Chironomid pupae accounted for 60% composition by number, 57% composition by weight for offshore-captured kokanee, 28% composition by number, 23% composition by weight for nearshore kokanee (Figure 14). The reverse trend was true for chironomid larvae. The stomach content composition for nearshore captures was 24% chironomid larvae by number, 26% by weight, 11% by number, and 17% by weight for offshore kokanee. Amphipods and Trichoptera were more abundant in nearshore captures. Trichoptera was particularly abundant in angled nearshore captures.

Kokanee captured by angling and by the downrigger were very similar in terms of percent composition of the diet by vertical distribution; the highest proportion of their diet was taken from the midwater column (70% and 78% respectively) (Table 13). Gill netted kokanee fed in near-equal proportions from the column (49%) and from the benthos (47%). Those captured by angling tended to take larger prey (mean weight 1.66 mg). Nearshore-captured kokanee had a slightly larger mean prey weight (1.30 mg) than did offshore-captured kokanee (1.07 mg). Nineteen kokanee captured in gill nets (9.7%) had empty stomachs when retrieved from the nets. None of the hook and line-captured kokanee had empty stomachs. Gill net-captured fish may regurgitate and evacuate their guts as a

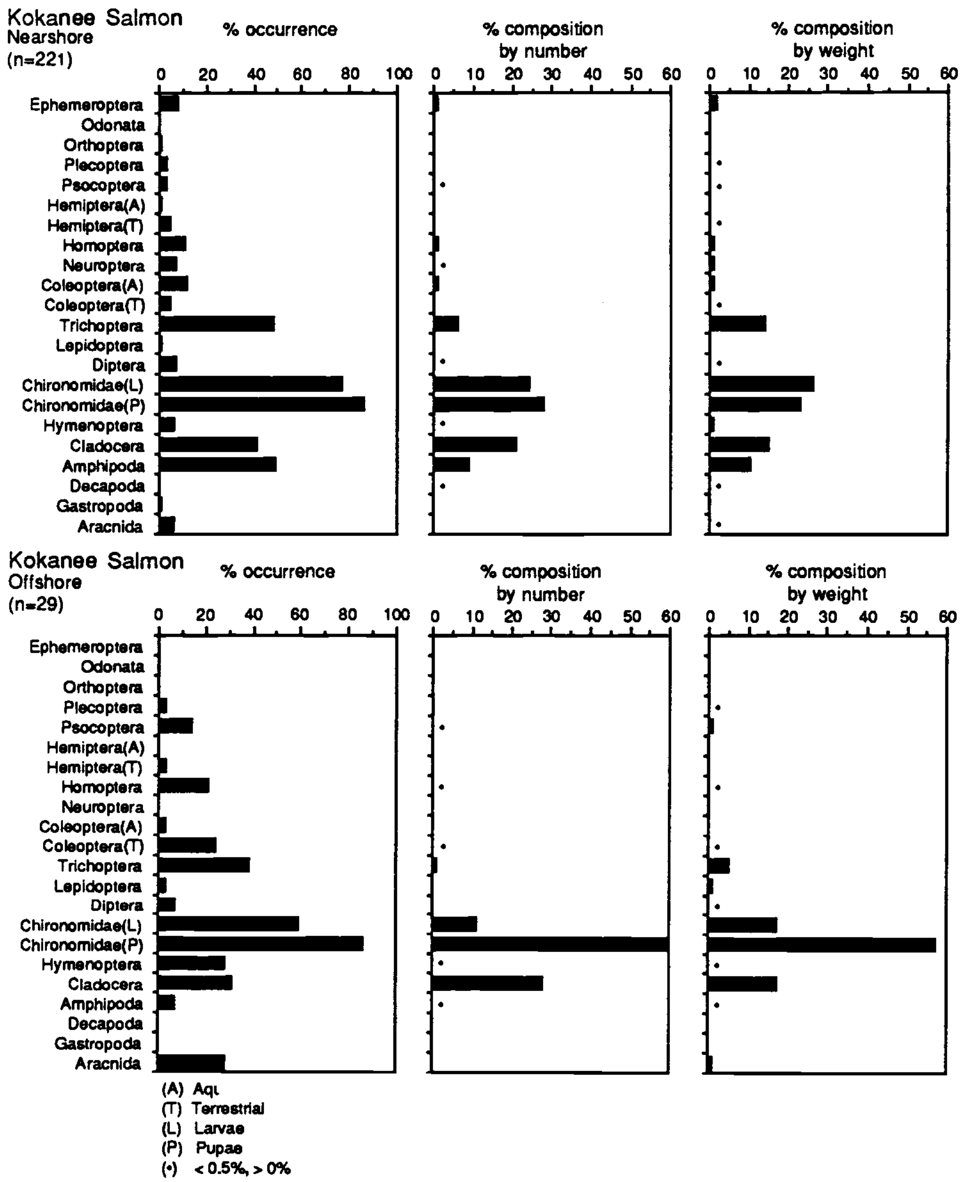


Figure 14. Percent Occurrence, Percent Composition by Number and Percent Composition by Weight, of Food Types, for Kokanee Salmon from Crater Lake, Oregon, by Location of Capture.

Table 13. Sample Size, Mean Weight, Percent Composition by Aquatic Versus Terrestrial Origin (by Weight), and by Vertical Distribution in the Water Column (by Weight) of Food Items for Kokanee Salmon from Crater Lake, Oregon, by Location and Method of Capture.

SUMMARY DATA FOR:	SAMPLE SIZE	MEAN WEIGHT OF FOOD ITEMS		PERCENT COMPOSITION BY VERTICAL DISTRIBUTION IN THE WATER COLUMN			PERCENT COMPOSITION BY AQUATIC VS. TERRESTRIAL ORIGIN	
KOKANEE SALMON	(N)	(MILLIGRAMS)	NUMBER EMPTY	SURFACE	COLUMN	BENTHOS	AQUATIC	TERRESTRIAL
Nearshore	221	1.300	19	5	52	43	98	2
Offshore	29	1.071	0	4	78	18	97	3
Captured by Gill Net	195	1.252	19	4	49	47	98	2
Captured by Angling	26	1.661	0	11	70	18	100	0
Captured by Downrigger	29	1.071	0	4	78	18	97	3

fright response. Food items remaining in their stomachs are subject to digestion until the fish are taken from the nets, processed, and preserved.

Rainbow trout captured by gill nets and by angling exhibited similar feeding habits in terms of percent occurrence and percent composition by number and weight (Figure 15). The former had a higher occurrence of food found on the benthos, while the latter had a higher proportion of the diet taken from the surface (Table 14). The mean weight of prey items taken by rainbow trout captured by angling was higher (14.09 mg) than for those taken by gill net (6.59 mg).

Distribution

The acoustic survey was conducted for an intensive one-week sampling period in early September 1987. The 1985 survey by Thorne and Marino (1985, unpublished report) indicated that fish distribution in Crater Lake was strongly biased toward shore. Therefore, a stratified random sampling design was used. The strata were nearshore (0 m to 100 m contour) and offshore (100 m to 589 m contour) zones of the lake and six four-hour periods of time, day and night, to assess diel distributional changes. Figure 16 indicates the approximate locations of day and night transects on Crater Lake. Figures 17 and 18 represent typical nearshore and offshore echograms.

A clear pattern of diel vertical migration was apparent in the offshore zone (Figure 19). Median fish depth ranged from 75 m during the day to 19 m at night, a 56 m daily vertical migration. The maximum depth of detection was 98.5 m. An opposite vertical migration is indicated by the nearshore data (Figure 19). Median nearshore fish depth ranged from 2 m in the day to 17 m at night. Near-constant boat speed was maintained; therefore, a measure of fish per hour from the echograms may reveal horizontal nearshore-offshore distribution changes with time (Figure 20). The increase in fish per hour at night in the nearshore zone may represent a horizontal shoreward migration, or it may represent an increase of

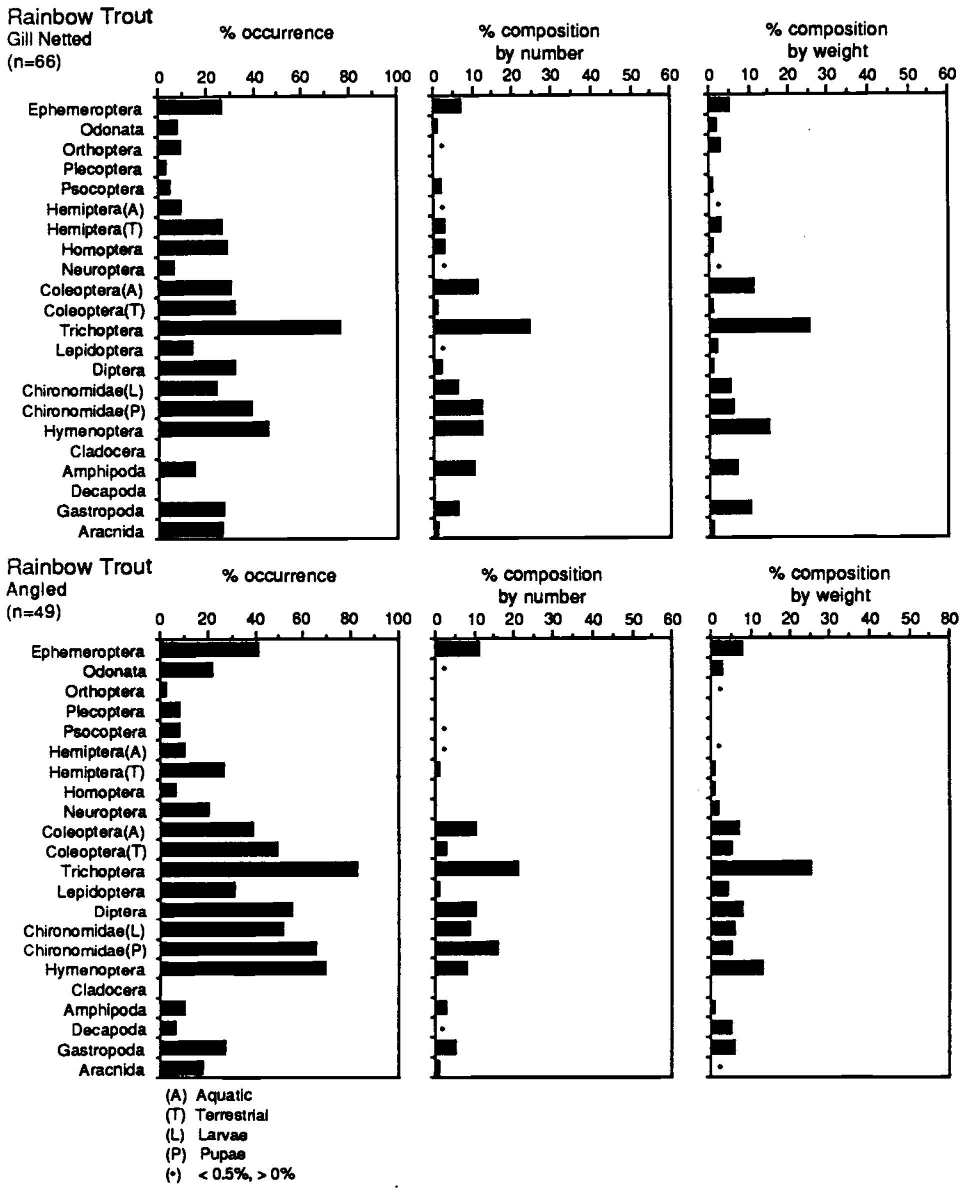


Figure 15. Percent Occurrence, Percent Composition by Number and Percent Composition by Weight, of Food Types, for Rainbow Trout from Crater Lake, Oregon, by Method of Capture.

