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CHIGNIK SALMON STUDIES:

CONSUMPTION OF SOCKEYE SALMON FRY BY JUVENILE COHO SALMON IN THE CHIGNIK LAKES, ALASKA: IMPLICATIONS FOR SALMON MANAGEMENT

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Gregory T. Ruggerone and Donald E. Rogers

ANNUAL REPORT
ANADROMOUS FISH PROJECT

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Director

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ABSTRACT

The consumption of recently emerged sockeye salmon by juvenile coho salmon in the Chignik lakes, Alaska, was estimated during 15 May to 5 August 1985-1987. Estimated daily consumption of sockeye by coho in Chignik Lake, based on a stomach evacuation (direct) method, increased from about 2.0 fry day^{-1} in late May to a maximum of 3.3 fry day^{-1} in June, then declined in July and early August (1.1 fry day^{-1}). The average daily consumption estimate for each year, based on a bioenergetic approach, was within 14% (range: 5-20%) of the direct method estimates, whereas bioenergetic estimates on a given day were generally within 30% of the direct estimates. The similarity in average consumption rates by these two independent methods tends to validate both estimates. Few coho were captured in nearby Black Lake and consumption of juvenile sockeye per coho was low.

Estimates of sockeye fry consumed by the coho population in Chignik Lake were based on two independent estimates of juvenile coho abundance, averaging 290,000, 230,000 and 340,000 coho during 1985, 1986 and 1987, respectively. The average of the estimates of sockeye fry consumed by these coho were 68 million, 24 million and 78 million fry or approximately 59% of the sockeye fry population during 1985, 1986 and 1987, respectively. Trends in the run size of adult coho and relative production of adult sockeye salmon returning to Chignik Lake during brood years 1971-1982 were inversely related, suggesting that predation by juvenile coho in Chignik Lake may have influenced the run size of adult sockeye.

Management of the coho salmon fishery has resulted in a relatively fixed rate of harvest and in increasingly large spawning escapements of coho during the past 16 yr. In contrast, a relatively fixed number of sockeye salmon have spawned. A management strategy resulting in a fixed annual escapement of coho is recommended to reduce and stabilize predation by coho on juvenile sockeye salmon in Chignik Lake.

INTRODUCTION

An important goal of fisheries biologists has been to identify the relative importance of mortality agents affecting Pacific salmon (*Oncorhynchus* sp.) during incubation, freshwater residence, seaward migration and marine residence (Thompson 1962; Larkin 1988). Of the 1,200-8,400 eggs produced by salmon (Bell 1980), <1% typically survive to successfully reproduce. Control of known mortality agents may be used by fisheries managers to enhance salmon production. For example, attempts have been made to improve salmon survival by regulating salmon spawning density (Ricker 1954), reducing stream flow fluctuations during incubation (West 1978), improving rearing habitat (Ministry of Environment 1980), adding nutrients to enhance salmon growth in streams (Mundie 1974) and lakes (Rogers et al. 1980; Hyatt and Stockner 1985), and removing predators of salmon (Foerster and Ricker 1941; Meachum and Clark 1979).

Predation is generally believed to be a major source of mortality for salmon after emergence from gravel (Foerster and Ricker 1941; Ricker 1941; Ruggerone and Rogers 1984); therefore, control of salmonid predators may lead to improved production. A special case of predator control may exist when both the predator and its prey are commercially valuable. For example, piscivorous coho salmon (*O. kisutch*) are often sympatric with pink (*O. gorbuscha*), chum (*O. keta*) and sockeye salmon (*O. nerka*). Coho may consume sockeye salmon in many Alaska and British Columbia lakes (e.g., Cultus and Karluk lakes: Ricker 1941; McIntyre et al. 1988), whereas pink and chum salmon are generally attacked by coho in coastal areas (Parker 1968, 1971; Jones et al. 1988). Management of salmon fisheries with knowledge of the predator-prey interactions could lead to improved returns of salmon.

In the Chignik lakes, Alaska (Fig. 1), sockeye salmon are closely managed and have supported a substantial commercial fishery ($\bar{x}$ = 960,000 adult fish yr^{-1}) since the late 1800s (INPFC 1979), whereas coho salmon are harvested at a lower level ($\bar{x}$ = 38,100 fish yr^{-1} since 1910) with lower effort and without consideration of their possible impacts on sockeye salmon. Roos (1960) first noted that juvenile coho in Chignik Lake consumed juvenile sockeye and suggested that coho might reduce sockeye abundance. Predation by coho on sockeye salmon in the lakes may have increased substantially in recent years, as the average run size of adult coho has increased 157% during 1979-1988 ($\bar{x}$ = 170,000 fish ± 24,000 S.E.) relative to the previous 6 yr ($\bar{x}$ = 66,000 fish ± 6,000 S.E., Ruggerone 1989a).