Table 14. Sample Size, Mean Weight, Percent Composition by Aquatic Versus Terrestrial Origin (by Weight), and by Vertical Distribution in the Water Column (by Weight), of Food Items, for Rainbow Trout from Crater Lake, Oregon, by Method of Capture.

SUMMARY DATA FOR:	SAMPLE SIZE	MEAN WEIGHT OF FOOD ITEMS		PERCENT COMPOSITION BY VERTICAL DISTRIBUTION			PERCENT COMPOSITION BY AQUATIC VS. TERRESTRIAL ORIGIN	
RAINBOW TROUT	(N)	(MILLIGRAMS)	NUMBER EMPTY	SURFACE	COLUMN	BENTHOS	AQUATIC	TERRESTRIAL
Captured by Gill net	66	6.59	2	31	10	59	70	30
Captured by angling	49	14.09	2	44	14	41	67	33

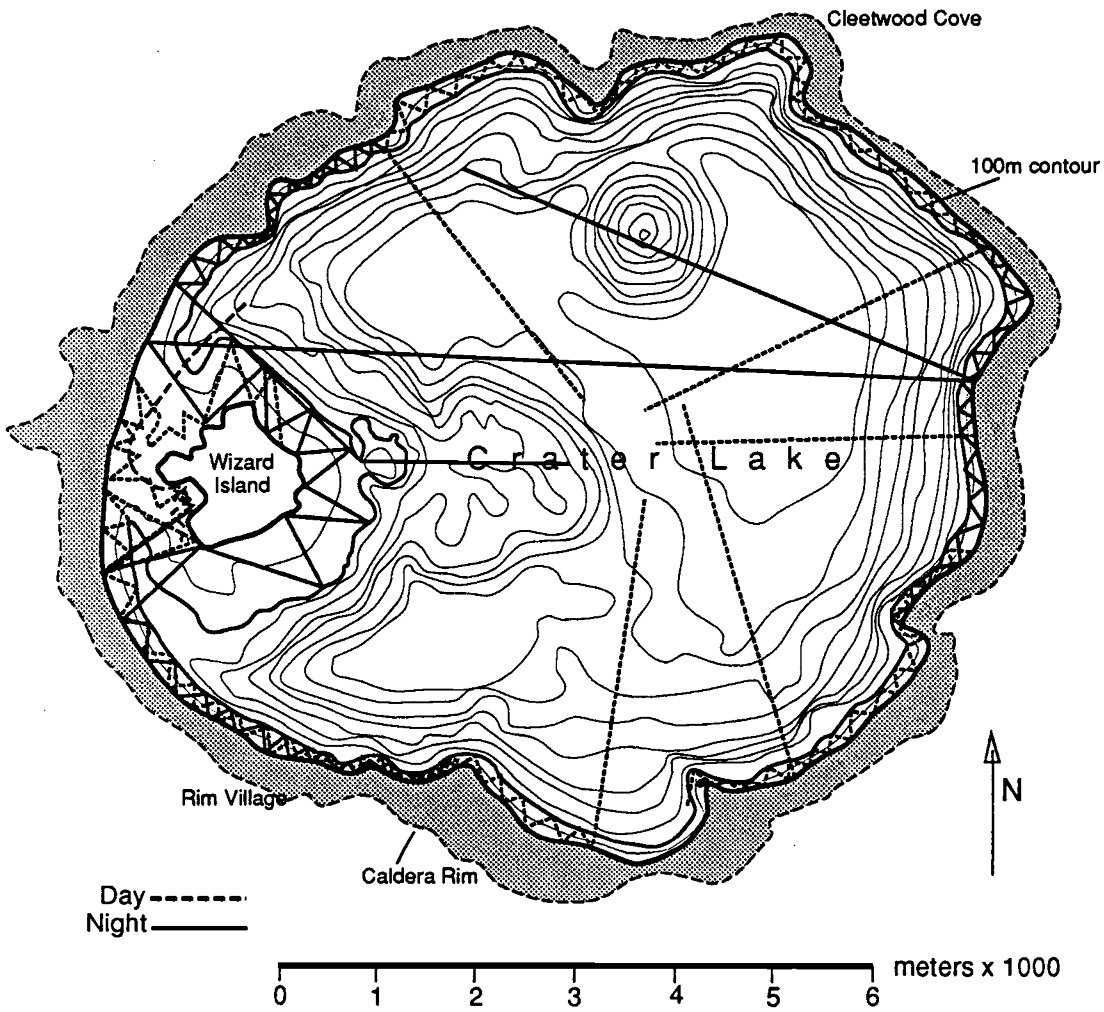


Figure 16. Map of Crater Lake, Oregon, with the Approximate Locations of Hydroacoustic Transects.

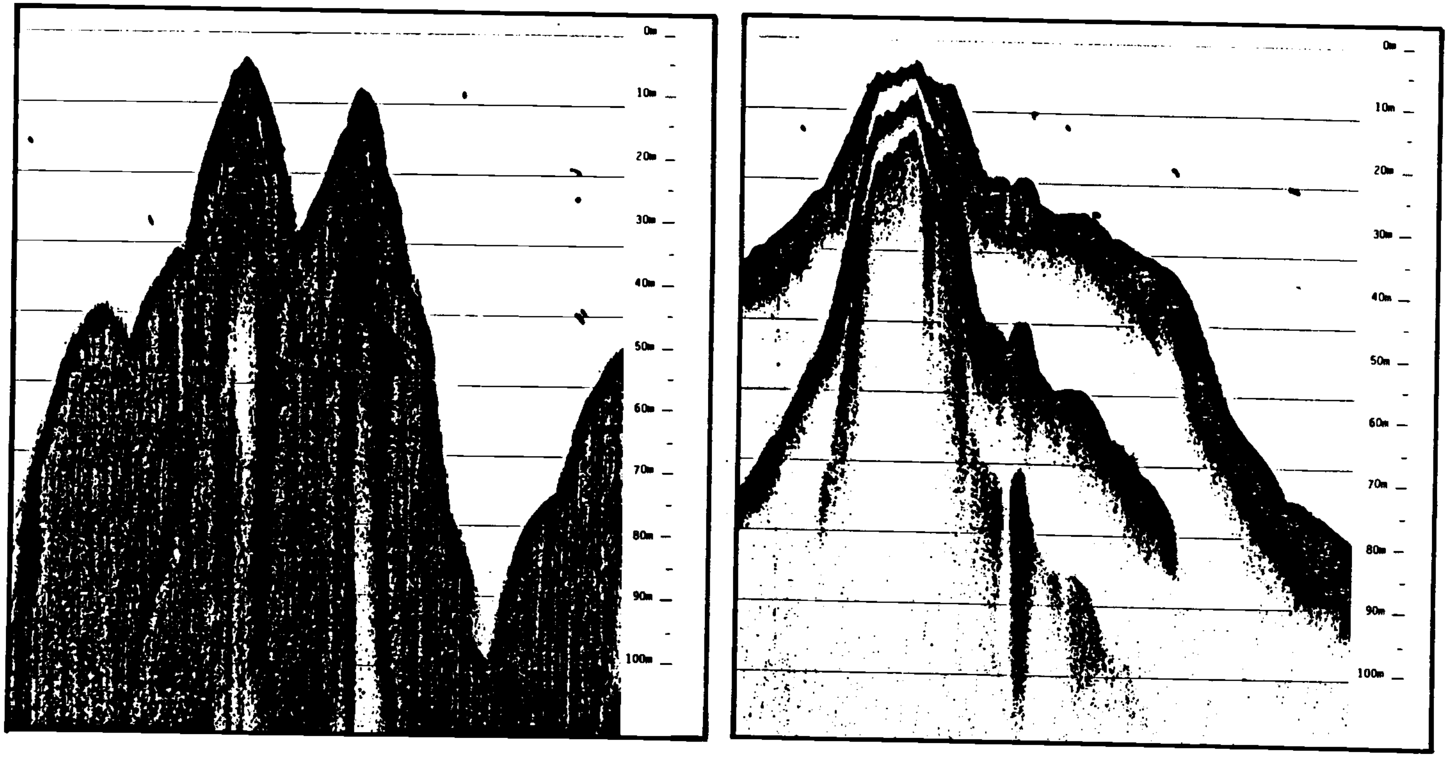


Figure 17. Sample Echograms from the Nearshore Zone (0 to 100 m Contour) of Crater Lake, Oregon, Recorded Around Midnight on September 6, 1987.

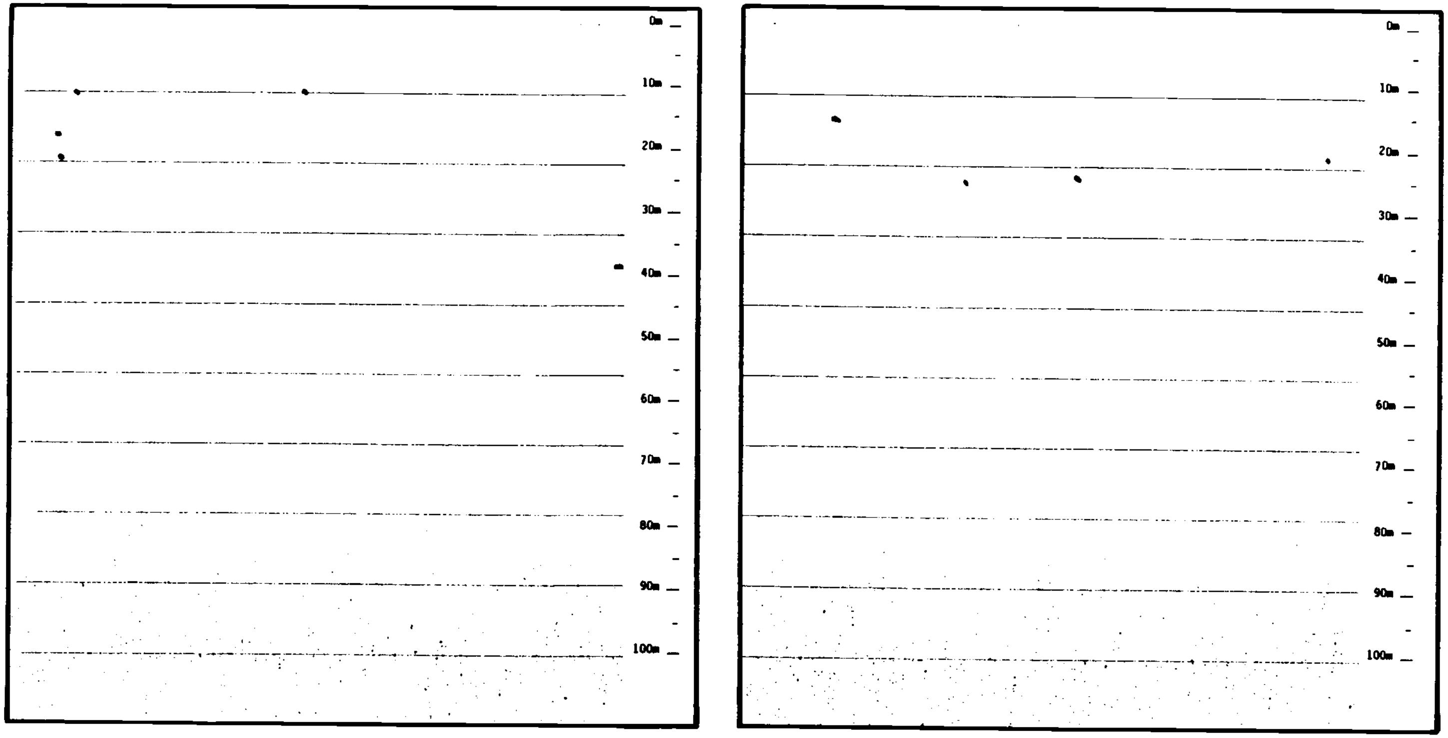


Figure 18. Sample Echograms from the Offshore Zone (100 to 589 m Contour) of Crater Lake, Oregon, Recorded Around Midnight on September, 1987.

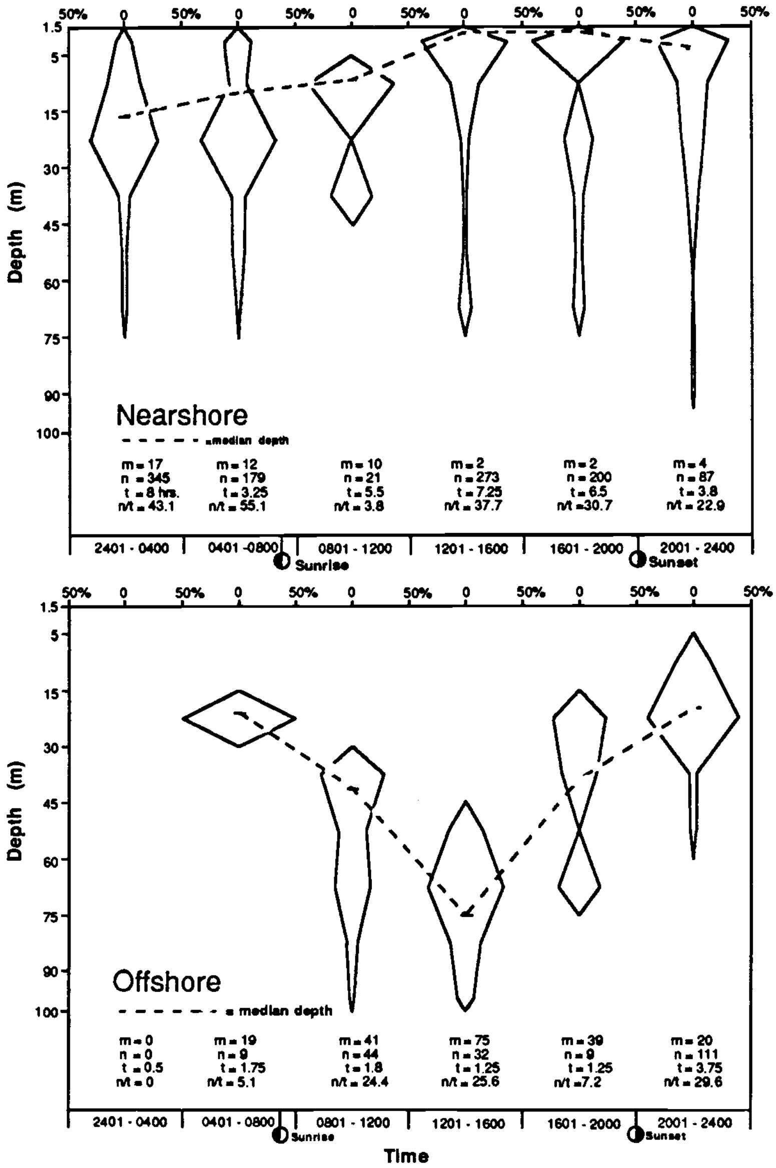


Figure 19. Diel Vertical Distribution Patterns of Nearshore and Offshore Fish in Crater Lake During the First Week of September 1987, Presented as Percentage of Total Sonar Contacts. m = Median Depth, n = Number of Fish Detections, t = Total Time of Transects in Each Time Period, n/t = Fish Detections Per Hour.

susceptibility of nearshore fish to the acoustic beam at night. If fish are strongly associated with the lake bottom (for foraging or for cover) during the day, their echoes may not be distinguishable from the bottom echoes. In the dark the fish may leave the substrate or drift away from the caldera wall where they can be detected (Thorne and Marino, 1985).

Fish capture techniques were used in conjunction with hydroacoustic data to assess fish distribution. Downrigger captures support the deeper depth occurrence of offshore fish during the day (Figure 21). The downrigger was fished offshore between 1200 hours and 2000 hours. Thirty-one fish were captured; all were kokanee. The median depth of capture was 65 m. The maximum depth of capture was 86.25 m. Angling occurred along the shoreline, during the day and in the evening. Most of the fish angled were rainbow trout. Twenty-one out of the twenty-five kokanee angled were captured after 1800 hours; twenty were captured after 1900 hours. Overnight gill net sets were successful in capturing kokanee salmon and rainbow trout.

The capture data, when combined with the acoustic data, suggests that the kokanee are mainly deep and offshore during the day and that they migrate to shallower water and possibly shoreward at night. The rainbow trout are captured nearshore during the day and night. The acoustic data indicates an upward migration of nearshore fish in the day.

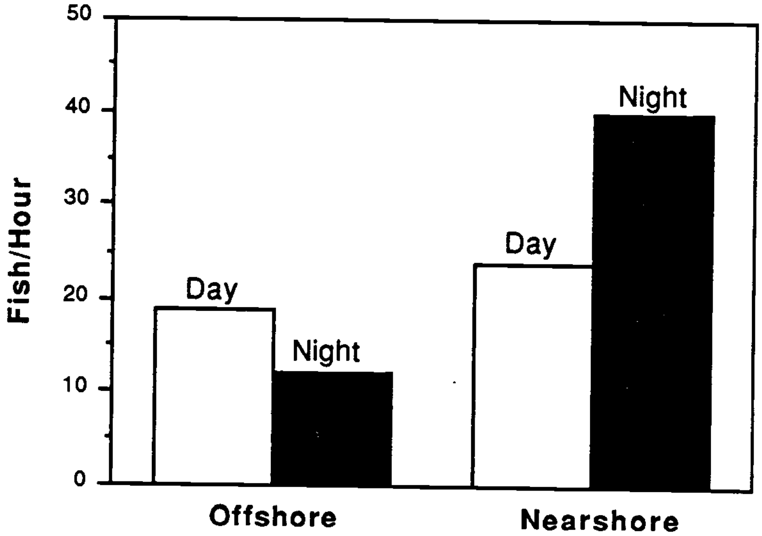


Figure 20. Total Sonar Contacts Per Hour (Fish/Hr), During the First Week of September 1987 in the Nearshore and Offshore Zones of Crater Lake During the Day and Night.

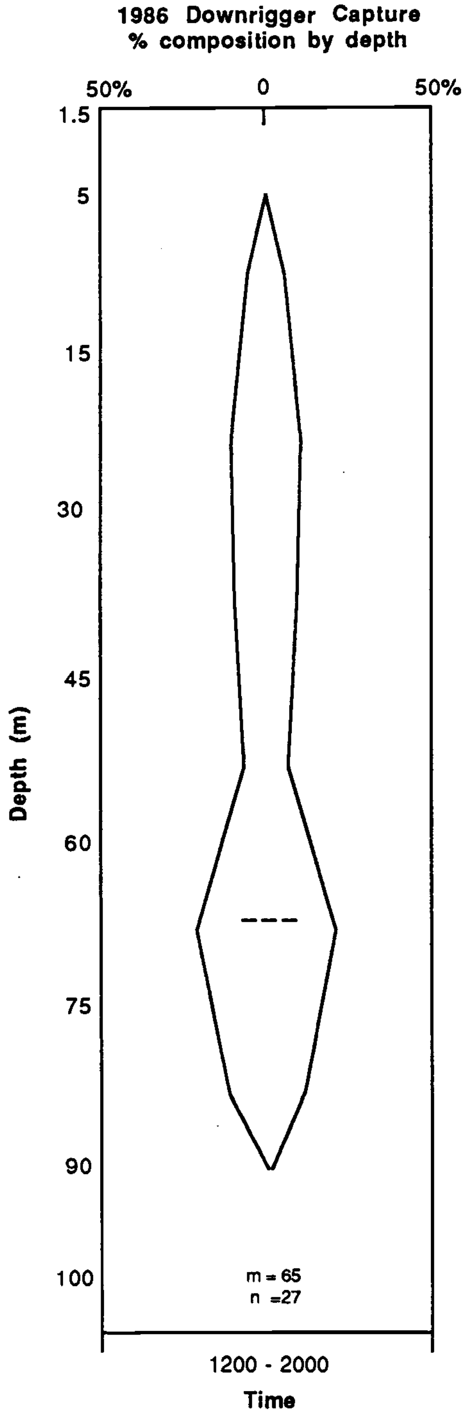


Figure 21. Vertical Distribution Pattern of Offshore Kokanee Salmon Captured by Downrigger in Crater Lake, Oregon, Presented as Percentages of Total Capture. The Broken Line Represents the Median Depth (m), Sample Size = n.

DISCUSSION

The primary goal of this thesis was to develop a better understanding of the ecological role of fish in Crater Lake. The work focused on the length, weight, age, growth, meristics and morphometrics, food habits, and distribution of adult kokanee salmon and rainbow trout. In this section these results and appropriate literature will be used to evaluate the ecology of Crater Lake fish populations relative to the limnological characteristics of the lake and to develop a general conceptual model of lake community structure and organization relative to kokanee salmon and rainbow trout.