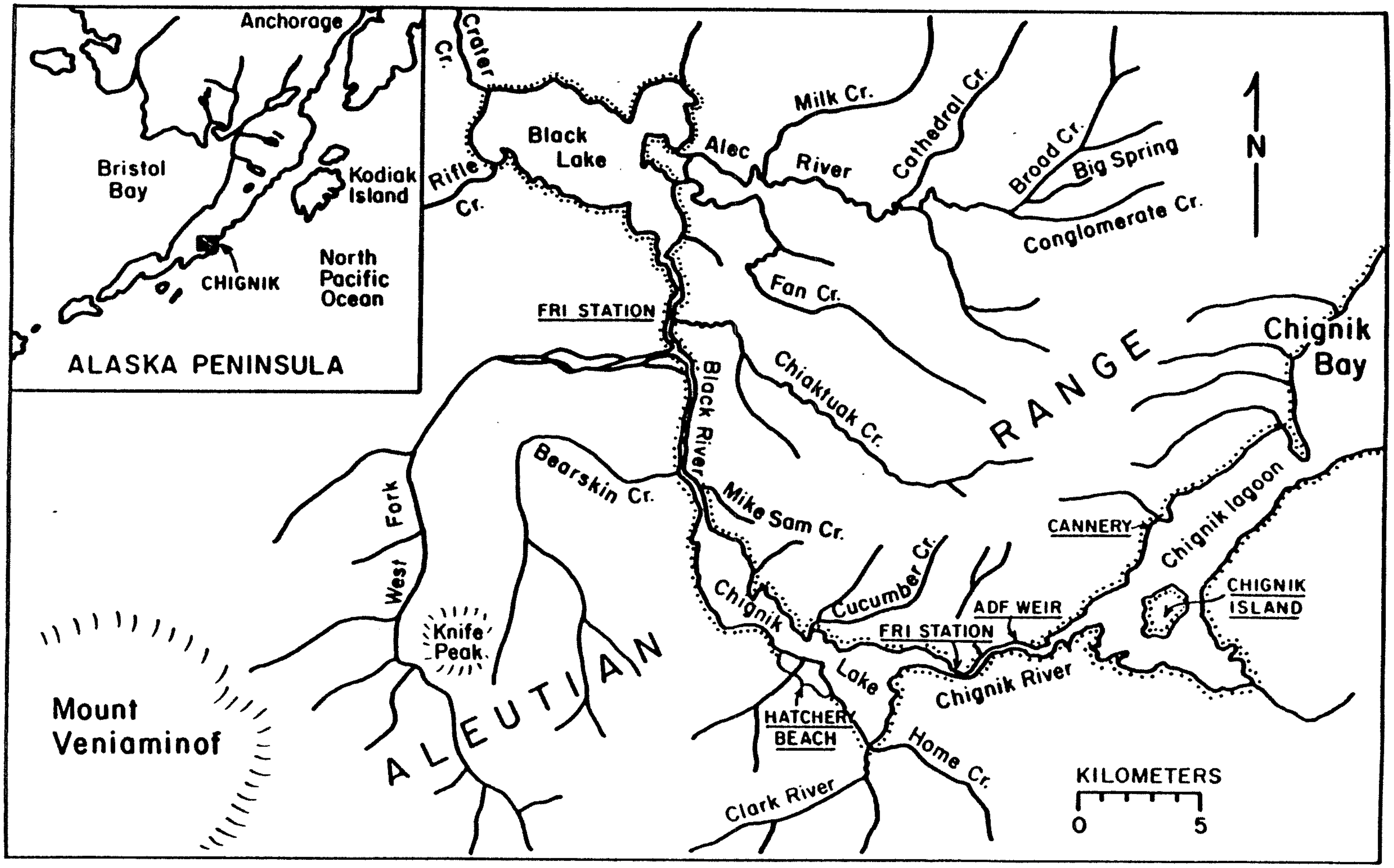

Figure 1. The Chignik lake system, Alaska.

The primary objective of this investigation was to estimate the importance of predation by coho salmon on sockeye abundance in Chignik and Black lakes and on subsequent returns of sockeye salmon. A secondary objective was to compare bioenergetic (Kitchell et al. 1977; Hewett and Johnson 1987) and stomach evacuation (Bajkov 1935; Elliott and Persson 1978) approaches for estimating daily food consumption by juvenile coho salmon.

MATERIALS AND METHODS

STOMACH CONTENT ANALYSIS

Juvenile coho salmon and other fishes were sampled by beach seine (35 m long x 4 m maximum depth, 17 m lead line, 3 mm mesh) with a stratified design during 1985-1987. Most sampling occurred between 1000 and 1600 h. Twelve stations representing five habitats in Chignik Lake were each fished once approximately every 10 days from mid-May to early August, 1986-1987 (Fig. 2). Six of these sampling stations were located within two sockeye beach spawning areas, which represented 5.6 km or 15% of the lake perimeter; the other six stations were located within three nonspawning areas (representing 12.4 km or 35% of the lake perimeter). An additional 55 beach seine sets were made at 10 locations representing the remaining 50% of the lake, which was believed to have few coho that consumed sockeye. In 1985, the five habitats were sampled at six rather than twelve locations. The captured fishes were identified and counted and fork length was measured on random subsamples of coho, sockeye and chinook salmon (*O. tshawytscha*) and Dolly Varden char (*Salvelinus malma*). Additional coho were saved for the analysis of stomach contents to achieve sample sizes of about 10 coho $\geq$ 70 mm fork length per station. Digestion and evacuation of prey from coho stomachs was reduced by immediately injecting 50% buffered formalin (~1 ml) into the stomach cavity of coho, then all subsampled fish were preserved in 10% buffered formalin. Coho in Black Lake were sampled by beach seine at 10 stations (Fig. 3) approximately every 14 days during 1985-1987.

Stomach contents of the coho were analyzed approximately 48 h after capture, at which time post-mortem shrinkage of body length was considered complete (Rogers 1964). Prey were identified as sockeye salmon fry, other fish species (age-1 sockeye,

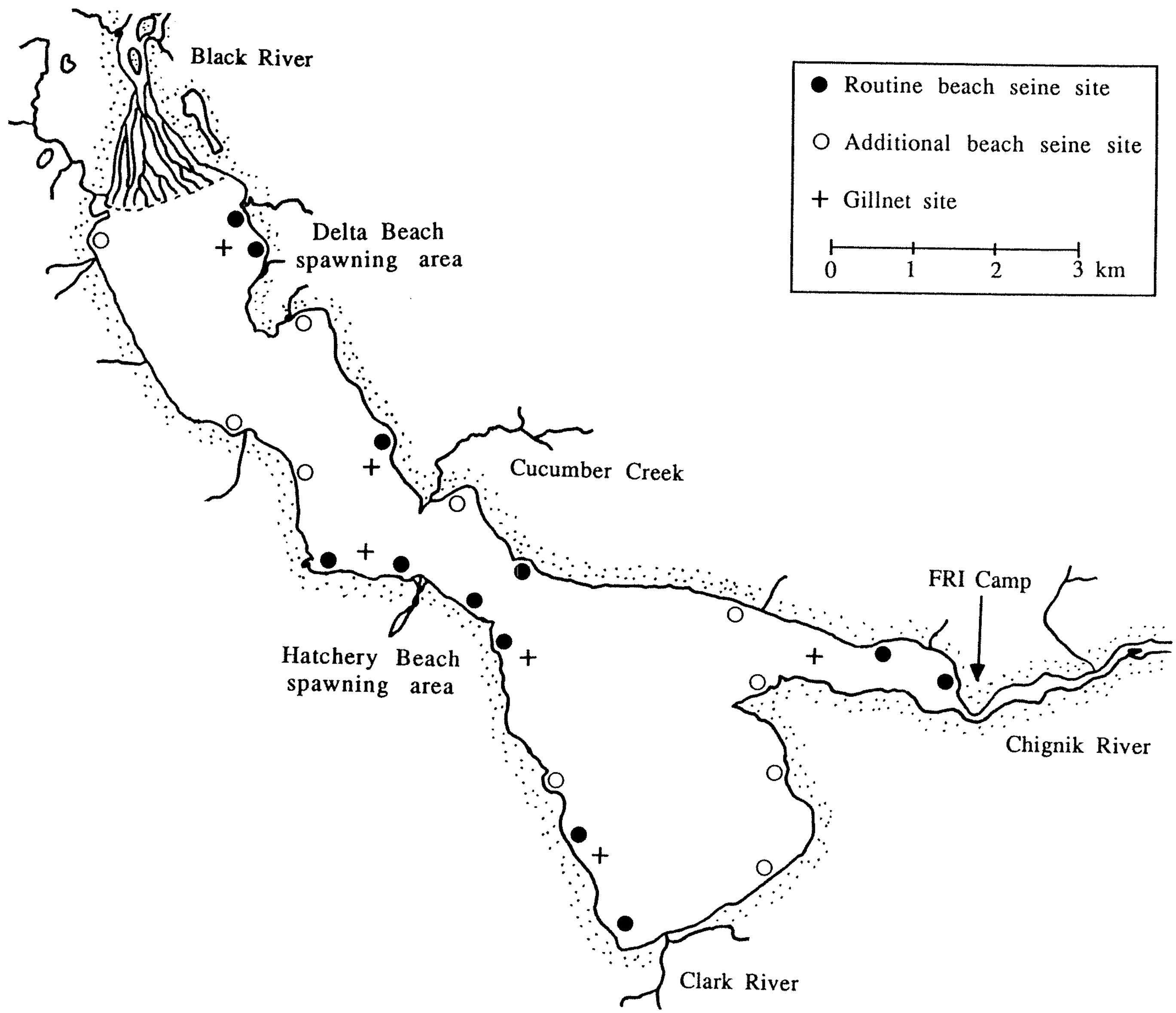

Figure 2. Locations of beach seine and gillnet stations at Chignik Lake.

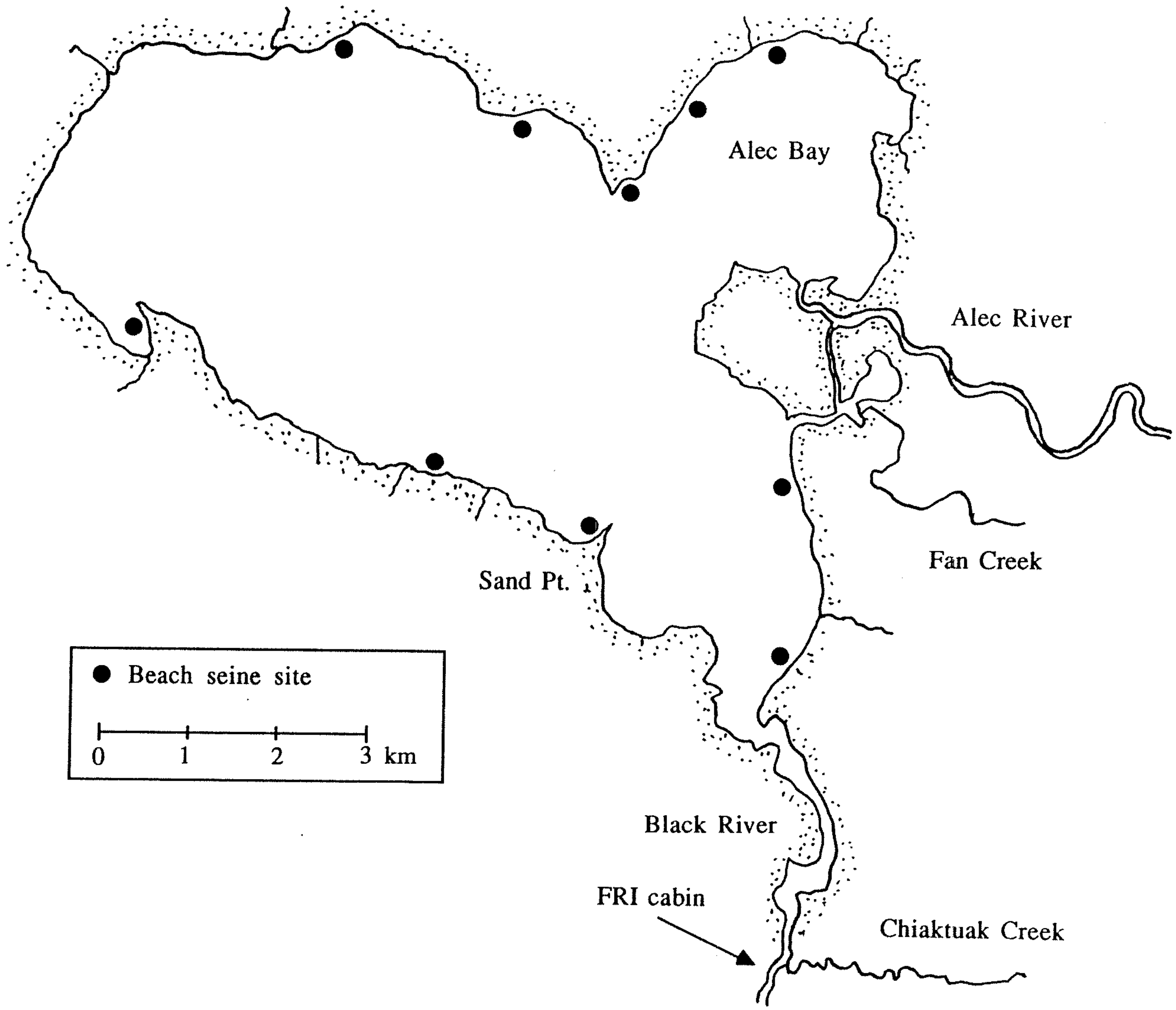

Figure 3. Locations of beach seine stations at Black Lake.

sculpin, coho fry or unidentified fish), insects, or uncommon prey, then blot dried and weighed separately to the nearest mg. Each coho was measured and scales from approximately 60 coho were removed at each 10- or 14-day sampling period in order to estimate age-specific growth, which was used to estimate food consumption by the bioenergetic method.

DISTRIBUTION OF COHO SALMON IN CHIGNIK LAKE

The horizontal and vertical distribution of coho in Chignik Lake was assessed by gill nets (2.6 cm stretch mesh, 2 m x 30 m). Three surface nets were placed at 20, 50, 100 or 150 m from shore at six beach seining areas (Fig. 2) during late May to early July, 1986-1988. Most nets were set parallel to shore and fished continuously for 24 h or more. Coho were counted and removed twice daily (~0900 and 2200 h) for approximately 18 days at each distance from shore. A vertical gill net (Knight and Margraf 1982) was also deployed overnight on 2 July 1986.

MORTALITY OF SOCKEYE FRY IN CHIGNIK LAKE

Daily consumption of sockeye by coho salmon was estimated by two independent methods. The first method (direct method) utilized stomach content data from each sampling location, gastric evacuation rates and Eggers' (1979) food consumption model:

$$\text{Daily meal} = 24(W)(r),$$

where (W) is the average weight of sockeye per coho and (r) is the exponential rate of evacuation. A diel feeding pattern was not observed in Chignik coho (Ruggerone 1989b), therefore the observed stomach contents of coho were assumed to represent the daily average. Rates of gastric evacuation were estimated from the following equation developed for coho feeding on juvenile sockeye salmon (Ruggerone 1989b, c):

$$\text{Evacuation rate } (r) = 0.133 + 0.021(\text{Temp.}) - 0.402(\text{Prey wt.}).$$

Temperature was measured at each sampling location and prey weight was the average of total prey consumed by those coho feeding on sockeye. The gastric evacuation model was developed by feeding coho a single meal of one or two sockeye fry, therefore the range of prey weight used in the equation was 0.169-0.500 g. Daily consumption of fry per coho was based on 0.169 g per fry, which was estimated from lengths of fry consumed by coho.

The second method for estimating daily consumption of sockeye by coho was based on a bioenergetic approach (Kitchell et al. 1977; Stewart et al. 1981, 1983; Hewett and Johnson 1987). This method utilized estimates of predator growth, caloric density of predator and prey, ambient temperature, relative prey composition, and a temperature-dependent algorithm for estimating food consumption (Thornton and Lessem 1978). Age-specific weight (g) of coho at the beginning and end of the sampling season was estimated from average coho weight[1] at each sampling period. Since peak seaward migration of coho occurs in early July and is generally comprised of the larger fish, estimates of coho growth were estimated from late May to mid-July. Consumption estimates of coho after mid-July were based on daily calories consumed during the last day that growth data were available, the temperature-dependent algorithm, and the proportion of sockeye fry in the diet. Average daily consumption of the coho population was estimated by weighting the age-specific consumption values by the proportion of age-1 and age-2 coho in the beach seine samples for each period.

Caloric density values of Chignik sockeye fry and coho parr were 811 ± 9 (S.E.) and 1000 ± 22 cal/g wet weight, respectively (Ruggerone 1989a). Caloric density of insects, primarily chironomids, was assumed to be 655 cal/g wet weight (Cummins and Wuycheck 1971; Elliott 1976). The caloric densities of other prey, which were minor components in the diet of coho, were assumed to be equivalent to sockeye fry.