Meristics and Morphometrics

Meristic and morphometric character analyses of the two species produced results much as expected. Kokanee salmon had narrower mouths and a greater number of gill rakers that were longer and closer together than those of rainbow trout. Gill raker counts were within the expected ranges for each species (Mottley, 1936; Vernon, 1957; Bidgood and Berst, 1967; Nelson, 1968; Kurenkou, 1977). Based on the literature, these characteristics suggest that kokanee are better suited than rainbow trout to feed on small prey. This is consistent with the observation that the mean weight of food items for Crater Lake kokanee was about eight times smaller than that of rainbow trout.

Offshore-captured kokanee had narrower mouths and narrower spaces between gill rakers than did nearshore-captured kokanee. Such differences, plus other characteristics such as timing and location of spawning, age composition, and differences in feeding habits, have been used to indicate the existence of two or more races of kokanee in lakes, e.g., Cultus Lake, B.C. (Ricker, 1938); Kootenay Lake, B.C. (Vernon, 1957); Odell Lake, Oregon (Averett and Espinosa, 1968); Lake Kronotskiy, USSR (Kurenkov, 1977); Pend Oreille Lake, Idaho (Rieman and Bowler, 1980); or Flathead Lake, Montana (Hanzel, 1984). Such a conclusion for Crater Lake kokanee is premature; morphological characteristics may vary with size, sex, and sexual maturity (Mottley, 1936; Bidgood and Berst, 1967), developmental environment (Lindsey, 1958; MacCrimmon and Kwain, 1968), or be biased by method of capture. Future morphological comparisons for taxonomic purposes at Crater Lake should use individuals of the same size, age, sex, degree of maturity, all captured by the same method.

Age

In contrast to the age-frequency composition of the rainbow trout population that exhibited no clear patterns, the kokanee population was dominated in number by one year class. Although it is not known why this occurred, this is not the first time year class dominance by kokanee has been observed in Crater Lake (Kibby, 1966, unpublished report). Dominant year classes in kokanee populations also have been reported in other lakes, e.g. Odell Lake (Lewis, 1971) and Flathead Lake (Hanzel, 1984), though the extent of the dominance was not as great as in Crater Lake.

Reproduction

Whether or not fish could successfully reproduce in Crater Lake was the subject of much early discussion. When stocking ceased in 1941, it became apparent that rainbow trout, brown trout, and kokanee salmon did successfully reproduce. This was first suggested from early scale analysis (Hasler and Farner, 1942), and later by the persistance of these populations. Kibby (1966, unpublished report) collected and archived the last recorded brown trout captured from the lake in 1966. The timing and location of spawning of kokanee salmon and rainbow trout in Crater Lake have not been described.

Kokanee salmon typically spawn between the ages II+ and IV+, though kokanee as old as age VI+ have been seen (Seely and McCammon, 1966). Kokanee generally spawn in the fall (Collins, 1971; Cordone et. al., 1971; Stober and Tyler, 1982.) but kokanee spawning peaks as early as July have been observed in Lake Kronotskiy, USSR (Kurenkov, 1977). Spawning extends into January in some lakes in the Pacific Northwest (Averett and Espinosa, 1968; Rieman and Bowler, 1980). For example, in Odell Lake, Oregon, one spawning group spawns from mid-September to early November; another group spawns from early December to mid-January (Averett and Espinosa, 1968).

Spawning may occur in inlet and outlet streams, and along shoreline beaches. Lakeshore areas with subsurface springs or upwelling water are preferred (Lewis, 1971; Kinsey, 1951); however, upwelling water is not necessary for spawning success (Olsen, 1968; Hassemer and Riemer, 1981; Stober and Tyler, 1982).

In Crater Lake, the timing and location of spawning for at least a small group of kokanee was documented for the first time on January 6, 1988. Forty-four kokanee were captured in a gill net set overnight at Eagle Point at the base of an avalanche chute. The kokanee ranged in condition from being full of loose eggs or milt to having recently spawned. The fish were dark olive green without the red coloration characteristic of spawning kokanee populations elsewhere (Averett and Espinosa, 1968). The caudal fins of females were worn with tattered fin rays exposed, presumably from digging redds. Spawning males had hooked jaws, and slightly humped backs. Later in the day on January 6 an avalanche of snow occurred at the site, prohibiting further investigation.

Rainbow trout may spawn as early as age I+ for males, and age II+ for females, but ages III+ to V+ are most common (Hartman, 1959). Rainbow trout are repeat spawners and have been observed to spawn at age VII+. Rainbow trout generally spawn in spring, but they may spawn virtually any month of the year. Dodge and MacCrimmon (1970) found, for example, that rainbow trout in the Great Lakes began to spawn in December. Individual trout have been reported to spawn twice a year (Hume, 1955). They will spawn in inlet and outlet streams, but there are few reports in the literature of successful shoreline spawning (Scott and Crossman, 1973).

In Crater Lake it appears that the peak in rainbow trout spawning activity is over by mid-June to July (Table 15). The main spawning season(s) has not been documented.

Growth

For many years the widely held belief that the fish in Crater Lake are starving because Crater Lake is a nearly sterile body of water has persisted. Previous and current fish investigations contradict this belief. Hubbard (1933, unpublished report) reported,

> "There is no truth to the often heard statement that Crater Lake trout are starved to death. The fish have plenty to eat in the lake and eat it . . . . The rainbows are a nice, plump oval. The fish are well-filled out and the flavor is unexcelled."

Hasler (1938) noted, "Growth of trout and salmon in the lake is exceptionally rapid." Hasler and Farner (1942) noted that growth in Crater Lake fishes was nearly at an optimum. Fish captured in 1986 and 1987 consistently possessed fat reserves, even those fish captured in April. These fish experienced comparable growth rates, as determined by length at age and back-calculated length at age, relative to other populations in oligotrophic lakes (Ricker, 1938; Carlander, 1969; Lindsay and Lewis, 1978) but slightly slower growth rates compared to that found by previous investigations on Crater Lake (Hasler, 1938; Hasler and Farner, 1942). It also appears that there were fewer large rainbow trout in 1986 and 1987 than in previous years (Hasler, 1938).

Food Habits

Kokanee are considered zooplanktivores and are found to rely heavily on zooplankton in their diets (Cordone et. al., 1971; Rieman and Bowler, 1980). When zooplankton abundance is low they have been

Table 15. Recorded Observations Relative to the Spawning and Reproduction of Crater Lake Fish.

1933, August 26

"10-inch rainbow trout . . . . Spawner, eggs ready to lay"
"16-inch rainbow trout . . . . Eggs well developed"

"With the exception of a few strafflers (sic) the spawning season for the rainbows in Crater Lake is prior to July 15 . . . the latest on record being August 26."

C.A. Hubbard
Professor of Biology
Pacific University
Forest Grove, Oregon

1937

Sex Ratios: Kokanee Salmon 67% Female
Rainbow Trout 69% Female

A.D. Hasler
Ranger-Naturalist

1940, July 27

"In July, 1939, I observed, in a catch taken by fishermen, two female rainbow trout which had spawned their eggs and several which had their eggs loose."

"It is quite apparent ½from independent observations by Superintendent Canfield (1934) and by D.S. Farner (1939, 1940)¾ that a certain portion of the female rainbow trout do not spawn their eggs but retain and possibly resorb (sic) them."

D.S. Farner
Ranger-Naturalist

1986

KOKANEE SALMON

June, July, August . . . . Many males with large gonads, filling half or more of body cavity.

Table 15 continued

August 5	Two females with ripening scanes of eggs. (213 mm, 232 mm, fork length)
Sex Ratio: 55% Female	
RAINBOW TROUT	
August 8	One female with a few retained eggs. Apparently spawned earlier. (353 mm, fork length) Present work.
Sex Ratio: 63% Female	
1987	
KOKANEE	
June-October	Males and females with developing gonads.
September	Males developing secondary sex characteristics.
October 7	Males and females developing secondary sex characteristics One male appeared spawned out, most males not ripe. No loose eggs.
Sex Ratio: 32% Female	
RAINBOW TROUT	
June 26	Two females, recently spawned (479 mm, 426 mm, fork length). Full of loose eggs (384 mm, fork length).
July 3	Full of loose eggs (381 mm, fork length).

Table 15 continued

August 28	Spawned previously, a few eggs remained in body cavity (348 mm fork length). Present work.
Sex Ratio: 75% Female	
1988	
KOKANEE	
January 6	44 Adults ranging in condition from full of loose eggs and milt, to recently having spawned sizes--230 to 330 mm, fork length. Present work.

found to feed on chironomid larvae and pupae and other benthic organisms to a lesser degree (Northcote and Lorz, 1966). Rainbow trout typically feed on benthic and terrestrial invertebrates, although piscivory is common and planktivory may occur (Scott and Crossman, 1973).

Results from previous food habits studies at Crater Lake varied considerably; however, some patterns may be noted. Daphnia have fluctuated greatly in importance in the diet of "silversides" and kokanee. Hubbard (1933, unpublished report) stated that Daphnia comprised 14% of the fish food. Brode (1935) found Daphnia in 74% of the stomachs (mostly "silversides") and 62% of the volume in 1934; for the years 1934-1936, 51% of the stomachs (mostly "silversides") contained Daphnia and they comprised 33.55% of total fish food by volume. In a later paper, Brode (1937, unpublished report) discussed the food habits of 224 fish (214 were silversides) in Crater Lake and hypothesized that there were four food habitat groups: Group 1, a plankton feeding group (120 fish) which fed primarily on Daphnia; Group 2, a shore feeding group (72 fish) which fed primarily on benthic macroinvertebrates; Group 3, which fed on plankton (Daphnia) and shore organisms, in this case almost solely amphipods, (24 fish); and Group 4 (8 fish) that fed on terrestrial insect adults taken from "wind streaks" on the lake surface. In 1940, Hasler and Farner (1942) found only one silverside stomach to contain Daphnia. They noted that the absence of Daphnia in 100 m to surface plankton tows was in contrast to their abundance in 1937 (Hasler, 1938). Patten and Thompson (1957, unpublished report) did not record any Daphnia in stomach samples of kokanee (although this may have been a result of sample preparation). They concluded that the important food types (by frequency and by volume) for kokanee were Amphipoda, Diptera (Chironomidae), and Trichoptera, and those for rainbow trout were Trichoptera, Hymenoptera, Gastropoda, Coleoptera, and Diptera (Chironomidae). Patten and Thompson also stated that "the kokanee usually preferred the smaller forms of the insect orders" and that "the stomach contents indicate that rainbow feed as actively at the surface as below . . . while most of the kokanee foods were taken below the surface."

Although the information from previous studies is sometimes sketchy, the general food habits for trout and salmon were similar to those recorded in 1986 and 1987. Kokanee fed heavily on taxa found in the midwater column and off the lake bottom. Rainbow trout fed off the lake bottom and on insects from the lake surface. Kokanee fed on a few food types, while rainbow trout fed on a wide variety of food types. Where their diets overlapped, kokanee tended to take smaller-bodied taxa. For example, over 95% of the chironomid larvae eaten by kokanee were of the genus Parametriocnemus, while only four rainbow stomachs were found to contain prey of this genus. It should be noted that salamanders and small fish were found in the stomachs of trout in earlier studies, but none were observed in the 1986 or 1987 samples.

The confusion over the identification of the silversides in earlier studies (prior to 1950) prohibits direct comparison of food habits for kokanee in the present study. That the importance of Daphnia in the diet of the salmon apparently varied with abundance in the lake is consistent with what was found in 1986 and 1987. The increased importance of Daphnia in the kokanee diet in 1987 corresponded with an increase in Daphnia abundance in the lake in 1987 (Karnaugh, 1988). Many of the same food groups were important to the salmon, though the relative importance fluctuated between studies. This was also the trend for rainbow trout.

Distribution

Distributions of fish are variable among and within lakes and represent responses to dynamic interactions among physical, chemical, and biological components of a lake ecosystem. Vertical and horizontal migrations of fish are common and are believed to be responses to the interaction among some combination of these components. The most pertinent components appear to be feeding habits closely linked to light intensity (Ricker, 1938; Northcote et al., 1964; McDonald, 1973), avoidance to predation (Eggers, 1978; Wurtsbaugh and Li, 1985), competition (Collins, 1971), behavioral thermoregulation (Finnel and Reed, 1969), and spawning (Lorz and Northcote, 1964).

It is difficult to evaluate the relative importance of these variables to the distribution patterns of fish because the interactions are not static and are very complex. In fact, distributions of kokanee salmon and rainbow trout in lakes are quite variable. Northcote et al. (1964) observed vertical diel migration of kokanee to reverse in succeeding years. In Lake Tahoe, relative abundance of kokanee and rainbow trout that were captured in offshore and nearshore gill net catches fluctuated seasonally (Cordone et al., 1971).

One of the most interesting aspects of the distribution of Crater Lake fish is the unusually deep occurrence and the great magnitude of diel migrations. The maximum depths of occurrences for kokanee reported in the literature include the following:

Horsetooth Reservoir, CO Horak and Tanner (1964)	28.5 m
Lake Tahoe, CA Cordone et al. (1971)	36.5 m
Odell Lake, OR Lewis (1922)	30.0 m
Flathead Lake, MO Hanzel (1984)	36.5 m

A maximum depth of 81 m was recorded for an acoustic target in 1985 in Crater Lake (Thorne and Marino, 1985, unpublished report) and 98.5 m in 1987. The maximum depth of capture of kokanee in Crater Lake was 86.25 m in 1987.

Fish exhibited large diel vertical migrations in the offshore zone of Crater Lake during the first week of September, 1987. These fish were found in deeper water during the day than at night, the median difference in depth being 56 m. A diel migration also was exhibited by nearshore fish, but they were found deeper at night than during the day, a 17 m difference in median depth. Based on capture records it appears that kokanee are primarily offshore and in deep water during the day, and then they move shoreward into shallower water at night. Rainbow trout appeared to remain nearshore in shallower water during the day than at night.

Nearshore vertical distribution of fish and diel migration patterns in September 1987 were similar to those found in August 1985 (Thorne and Marino, 1985). Offshore vertical distribution and diel migration patterns differed, however. Thorne and Marino (1985, unpublished report) concluded that offshore fish migrated into shallower depths during the day and into deeper water at night. The opposite pattern was observed in 1987. A shoreward migration at night by offshore fish was suggested from the results of both studies.

The deep water occurrences of offshore fish may be related to the deep penetration of light in Crater Lake, and perhaps the deep water occurrences of chlorophyll and zooplankton. There does not appear to be a relationship between fish distribution and temperature, dissolved oxygen, or pH because the thermocline was shallow and dissolved oxygen and pH were fairly uniform throughout the water column. It appears that the distributions of Crater Lake fish were most closely associated with feeding habits. Kokanee salmon are believed to feed primarily on cladocerans and chironomids in the deep water offshore zone during the day and to migrate to shallower water and shoreward to feed at dawn and dusk. Rainbow trout appeared to feed primarily in the nearshore area of the lake, rising to shallower depths during the day and feeding heavily on insects from the lake surface.

Conceptual Framework

From the above review it can be concluded that the ecology of the two fish species in Crater Lake is different. Kokanee salmon and rainbow trout differed most notably in morphology, age structure, timing of reproduction, food habits, and distribution in the lake. Differences in feeding habits and distributions are likely a response, in part, to morphological and behavioral differences between kokanee salmon and rainbow trout. Direct and indirect interactions between the two species may also account for some proportion of the observed differences. Kokanee salmon and rainbow trout likely play different ecological roles within the lake community primarily as an expression of their trophic relations.

In recent years there has been a considerable amount of work on the dynamics of trophic interactions of limnetic lake communities (Hrbacek, et al., 1961; Henrikson et al., 1980; Benndorf et al., 1984; Shapiro and Wright, 1984; Carpenter et al., 1985; McQueen et al., 1986). Much of this work emphasized how fish affect community structure and organization through direct and indirect interactions. Historically this discussion has focused on two seemingly contradictory views. The first view conceptualizes lake ecosystems as being driven from the "bottom up" (producer controlled), where nutrient loading determines the productivity and biomass of phytoplankton, zooplankton, planktivorous fish, and piscivorous fish. The second view conceptualizes lakes as being driven from the "top down" (consumer controlled), where the top consumer, often a piscivorous fish, influences the community structure and biomass of lower trophic levels. These interactions affect the availability of dissolved nutrients and nutrient recycling rates (Hrbacek et al., 1961; Henrikson et al., 1980; Shapiro and Wright, 1984). Both the top down and bottom up pathways may affect water clarity, primarily as a function of changes in the phytoplankton community (Henrikson et al., 1980; Shapiro, 1980; Benndorf et al., 1984; Shapiro and Wright, 1984).

More recently it has been recognized that the structure and organization of lake communities is a dynamic response to controls and interactions from both the top down and the bottom up (Carpenter et al., 1985; Benndorf et al., 1986). McQueen et al., (1986) found the bottom up controls to be strongest at the bottom of the food web (nutrients to phytoplankton to zooplankton) and to weaken as one moves up the food web. Conversely, top down effects are strongest between top consumers and weaken as one moves down the food web. The predictability of responses of community subunits weakens as you move away from the controls.

Trophic interactions are as dynamic in the benthic subcommunity as well. Fish introductions may alter benthic community structure and organization through a variety of poorly understood pathways. These changes may be expressed as local extinctions (Riemers, 1979), changes of within-lake distributions (Macan, 1966a; Macan, 1966b), reduced mean weights of prey species, or as reduced biomass of benthic prey populations (Post and Cucin, 1984).

It seems clear that fish have the potential of altering the nutrient and energy flows through trophic interactions within and between the benthic community and the limnetic community. In addition to feeding on prey found in one community or the other, fish intercept many larval and pupal forms before they leave the lake as adults, and they intercept both aquatic and terrestrial adult life stages at the lake surface. Excretions from the fish help to recycle nutrients within and between the two communities (Tatrai, 1987).

It is beyond the scope of this thesis to evaluate these interactions in Crater Lake; however, with the conceptual framework presented and the ecological data collected on Crater Lake fish, a conceptual model has been developed for simplified trophic interactions within the lake (Figure 22).

The limnetic invertebrate community is relatively simple and void of invertebrate predators. Recently the limnetic zooplankton community has been dominated in number by rotifers, although Daphnia appear to be increasing in number. Previous zooplankton investigations between 1896 and 1969 found Daphnia abundance to range from rare to very abundant and dominance to shift between rotifers, Bosmina and Daphnia (see Karnaugh, 1988, for a review of previous zooplankton investigations). The effect of kokanee on the zooplankton community structure in Crater Lake is unknown, however the current community structure is consistant with that of a

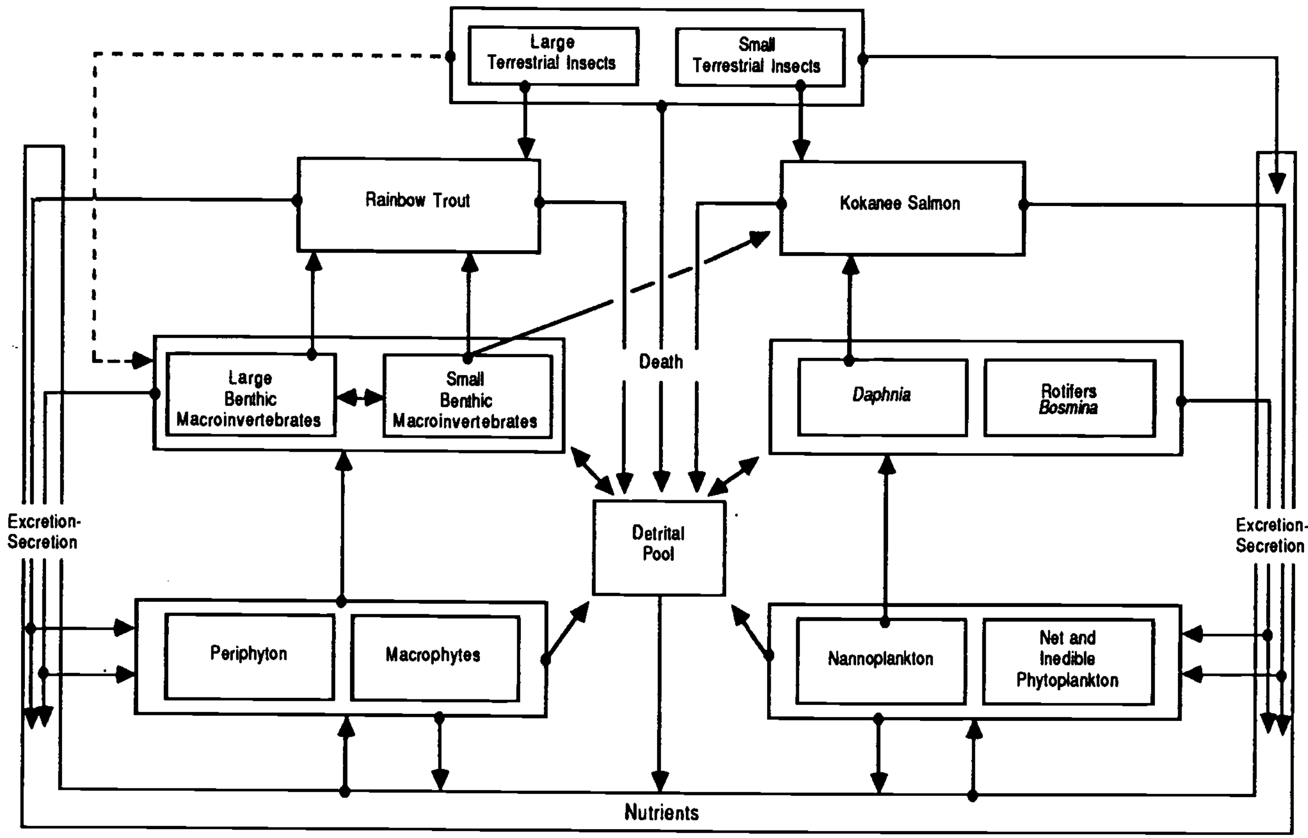


Figure 22. Conceptual Model of Simplified Trophic Interactions Relative to Adult Kokanee Salmon and Rainbow Trout in Crater Lake, Oregon.

zooplankton community under predatory control; preferential feeding by zooplanktivorous fish causes a shift in zooplankton community structure from large bodied cladocerans to small bodied cladocerans and rotifers (Brooks and Dodson, 1965). Kokanee salmon are the dominant vertebrate in the limnetic zone, although rainbow trout undoubtedly occur.