Two independent estimates of coho abundance were used for estimating numbers of sockeye fry consumed by coho in Chignik Lake during spring and summer. Coho abundance was estimated by extrapolating beach seine catches to a predetermined habitat area, based on the area swept by the beach seine (~500 m^2 based on field measurements). Daily mortality of sockeye fry, based on the area swept method for estimating coho abundance, was estimated from 15 May to 5 August by the following equation:

$$\text{Daily fry mortality} = 1.6 \sum_{i=1}^{5} (F_i\ C_i\ B_i\ D),$$

where F_i is the average number of fry consumed per coho per day at habitat (i) (based on the direct or bioenergetic methods), C_i is the average number of coho ≥70 mm in the beach seine set, B_i is the ratio of total area in habitat (i) to area swept by a beach seine and D is a multiplication factor based on the offshore distribution of coho captured in the gill

[1]Coho weight was estimated from length measurements based on the following regression: coho wt. (live) = 0.00001888(coho length, preserved)$^{2.896}$, n = 453, R^2 = 0.99.

nets. We assumed that the five sampled habitats represented 50% of the lake perimeter. Fry consumed per coho per day in the remaining portion of the lake was estimated as being equal to that in the routinely sampled habitats (the ratio of fry consumed per coho at nonroutine vs. routine stations was 1.01 ± 0.27 S.E.) but coho abundance was estimated to be 60% less than that at routine stations based on 55 beach seine sets at 10 additional locations (Fig. 2). Thus, the fry mortality in 50% of the lake was multiplied by 1.6 rather than two. Daily consumption of sockeye fry by coho between sampling dates was estimated by linear interpolation.

The second method (reconstruction method) for estimating juvenile coho abundance in Chignik Lake was based on coho run size (catch and escapement) during the following year (Ruggerone 1989a). This method of estimating fry mortality is summarized by the following equation:

$$\text{Daily fry mortality} = \frac{\sum_{i=1}^{5} (F_i\ C_i\ B_i\ D)}{\sum_{i=1}^{5} (C_i\ B_i\ D)} \quad ((0.2)(A)(0.55)(P_k) + N_k).$$

The fractional part of the equation represents the weighted mean fry consumed per coho per day; fry mortality was also estimated by substituting this fraction with the average daily consumption by coho based on the bioenergetic method. Abundance of presmolt coho (i.e., coho rearing in the lake prior to seaward migration) was estimated from coho run size (A), the proportion of presmolts in Chignik Lake (0.55) relative to Black Lake and an assumed marine survival of 20%.[2] The proportion of coho in Chignik Lake relative to Black Lake was estimated from beach seine catches of coho ≥70 mm and the proportion of coho habitat sampled by the seine in each lake. Coho habitat in Black Lake was assumed to include the entire lake (41.1 km^2) because of its shallow depth, whereas coho habitat in Chignik Lake was estimated by gill nets. The proportion of the presmolt population remaining in the lake (P) on day k was estimated from coho smolt migration timing in Chignik River (Ruggerone 1989a). An estimated 78% and 8% of the presmolt population remained in the lake on 1 July and 1 August, respectively. Abundance of piscivorous yearling coho that did not migrate (N_k) was estimated from the proportion of yearling coho <70 mm (i.e., nonsmolts) in the lake on or near 1 June and

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[2]The 20% marine survival of Chignik coho was based on the highest marine survival of wild coho in Puget Sound, Washington (range: 15-20%, T. Flint, Washington Department of Fisheries, pers. comm.) because approximately 70% of the Chignik coho are age-2 whereas Puget Sound coho are primarily age-1.

the time needed to exceed 70 mm (i.e., the length when piscivory becomes common, Ruggerone 1989a), based on an estimated growth rate of 0.42 mm day^{-1} for age-1 coho.

PREDATION EFFECTS ON SOCKEYE RUN SIZE

The effect of coho predation in Chignik Lake on returns of adult sockeye salmon was examined by comparing returns of sockeye during brood year (t) with coho run size during year (t+2) because most predation on emerging sockeye was by presmolt coho prior to seaward migration and because coho at Chignik spend one winter at sea. For example, sockeye fry produced by the 1980 brood would have been consumed by coho that returned to Chignik as adults in 1982. Relative production of adult sockeye salmon[3] was compared with coho run size during 1973-1982.

RESULTS

STOMACH CONTENT ANALYSIS

Over 268 beach seine hauls for coho salmon in Chignik Lake and 84 hauls in Black Lake were examined during 1985-1987. Juvenile coho (≥70 mm) in Chignik Lake were readily captured (~42 coho per set) during each year of sampling and the stomach contents of 2,141 coho were examined (Table 1). In contrast, fewer than three coho per beach seine set were typically captured in Black Lake (Table 2) and only 150 coho were examined for stomach contents. In Black Lake, the number and weight of sockeye fry observed in coho averaged <0.1 fry and 0.01 g per coho, respectively. Daily consumption of sockeye fry by coho in Black Lake was not estimated because few coho were captured, probably because of their diffuse distribution in the shallow lake. Relatively few fry in Black Lake appeared to be consumed by coho salmon.

In Chignik Lake, the average number of sockeye fry observed in coho stomachs increased from about 0.7 fry in late May to a maximum of 1.7 fry in June, then declined throughout July and early August (0.3 fry per coho; Fig. 4). Average weight of fry observed in coho followed a similar seasonal trend: 0.08 g in late May, 0.19 g in June,

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[3]Relative production of adult sockeye salmon was calculated as:
Relative production = ln (observed R/S) - ln (predicted R/S),
where the predicted return per spawner (R/S) was based on the Ricker recruitment curve for Chignik Lake sockeye during brood years 1922-1982 (Ruggerone 1989a).

Table 1. Summary of coho salmon catch statistics from beach seine hauls in Chignik Lake.

Year	Date	No. stations	Time (h)	Ave. temp. (°C)	Ave. secchi depth (m)	No. coho examined[1]	Ave. length (mm)[2]	% age-2 coho[2]	Coho per set[2]
1985	5/25	5	1530-1900	4.6	4.0	63	97	11	152 ± 132
	5/31	5	1115-1500	5.7	3.6	56	102	78	17 ± 10
	6/10	6	1045-1530	5.8	3.0	48	110	82	27 ± 20
	6/19	6	1200-1700	8.6	2.6	66	111	89	241 ± 200
	6/27	5	1130-1515	8.4	2.3	76	108	89	69 ± 51
	7/07	6	1530-2115	11.1	1.7	64	116	76	48 ± 11
	7/16	5	1215-1515	10.0	1.8	63	116	67	18 ± 4
	7/26	5	1300-1630	11.7	1.5	83	101	23	14 ± 4
	8/02	6	1130-1515	12.4	2.2	51	95	16	9 ± 3
	9/01	6	1130-1530	10.4	1.2	20	86	9	4 ± 1
1986	5/17	11	1030-1700	6.2	3.1	43	81	15	5 ± 3
	5/24	12	1000-1800	7.7	3.7	82	77	21	28 ± 12
	6/04	18	0800-2400	6.0	3.3	228	89	47	57 ± 24
	6/14	11	1040-1515	5.6	2.2	52	90	33	7 ± 3
	6/25	11	1100-1450	6.9	1.4	36	98	39	4 ± 2
	7/06	12	1030-1445	8.9	1.9	95	108	41	10 ± 2
	7/16	12	1100-1545	9.4	2.2	74	102	20	15 ± 5
	7/26	12	1000-1345	10.8	1.3	55	100	7	7 ± 3
	8/03	12	0930-1400	11.0	1.1	29	81	0	3 ± 1
1987	5/21	12	1100-1800	7.2	2.8	92	95	52	54 ± 20
	6/03	18	0600-2400	7.8	2.8	290	99	51	163 ± 44
	6/11	12	1015-1545	7.9	2.3	84	100	42	24 ± 10
	6/22	12	1030-1500	7.1	2.4	123	108	36	52 ± 23
	7/01	12	1000-1445	8.0	2.3	68	109	38	9 ± 3
	7/09	12	1100-1530	10.8	1.6	97	98	5	24 ± 12
	7/19	12	1100-1530	10.2	2.3	85	94	17	18 ± 7
	7/27	12	1130-1630	14.3	0.8	18	96	7	6 ± 2