Little is known about the benthic community in Crater Lake. Periphyton and macrophytes are relatively sparce along the shoreline and moss exists to depths of 120 m. Most of the available knowledge about benthic macroinvertebrates has come almost solely from food habit analysis of fish. Both rainbow trout and kokanee salmon interact with the benthic community.

The model indicates that the food web in Crater Lake is not simply a benthic-rainbow trout and limnetic-kokanee salmon system. It is much more complicated. In fact, kokanee salmon greatly increase the diversity of the interactions among the limnetic, benthic, and terrestrial components of the food web, especially prey of small body size. Rainbow trout also are important to the food web, but the focus is on prey of large body size from the benthic and terrestrial components.

While this conceptual model may be heuristically useful, it must be emphasized that lake systems have a high level of complexity. Interactions among life history types and habitat types are not static but are dynamic and ever-evolving. Exhibited life history patterns are in part an expression of the developmental environment of the population and may change with evolving environments as well as in sympatry with other species or groups of species (William Liss, Oregon State University, Department of Fisheries and Wildlife, personal communication).

The concepts presented above are of interest in fisheries sciences because the stocking of fish and invertebrates is a well-practiced management technique to supplement local faunas in order to improve fishing (Li and Moyle, 1981) and more recently in order to improve water quality in environmentally degraded systems (Benndorf, et al., 1984). The ecological implications of fish introductions are poorly understood (Goetze, et al., 1988) and are of growing concern as naturally fishless areas continue to be stocked and are diminishing in number.

An interesting opportunity exists at Crater Lake to follow the apparently cyclic abundances of kokanee salmon and members of the limnetic zooplankton community. Investigation of abundance, distribution, and diel migrations of fish and zooplankton should be expanded, in conjunction with continued food habits analysis, throughout the summer sampling season and during other times of the year if possible. Attempts to sample juvenile fish by previous investigators were unfruitful; none the less, the collection of juveniles and the further description of reproduction, would greatly expand the ecologic knowledge on Crater Lake fish.

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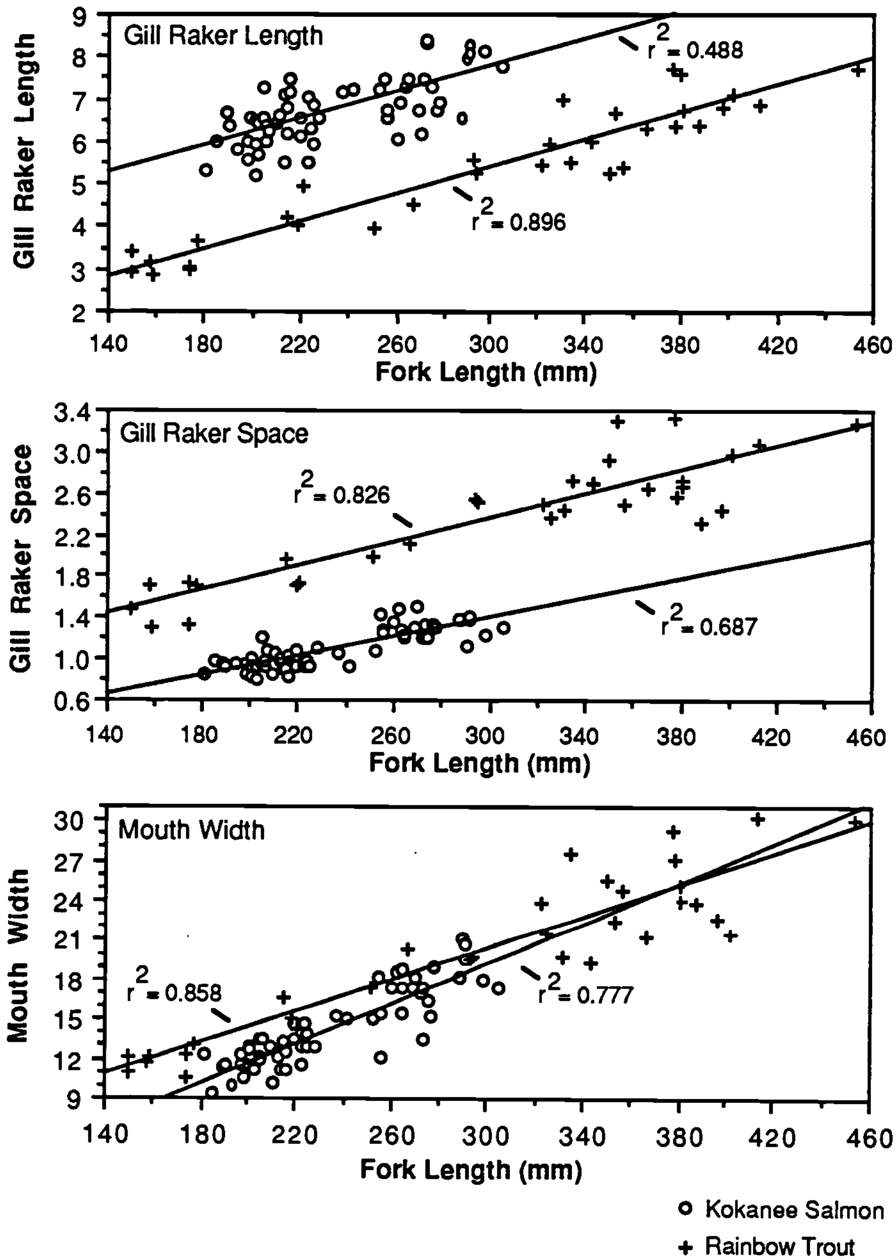
APPENDICES

Appendix I. Relationships Between Gill Raker Length and Fork Length, Gill Raker Space and Fork Length, and Mouth Width and Fork Length for Kokanee Salmon and Rainbow Trout, Crater Lake, Oregon.


Gill Raker Length
Gill Raker Length
r^2 = 0.488
r^2 = 0.896
Fork Length (mm)
Gill Raker Space
Gill Raker Space
r^2 = 0.826
r^2 = 0.687
Fork Length (mm)
Mouth Width
Mouth Width
r^2 = 0.858
r^2 = 0.777
Fork Length (mm)
Kokanee Salmon
Rainbow Trout

Appendix II. A) Percent occurrence, B) Percent composition by number, and C) percent composition by weight of food types from the food habits analysis of Crater Lake fish. Table headings consist of the first four letters of each food type; an "A" at the end denotes aquatic taxa, a "T" denotes terrestrial taxa, an "L" denotes larval life stage, and a "P" denotes pupal life stage.

A) PERCENT OCCURRENCE

DISCRIPTION	COUNT	EPHE	ODON	ORTH	PLEC	PSOC	HEMIA	HEMIT	HOMO	NEUR	COLEA	COLET
SUMMARY FOR ALL KOKANEE	269	6.7	0.0	0.0	2.6	3.7	0.7	4.5	11.5	5.6	10.0	6.3
SUMMARY FOR ALL RAINBOWS	120	31.7	13.3	6.7	3.3	5.8	9.2	25.0	18.3	11.7	33.3	39.2
SUMMARY FOR 1986 KOKANEE	105	13.1	0.0	0.0	6.7	7.6	0.0	2.9	14.3	8.6	12.4	11.4
SUMMARY FOR 1987 KOKANEE	165	2.4	0.0	0.0	0.0	6.0	1.2	5.5	8.5	3.6	9.1	3.0
SUMMARY FOR 1986 RAINBOW	59	18.6	13.6	6.8	1.7	8.5	0.0	16.9	8.5	5.1	50.8	35.6
SUMMARY FOR 1987 RAINBOW	61	40.9	13.1	6.5	4.9	1.6	18.0	32.7	26.2	18.0	18.0	37.7
SUMMARY FOR KOKANEE BY AGE												
AGE 2	99	11.1	0.0	0.0	6.1	7.1	0.0	2.0	13.1	6.1	11.1	9.1
AGE 3	105	4.8	0.0	0.0	1.0	0.0	1.0	5.7	9.5	5.7	12.4	5.7
SUMMARY FOR RAINBOWS BY AGE												
AGE 1	12	41.6	16.6	0.0	0.0	8.3	8.3	33.3	25.0	5.0	25	25.0
AGE 2	40	15.0	5.0	10.0	2.5	7.5	5.0	22.5	25.0	2.5	42.5	47.5
AGE 3	23	39.1	17.3	4.3	4.3	4.3	8.6	26.0	21.7	17.3	34.7	34.7
AGE 4	10	60.0	20.0	0.0	0.0	0.0	30.0	30.0	0.0	20.0	40.0	40.0
AGE 5	9	33.3	44.4	0.0	0.0	22.2	22.2	22.2	11.1	33.3	11.1	44.4
AGE 6	6	66.6	33.3	0.0	0.0	0.0	16.6	33.2	0.0	33.3	50.0	33.3
SUMMARY FOR KOKANEE BY LENGTH												
LENGTH 1 (200-249mm)	83	13.3	0.0	0.0	6.0	8.4	0.0	2.4	10.8	7.2	12.0	6.0
LENGTH 2 (250-300mm)	83	6.0	0.0	0.0	0.0	0.0	1.2	7.2	8.4	4.8	13.3	3.6
SUMMARY FOR RAINBOW BY LENGTH												
LENGTH 1 (200-249mm)	24	29.2	8.3	4.2	4.2	8.3	8.3	29.2	25.0	0.0	45.8	58.3
LENGTH 2 (250-300mm)	20	10.0	15.0	20.0	5.0	5.0	0.0	45.0	20.0	10.0	25.0	35.0
SUMMARY FOR LITTORAL KOKANEE	221	8.1	0.0	0.5	2.7	2.7	0.9	5.0	11.3	6.8	12.2	5.0
SUMMARY FOR PELAGIC KOKANEE	29	0.0	0.0	0.0	3.4	13.8	0.0	3.4	20.7	0.0	3.4	24.1
SUMMARY FOR GILL NET KOKANEE	195	6.2	0.0	0.5	1.5	2.6	1.0	5.1	12.3	6.7	9.2	5.1
SUMMARY FOR ANGLED KOKANEE	26	23.1	0.0	0.0	11.5	3.8	0.0	3.8	3.8	7.7	34.6	3.8
SUMMARY FOR DOWNRIGGER KOKANEE	29	0.0	0.0	0.0	3.4	13.8	0.0	3.4	20.7	0.0	3.4	24.1
SUMMARY FOR GILL NET RAINBOW	66	25.8	7.6	9.1	3.0	4.5	9.1	25.8	28.8	6.1	30.3	31.8
SUMMARY FOR ANGLED RAINBOW	49	40.8	22.4	2.0	8.2	8.2	10.2	25.6	6.1	20.4	38.8	49.0

DISCRIPTION	COUNT	TRIC	LEPI	DIPT	CHIRL	CHIRP	HYME	CLAD	AMPH	DECA	GAST	ARAC
SUMMARY FOR ALL KOKANEE	269	43.1	0.7	6.3	74.0	72.1	7.8	36.8	41.3	0.0	0.4	7.8
SUMMARY FOR ALL RAINBOWS	120	75.8	20.0	38.3	35.0	49.2	54.2	0.0	13.3	2.5	25.8	21.7
SUMMARY FOR 1986 KOKANEE	105	59.0	1.9	7.6	65.7	81.9	13.3	18.3	32.4	0.0	0.0	10.5
SUMMARY FOR 1987 KOKANEE	165	32.7	6.0	4.2	72.7	65.6	4.2	49.7	45.5	0.0	6.0	6.1
SUMMARY FOR 1986 RAINBOW	59	69.5	18.6	54.2	47.5	54.2	61.0	0.0	8.5	1.7	15.3	16.9
SUMMARY FOR 1987 RAINBOW	61	81.9	21.3	26.2	22.9	37.7	47.5	0.0	16.3	3.2	36.0	26.2
SUMMARY FOR KOKANEE BY AGE												
AGE 2	99	53.5	1.0	8.1	67.7	81.0	11.1	17.2	35.4	0.0	0.0	10.1
AGE 3	105	38.1	1.0	5.7	69.5	72.4	3.8	44.8	51.4	0.0	0.0	7.6
SUMMARY FOR RAINBOWS BY AGE												
AGE 1	12	91.6	16.2	33.3	41.6	41.6	33.0	0.0	8.3	0.0	50.0	8.3
AGE 2	40	72.5	17.5	47.5	40.0	45.0	62.5	0.0	10.0	0.0	17.5	25.0
AGE 3	23	73.9	21.7	34.7	34.7	60.8	56.5	0.0	21.7	0.0	26.0	39.1
AGE 4	10	90.0	30.0	50.0	40.0	50.0	60.0	0.0	20.0	0.0	1.0	0.0
AGE 5	9	100.0	44.4	66.6	11.1	66.6	55.5	0.0	11.1	11.1	33.3	22.2
AGE 6	6	83.3	33.3	50.0	33.3	83.3	83.3	0.0	16.6	16.6	50.0	50.0
SUMMARY FOR KOKANEE BY LENGTH												
LENGTH 1 (200-249mm)	83	50.6	1.2	6.0	67.5	80.7	12.0	18.1	34.9	0.0	0.0	9.6
LENGTH 2 (250-300mm)	83	38.6	0.0	4.8	72.3	73.5	3.6	48.2	57.8	0.0	0.0	9.6
SUMMARY FOR RAINBOW BY LENGTH												
LENGTH 1 (200-249mm)	24	83.3	12.5	50.0	41.7	41.7	66.7	0.0	8.3	0.0	8.3	25.0
LENGTH 2 (250-300mm)	20	60.0	20.0	25.0	25.0	50.0	50.0	0.0	15.0	0.0	35.0	35.0
SUMMARY FOR LITTORAL KOKANEE	221	48.0	0.9	6.8	76.9	85.5	6.3	40.7	48.9	0.0	0.5	5.9
SUMMARY FOR PELAGIC KOKANEE	29	37.9	3.4	6.9	58.6	86.2	27.6	31.0	6.9	0.0	0.0	27.6
SUMMARY FOR GILL NET KOKANEE	195	44.1	1.0	6.7	78.5	74.9	5.6	44.1	50.8	0.0	0.5	6.2
SUMMARY FOR ANGLED KOKANEE	26	76.9	0.0	7.7	65.4	88.5	11.5	15.4	34.6	0.0	0.0	3.8
SUMMARY FOR DOWNRIGGER KOKANEE	29	37.9	3.4	6.9	58.6	86.2	27.6	31.0	6.9	0.0	0.0	27.6
SUMMARY FOR GILL NET RAINBOW	66	75.8	13.6	31.8	24.2	39.4	45.5	0.0	15.2	0.0	27.3	25.8
SUMMARY FOR ANGLED RAINBOW	49	81.6	30.6	55.1	51.0	65.3	69.4	0.0	10.2	6.1	26.5	18.4

B) PERCENT COMPOSITION BY NUMBER

DISCRIPTION	COUNT	EPHE	ODON	ORTH	PLEC	PSOC	HEMIA	HEMIT	HOMO	NEUR	COLEA	COLET
SUMMARY FOR ALL KOKANEE	269	1.0	0.0	0.0	0.0	0.3	0.0	0.0	0.8	0.2	0.5	0.0
SUMMARY FOR ALL RAINBOWS	120	7.9	0.5	0.2	0.0	0.9	0.2	1.7	1.5	0.2	10.1	2.0
SUMMARY FOR 1986 KOKANEE	105	2.3	0.0	0.0	0.0	0.8	0.0	0.0	1.0	0.4	0.4	0.0
SUMMARY FOR 1987 KOKANEE	165	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.6	0.0
SUMMARY FOR 1986 RAINBOW	59	2.3	0.6	0.1	0.0	1.7	0.0	0.2	0.4	0.1	17.8	2.2
SUMMARY FOR 1987 RAINBOW	61	13.4	0.4	0.4	0.0	0.1	0.5	3.1	2.6	0.3	2.6	1.8
SUMMARY FOR KOKANEE BY AGE												
AGE 2	99	1.7	0.0	0.0	0.0	0.8	0.0	0.0	0.1	0.4	0.8	0.0
AGE 3	105	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.2	0.0
SUMMARY FOR RAINBOWS BY AGE												
AGE 1	12	4.7	0.5	0.0	0.0	0.2	0.5	4.0	1.4	0.0	12.2	0.6
AGE 2	40	2.8	0.0	0.1	0.0	2.4	0.1	2.1	2.9	0.0	12.9	1.2
AGE 3	23	9.2	0.6	0.9	0.0	0.0	0.4	1.6	1.6	0.2	6.7	1.2
AGE 4	10	20.8	0.2	0.0	0.0	0.0	0.6	0.7	0.0	0.2	7.7	1.7
AGE 5	9	12.7	0.3	0.0	0.0	0.5	0.1	0.3	0.1	0.3	8.3	8.1
AGE 6	6	10.3	4.2	0.1	0.0	0.0	0.5	0.2	0.0	0.6	2.1	4.7
SUMMARY FOR KOKANEE BY LENGTH												
LENGTH 1 (200-249mm)	83	2.1	0.0	0.0	0.0	0.9	0.0	0.0	0.1	0.5	1.0	0.0
LENGTH 2 (250-300mm)	83	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.2	0.0
SUMMARY FOR RAINBOW BY LENGTH												
LENGTH 1 (200-249mm)	24	5.7	0.0	0.1	0.0	0.2	0.1	2.9	3.7	0.0	19.0	1.3
LENGTH 2 (250-300mm)	20	4.4	0.2	0.2	0.0	0.1	0.0	1.9	0.6	0.1	7.8	2.8
SUMMARY FOR LITTORAL KOKANEE	221	1.1	0.0	0.0	0.0	0.3	0.0	0.0	0.9	0.2	0.5	0.0
SUMMARY FOR PELAGIC KOKANEE	29	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.2	0.0	0.0	0.1
SUMMARY FOR GILL NET KOKANEE	195	1.0	0.0	0.0	0.0	0.3	0.0	0.0	1.0	0.2	0.4	0.0
SUMMARY FOR ANGLED KOKANEE	26	1.8	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	1.4	0.0
SUMMARY FOR DOWNRIGGER KOKANEE	29	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.2	0.0	0.0	0.1
SUMMARY FOR GILL NET RAINBOW	66	6.6	0.5	0.4	0.0	1.5	0.3	2.7	2.7	0.1	10.6	1.1
SUMMARY FOR ANGLED RAINBOW	49	10.5	0.4	0.0	0.0	0.1	0.2	0.5	0.1	0.4	10.2	3.4