[1]Stomach content analysis only; does not include all measured fish
[2]Coho ≥70 mm ± S.E..

Table 2. Summary of coho salmon catch statistics from beach seine hauls in Black Lake.

Year	Date	No. stat- tions	Time (h)	Ave. temp. (°C)	Ave. Secchi depth (m)	No. coho examined[1]	Ave. length (mm)[2]	% age-2 coho[2]	Coho per set[2]	Fry per coho[2]	Fry wt per coho (g)[2]
1985	5/27	2	1130-1230	10.0	1.5	1	87	0	<1	0.0	0.0
	6/01	6	1200-1800	8.6	1.4	0	–	0	0	–	–
	6/20	6	1845-2200	10.9	1.8	22	108	59	4 ± 2	0.1 ± 0.1	0.08 ± 0.07
	7/11	9	1315-2345	16.3	2.4	20	97	30	3 ± 2	0.0	0.0
	7/22	12	1315-2030	13.2	0.9	44	81	0	4 ± 2	<0.1	<0.01
1986	6/07	10	1145-1615	8.8	0.8	7	80	0	<1	0.0	0.0
	6/28	10	1230-1600	10.0	0.8	9	84	0	<1	0.3 ± 0.3	0.03 ± 0.03
	7/24	10	1230-1700	14.9	1.5	24	103	0	6 ± 5	0.0	0.0
1987	6/20	10	1400-1845	10.0	1.5	2	68	0	<1	0.0	0.0
	7/07	9	1645-2000	14.0	1.6	21	79	0	6 ± 4	0.0	0.0

[2]Coho ≥70 mm ± S.E.

and 0.04 g in July and early August. The highest numbers and weights of fry were observed in coho stomachs during 1985 (1.4 fry, 0.16 g), followed by 1987 (0.9 fry, 0.8 g) and 1986 (0.4 fry, 0.04 g).

Numbers of sockeye fry consumed per day by coho were nearly four times higher than the observed number of fry in coho stomachs, based on a fry weight of 0.169 g. Daily consumption of sockeye fry based on observed prey weight and stomach evacuation rates of coho (direct method) averaged 2.0 fry in late May, 3.3 fry in June, and 1.1 fry in July and early August (Fig. 5). Average fry consumed per coho per day was greatest in 1985 (2.8 fry) and 1987 (2.4 fry) relative to consumption in 1986 (1.0 fry).

Daily consumption of sockeye fry by coho based on the bioenergetic method followed a seasonal trend similar to that shown by the direct method (Fig. 5). The average daily consumption estimated by the bioenergetic method during each year were within 14% (range: 5-20%) of the direct method estimates (absolute $\bar{d} = 0.25$ fry day^{-1}) whereas bioenergetic estimates on a given day were within 30% ± 18% S.D. of the direct estimates. Daily fry consumption estimated from the bioenergetic method was slightly greater than that from the direct method during 1986 ($\bar{d} = 0.19$ fry day^{-1}) and 1987 ($\bar{d} = 0.10$ fry day^{-1}) but less in 1985 ($\bar{d} = -0.61$ fry day^{-1}). Only the difference in 1986 was statistically significant (paired t-test, $p < 0.05$, df = 8). Growth rates of coho used in the bioenergetic approach are shown in Fig. 6; growth of age-1 and age-2 coho averaged 0.12 g day^{-1} and 0.19 g day^{-1}, respectively.

DISTRIBUTION OF COHO IN CHIGNIK LAKE

Gill nets set 20, 50, 100 and 150 m from the lake shoreline indicated that coho were most abundant near shore. A total of 768 coho were captured by gill nets during 1986-1988. Approximately 45 coho per 24 h were captured in the nearshore gill net compared to 12 coho per 24 h at 50 m, 10 coho per 24 h at 100 m and 6 coho per 24 h at 150 m from shore (Fig. 7a). In 1988, sockeye salmon were consumed by 69% of the coho in the nearshore gill net compared to to 57% of the coho in the offshore nets. The night of sampling for vertical distribution of coho suggested that approximately 50% of the coho (36 fish captured) were within 2 m of the surface; all coho were in the top 15 m of the 30 m vertical gill net (Fig. 7b).

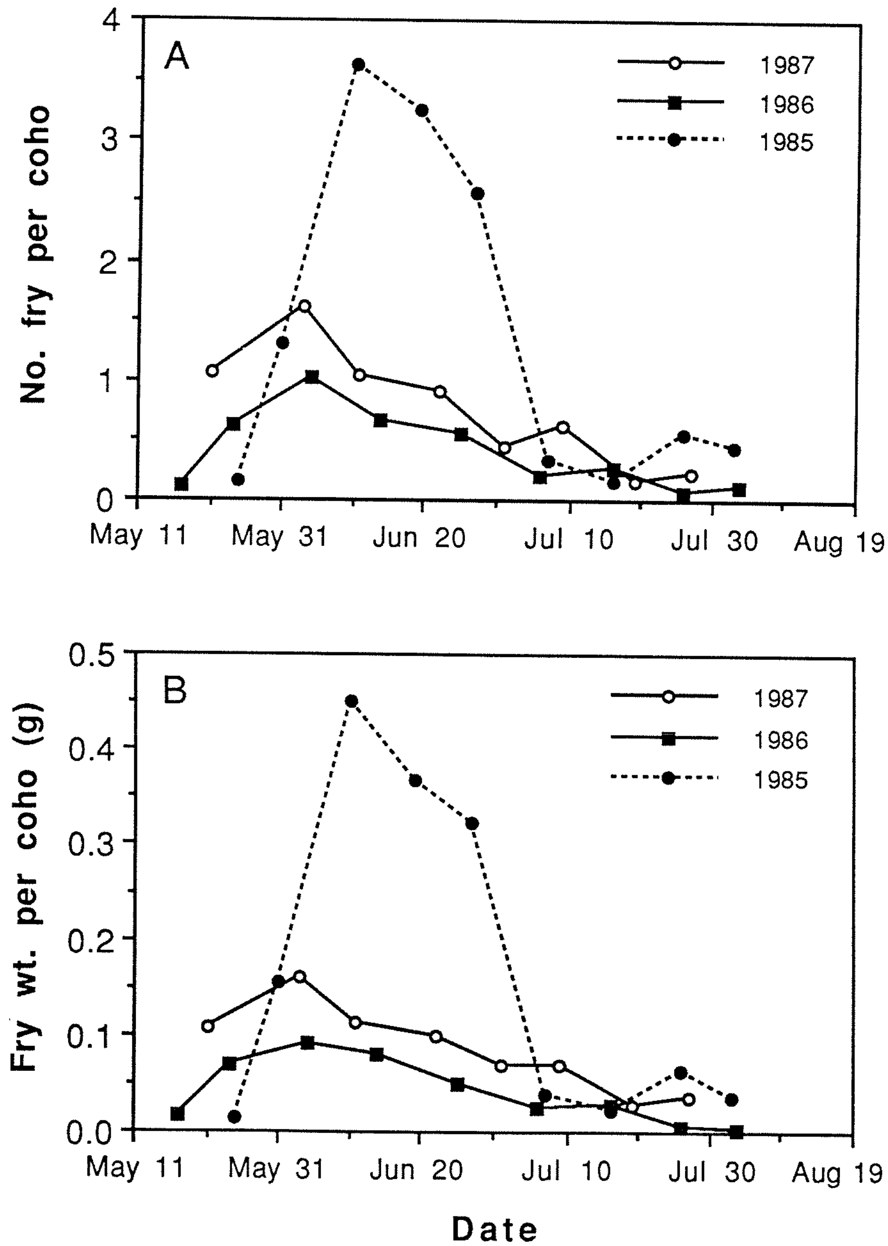

Figure 4. Number and weight of sockeye salmon fry observed in stomachs of coho at Chignik Lake, 1985-1987.

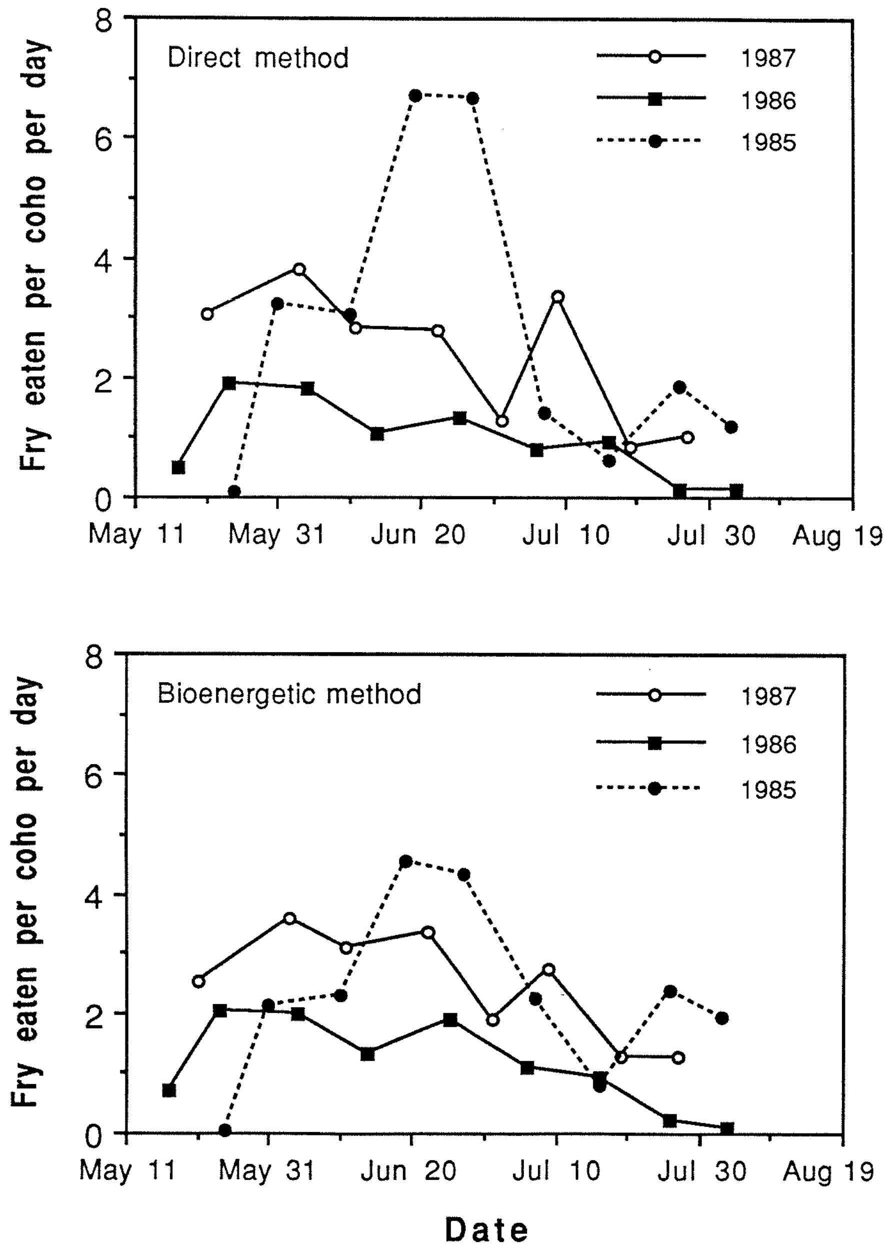

Figure 5. Number of sockeye salmon fry consumed per coho salmon per day at Chignik Lake during 1985-1987, based on the direct and bioenergetic methods.