DISCRIPTION	COUNT	TRIC	LEPI	DIPT	CHIRL	CHIRP	HYME	CLAD	AMPH	DECA	GAST	ARAC
SUMMARY FOR ALL KOKANEE	269	5.6	0.0	0.1	22.6	31.4	0.4	21.3	8.0	0.0	0.3	0.0
SUMMARY FOR ALL RAINBOWS	120	22.2	0.6	4.8	7.3	13.4	10.1	0.0	6.8	0.1	5.5	0.6
SUMMARY FOR 1986 KOKANEE	105	8.8	0.0	0.1	10.6	49.7	1.0	9.4	8.7	0.0	0.0	0.1
SUMMARY FOR 1987 KOKANEE	165	3.6	0.0	0.0	30.3	19.7	0.0	28.9	7.6	0.0	0.5	0.0
SUMMARY FOR 1986 RAINBOW	59	19.4	0.6	8.7	10.2	12.3	8.8	0.0	4.3	0.1	4.8	0.3
SUMMARY FOR 1987 RAINBOW	61	24.8	0.7	0.9	4.5	14.5	11.3	0.0	9.2	0.1	6.1	0.9
SUMMARY FOR KOKANEE BY AGE												
AGE 2	99	8.1	0.0	0.0	18.1	48.0	0.0	8.2	7.3	0.0	0.0	0.1
AGE 3	105	5.1	0.0	0.1	24.7	28.2	0.0	21.3	10.9	0.0	0.0	0.0
SUMMARY FOR RAINBOWS BY AGE												
AGE 1	12	22.5	0.4	5.1	21.3	3.6	6.4	0.0	3.1	0.0	13.6	0.0
AGE 2	40	19.8	0.5	6.8	6.9	10.8	13.3	0.0	8.7	0.0	2.8	0.9
AGE 3	23	16.5	1.3	5.3	6.8	20.0	9.1	0.0	7.0	0.0	6.3	1.2
AGE 4	10	20.3	0.4	1.1	0.7	18.1	10.2	0.0	16.4	0.0	1.0	0.0
AGE 5	9	19.6	0.8	2.4	5.2	8.4	8.5	0.0	5.4	0.1	8.4	0.4
AGE 6	6	33.3	0.2	2.7	4.9	14.2	5.9	0.0	0.5	0.7	13.4	0.4
SUMMARY FOR KOKANEE BY LENGTH												
LENGTH 1 (200-249mm)	83	7.7	0.0	0.0	19.5	46.3	0.0	9.8	7.2	0.0	0.0	0.1
LENGTH 2 (250-300mm)	83	6.2	0.0	0.0	27.6	22.7	0.0	22.1	11.6	0.0	0.0	0.0
SUMMARY FOR RAINBOW BY LENGTH												
LENGTH 1 (200-249mm)	24	25.9	0.1	6.1	4.9	9.9	13.2	0.0	5.8	0.0	0.0	1.1
LENGTH 2 (250-300mm)	20	2.3	1.4	3.5	4.7	16.5	16.7	0.0	14.1	0.0	6.5	1.5
SUMMARY FOR LITTORAL KOKANEE	221	6.3	0.0	0.1	24.2	28.1	0.4	20.6	9.0	0.0	0.3	0.0
SUMMARY FOR PELAGIC KOKANEE	29	0.5	0.0	0.0	10.6	59.7	0.1	28.0	0.1	0.0	0.0	0.3
SUMMARY FOR GILL NET KOKANEE	195	3.5	0.0	0.1	26.4	27.1	0.5	21.3	8.7	0.0	0.4	0.0
SUMMARY FOR ANGLED KOKANEE	26	28.9	0.0	0.0	5.9	35.9	0.0	14.3	11.5	0.0	0.0	0.0
SUMMARY FOR DOWNRIGGER KOKANEE	29	0.5	0.0	0.0	10.6	59.7	0.1	28.0	0.1	0.0	0.0	0.3
SUMMARY FOR GILL NET RAINBOW	66	23.7	0.4	1.6	6.4	12.3	12.4	0.0	9.8	0.0	6.3	0.6
SUMMARY FOR ANGLED RAINBOW	49	20.6	0.9	9.5	9.4	16.3	8.0	0.0	3.3	0.2	4.9	0.7

C) PERCENT COMPOSITION BY WEIGHT

DISCRIPTION	COUNT	EPHE	ODON	ORTH	PLEC	PSOC	HEMIA	HEMIT	HOMO	NEUR	COLEA	COLET
SUMMARY FOR ALL KOKANEE	269	1.4	0.0	0.0	0.1	0.3	0.0	0.1	0.5	1.2	0.5	0.1
SUMMARY FOR ALL RAINBOWS	120	6.2	2.4	1.7	0.0	0.4	0.2	2.3	0.8	0.7	8.8	2.7
SUMMARY FOR 1986 KOKANEE	105	3.0	0.0	0.0	0.1	0.7	0.0	0.0	0.2	2.6	0.3	0.2
SUMMARY FOR 1987 KOKANEE	165	0.3	0.0	0.0	0.0	0.0	0.0	0.1	0.6	0.3	0.7	0.1
SUMMARY FOR 1986 RAINBOW	59	1.8	2.3	0.7	0.0	0.7	0.0	1.0	0.5	0.0	16.4	3.5
SUMMARY FOR 1987 RAINBOW	61	10.4	2.5	2.7	0.0	0.0	0.5	3.5	1.2	1.3	1.5	1.9
SUMMARY FOR KOKANEE BY AGE												
AGE 2	99	2.4	0.0	0.0	0.1	0.7	0.0	0.0	0.0	1.8	0.3	0.2
AGE 3	105	1.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.5	0.4	0.2
SUMMARY FOR RAINBOWS BY AGE												
AGE 1	12	2.7	4.5	0.0	0.0	0.0	0.2	2.4	0.5	0.0	10.4	0.2
AGE 2	40	2.9	0.3	1.9	0.0	1.1	0.1	2.8	2.0	0.0	11.2	2.3
AGE 3	23	10.5	3.7	3.0	0.0	0.0	0.6	1.5	0.4	2.0	6.4	1.2
AGE 4	10	15.1	1.1	0.0	0.0	0.0	0.3	4.0	0.0	0.2	2.6	3.9
AGE 5	9	7.9	2.7	0.0	0.0	0.0	0.1	0.4	0.0	0.1	8.9	11.6
AGE 6	6	3.2	12.6	1.3	0.0	0.0	0.1	0.6	0.0	0.3	0.3	2.2
SUMMARY FOR KOKANEE BY LENGTH												
LENGTH 1 (200-249mm)	83	2.9	0.0	0.0	0.2	0.8	0.0	0.0	0.0	2.1	1.0	0.0
LENGTH 2 (250-300mm)	83	1.3	0.0	0.0	0.0	0.0	0.0	0.1	0.0	0.5	0.4	0.1
SUMMARY FOR RAINBOW BY LENGTH												
LENGTH 1 (200-249mm)	24	5.5	0.5	1.0	0.0	0.0	0.1	4.6	3.0	0.0	17.2	2.2
LENGTH 2 (250-300mm)	20	4.6	0.7	4.8	0.0	0.0	0.0	2.4	0.5	0.0	7.7	3.8
SUMMARY FOR LITTORAL KOKANEE	221	1.5	0.0	0.0	0.1	0.2	0.0	0.1	0.5	1.3	0.6	0.1
SUMMARY FOR PELAGIC KOKANEE	29	0.0	0.0	0.0	0.1	0.6	0.0	0.0	0.1	0.0	0.0	0.3
SUMMARY FOR GILL NET KOKANEE	195	1.4	0.0	0.0	0.0	0.2	0.0	0.1	0.6	1.5	0.6	0.1
SUMMARY FOR ANGLED KOKANEE	26	2.4	0.0	0.0	0.2	0.0	0.0	0.1	0.0	0.4	1.1	0.0
SUMMARY FOR DOWNRIGGER KOKANEE	29	0.0	0.0	0.0	0.1	0.6	0.0	0.0	0.1	0.0	0.0	0.3
SUMMARY FOR GILL NET RAINBOW	66	5.2	2.3	2.9	0.0	0.7	0.4	3.1	1.1	0.1	10.6	1.4
SUMMARY FOR ANGLED RAINBOW	49	8.2	2.8	0.1	0.0	0.0	0.1	1.4	0.5	1.5	7.4	4.7

DISCRIPTION	COUNT	TRIC	LEPI	DIPT	CHIRL	CHIRP	HYME	CLAD	AMPH	DECA	GAST	ARAC
SUMMARY FOR ALL KOKANEE	269	13.0	0.2	0.1	24.7	26.3	0.5	14.7	8.5	0.0	0.4	0.2
SUMMARY FOR ALL RAINBOWS	120	24.7	2.9	3.7	5.3	5.4	13.8	0.0	4.4	1.9	7.9	0.3
SUMMARY FOR 1986 KOKANEE	105	19.7	0.3	0.2	11.8	40.8	1.1	4.0	8.0	0.0	0.0	0.3
SUMMARY FOR 1987 KOKANEE	165	8.7	0.1	0.0	33.0	17.1	0.1	21.5	8.8	0.0	0.6	0.2
SUMMARY FOR 1986 RAINBOW	59	23.8	2.1	7.1	7.1	3.2	14.6	0.0	2.8	1.6	5.4	0.3
SUMMARY FOR 1987 RAINBOW	61	25.7	3.8	0.3	3.6	7.6	13.0	0.0	6.0	2.2	10.3	0.4
SUMMARY FOR KOKANEE BY AGE												
AGE 2	99	16.8	0.3	0.1	19.2	39.1	0.1	4.6	7.2	0.0	0.0	0.3
AGE 3	105	11.7	0.0	0.2	26.7	23.0	0.0	16.0	11.5	0.0	0.0	0.2
SUMMARY FOR RAINBOWS BY AGE												
AGE 1	12	22.6	3.9	2.2	16.8	1.6	6.9	0.0	3.5	0.0	21.6	0.0
AGE 2	40	23.0	1.9	5.8	5.7	2.8	19.6	0.0	6.2	0.0	4.9	0.5
AGE 3	23	19.5	3.9	5.0	5.1	12.1	11.5	0.0	2.8	0.0	6.1	0.5
AGE 4	10	25.1	2.5	1.6	0.4	9.4	19.4	0.0	13.1	0.0	1.4	0.0
AGE 5	9	24.9	4.2	1.1	1.5	0.4	11.6	0.0	0.4	6.2	7.5	0.4
AGE 6	6	44.6	0.8	0.5	1.7	0.9	4.1	0.0	0.0	10.6	16.0	0.2
SUMMARY FOR KOKANEE BY LENGTH												
LENGTH 1 (200-249mm)	83	13.9	0.4	0.1	20.9	40.2	0.1	5.4	6.9	0.0	0.0	0.3
LENGTH 2 (250-300mm)	83	11.9	0.0	0.1	30.1	18.1	0.1	16.1	12.7	0.0	0.0	0.3
SUMMARY FOR RAINBOW BY LENGTH												
LENGTH 1 (200-249mm)	24	27.4	0.8	5.2	4.7	2.1	23.4	0.0	1.2	0.0	0.4	0.5
LENGTH 2 (250-300mm)	20	5.9	4.5	3.4	3.7	5.2	13.1	0.0	11.9	0.0	12.1	0.6
SUMMARY FOR LITTORAL KOKANEE	221	14.0	0.0	0.1	25.7	22.8	0.6	14.5	9.5	0.0	0.4	0.1
SUMMARY FOR PELAGIC KOKANEE	29	5.2	1.0	0.1	17.4	56.7	0.2	17.3	0.2	0.0	0.0	0.8
SUMMARY FOR GILL NET KOKANEE	195	10.3	0.1	0.1	28.2	21.6	0.6	15.6	9.8	0.0	0.5	0.1
SUMMARY FOR ANGLED KOKANEE	26	44.6	0.0	0.0	5.5	32.3	0.2	6.1	7.2	0.0	0.0	0.0
SUMMARY FOR DOWNRIGGER KOKANEE	29	5.2	1.0	0.1	17.4	56.7	0.2	17.3	0.2	0.0	0.0	0.8
SUMMARY FOR GILL NET RAINBOW	66	25.3	2.1	0.7	5.1	6.3	15.3	0.0	7.1	0.0	10.0	0.5
SUMMARY FOR ANGLED RAINBOW	49	24.6	4.4	8.1	6.1	4.9	13.2	0.0	1.2	4.8	5.9	0.2