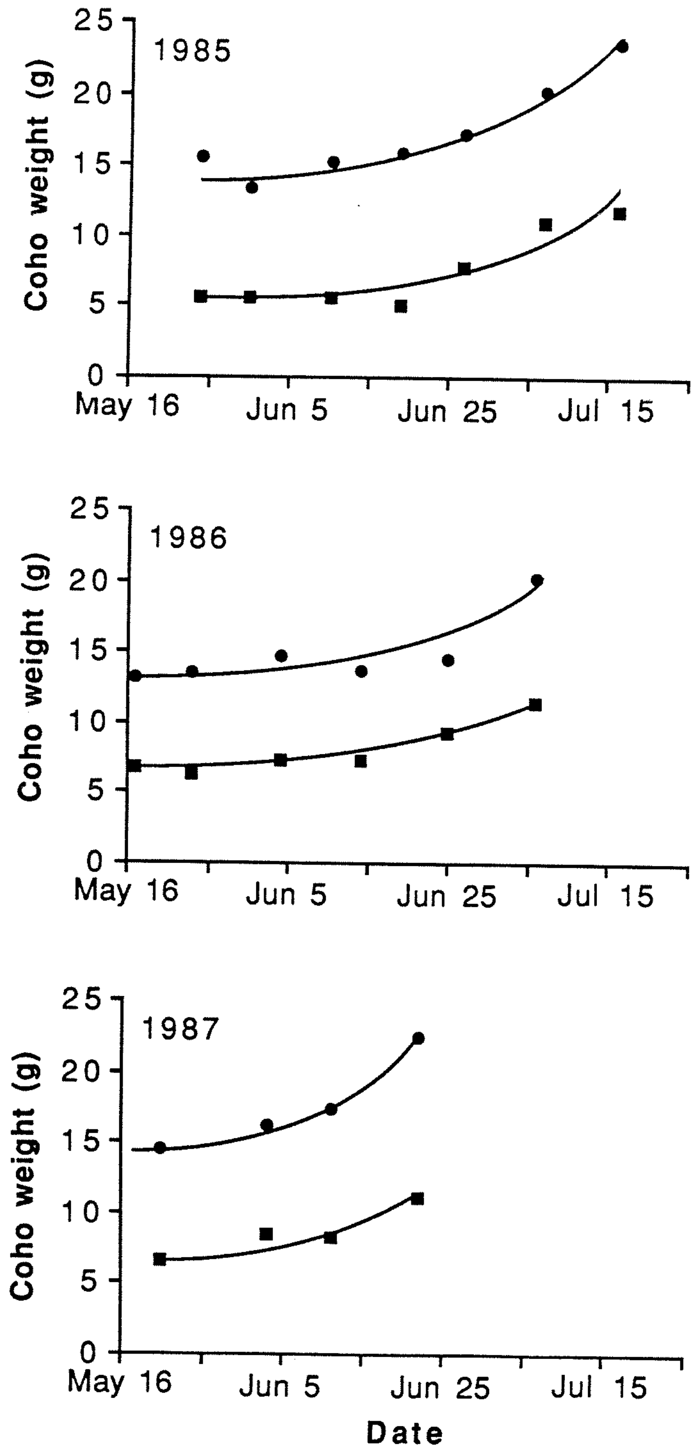

Figure 6. Growth of age-1 (■) and age-2 (●) coho salmon in Chignik Lake during spring and summer, 1985-1987. Lines drawn by eye.

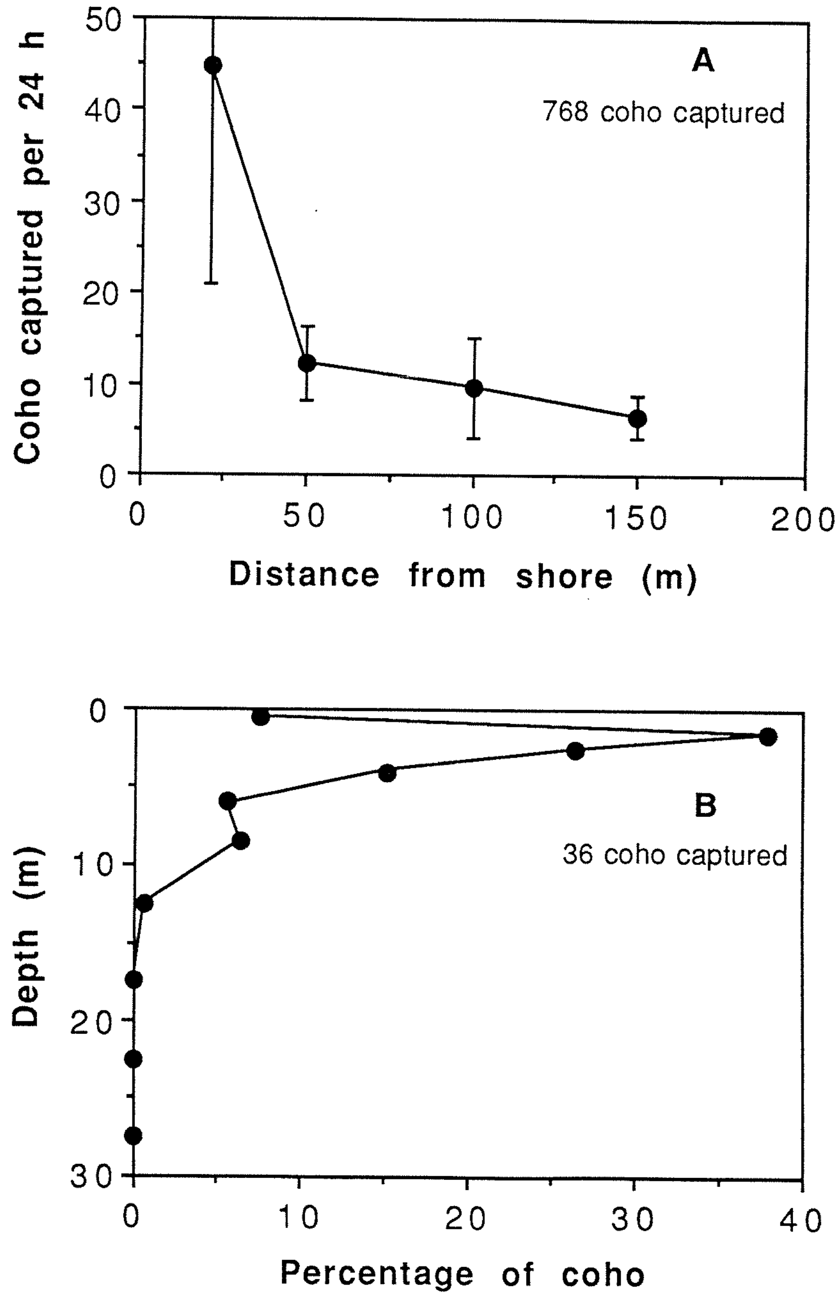

Figure 7. Horizontal and vertical distribution of juvenile coho salmon in Chignik Lake. Values are daily means ± S.E..

We estimated that coho within 25 m of the shore represented approximately 33% of the coho population in the lake, based on the relationship between coho density and distance from the shore, the vertical distribution of coho and the water depth at the nearshore gill net (~3 m) relative to the offshore nets (10-30 m). Therefore, beach seine catches of coho, which extended 25 m offshore, were multiplied by three when estimating coho abundance by the area swept method.

COHO ABUNDANCE

Estimated coho abundance in Chignik Lake differed markedly depending on the method of estimation and year. Prior to the seaward migration of coho in mid-June, coho abundance during 1985-1987 ranged from 100,000 to 460,000 fish based on the area swept by the beach seine and from 450,000 to 670,000 fish based on reconstruction of coho abundance from adult run size during the following year (Fig. 8). The abundance of coho estimated from the reconstruction method was generally twice that of the area swept method. Average population size of juvenile coho during 1985, 1986 and 1987 was 290,000, 230,000 and 340,000 coho, respectively, based on the average of the two methods. Approximately 30% of the initial piscivorous coho population (≥70 mm) remained in Chignik Lake in late July, including nonsmolting coho.

MORTALITY OF SOCKEYE FRY IN CHIGNIK LAKE

The number of sockeye fry consumed by coho during the summer, based on the average of the four estimates, increased from about 0.66 million fry day^{-1} in late May (±0.17 S.E.) to a maximum of 1.35 million fry day^{-1} in June (±0.25), then declined throughout July and early August (0.24 million fry day^{-1} ± 0.06; Fig. 9). Annual consumption of sockeye fry by the coho population between 15 May and 5 August, based on the four estimates, averaged 68 million, 24 million and 78 million fry during 1985, 1986 and 1987, respectively (Table 3). Mortality estimates based on the direct and bioenergetic methods were nearly identical in 1986 and 1987 (<10% difference), whereas in 1985 fry mortality based on the bioenergetic method was 70% of the direct method estimate. Estimates of mortality based on the area swept method of estimating coho abundance were approximately 55% less than those estimated by the reconstruction method. Approximately 90% of sockeye mortality was attributed to coho that migrated to sea during the year of investigation.

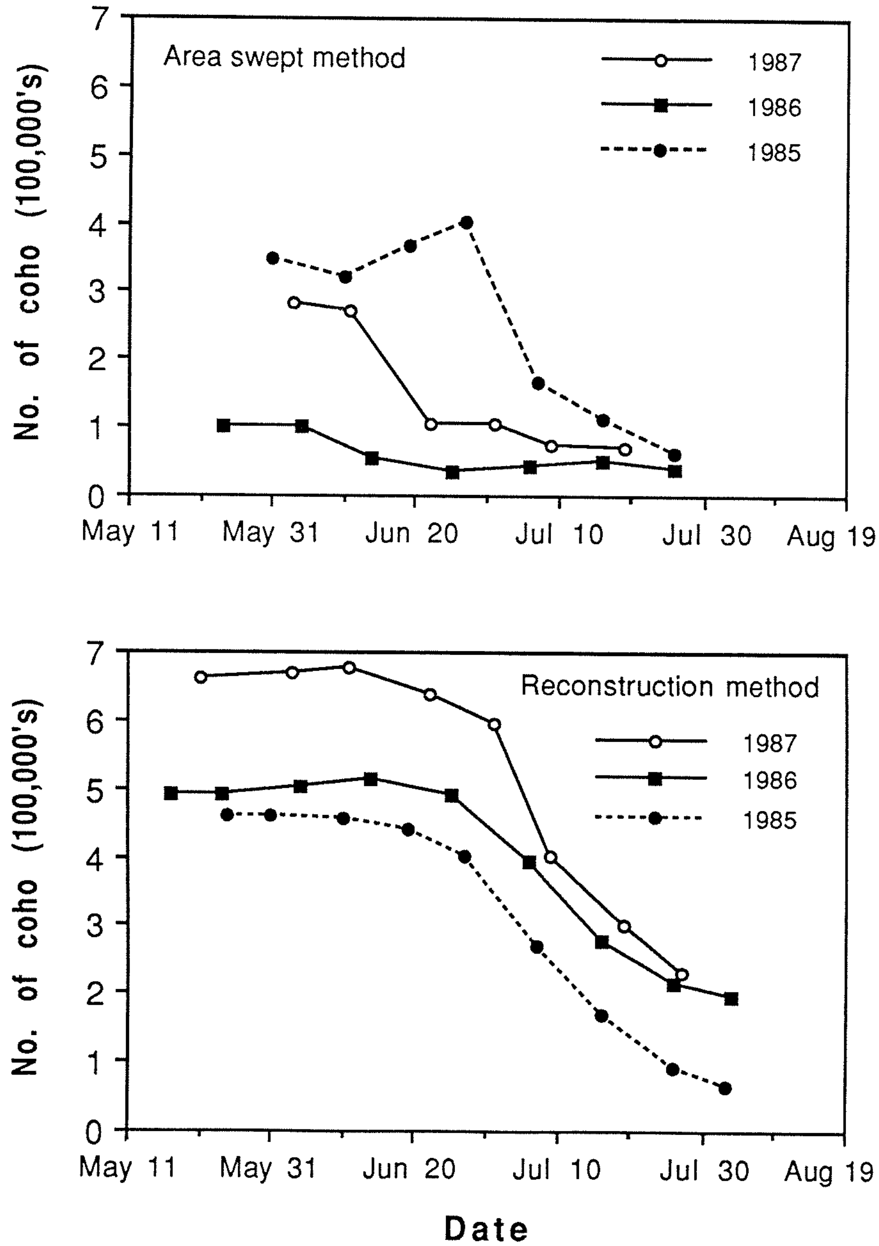

Figure 8. Number of coho salmon ≥ 70 mm in Chignik Lake, 1985-1987, based on the area swept by the beach seine and the reconstruction of juvenile coho abundance from adult coho run size during the following year. Area swept data are smoothed by a moving average of three.

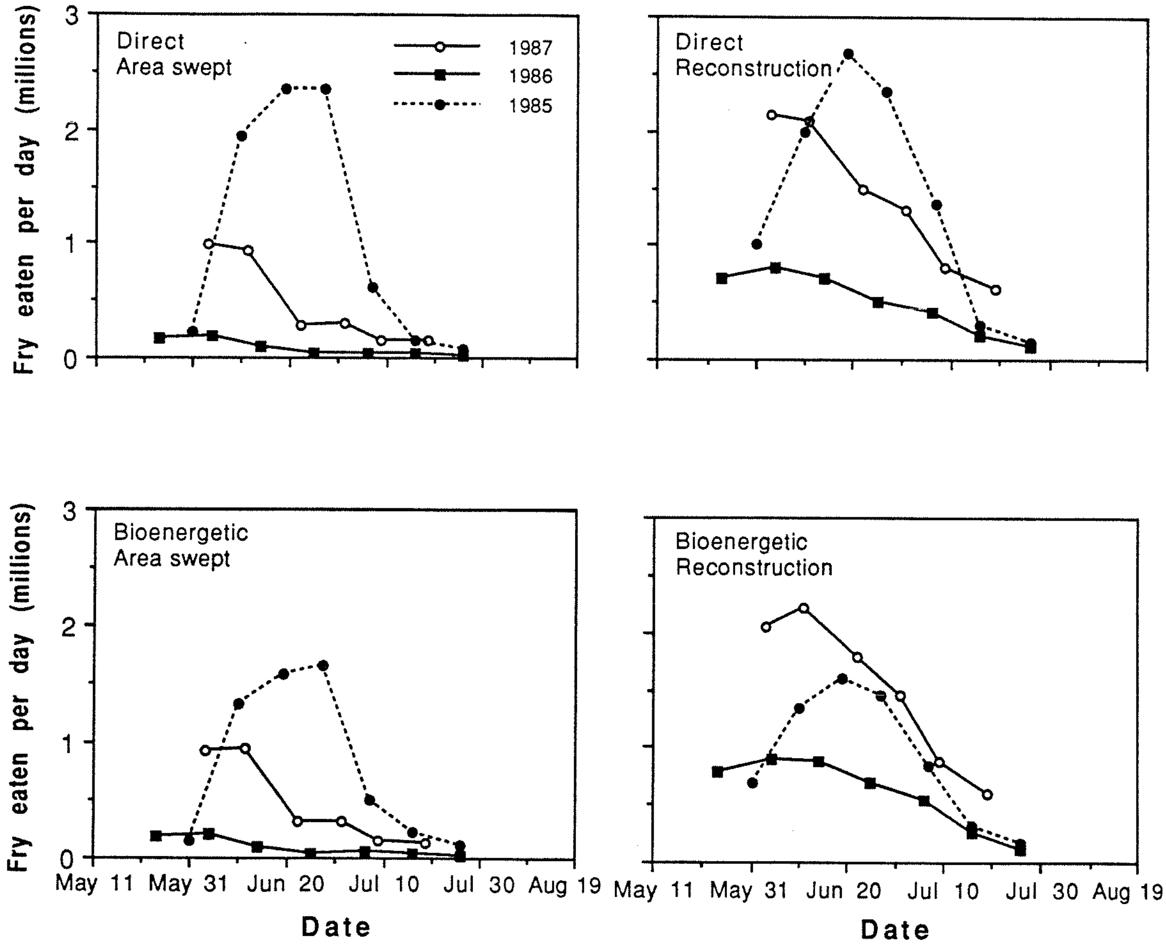

Figure 9. Number of sockeye salmon fry consumed per day by coho, 1985-1987, based on the direct/area swept, direct/reconstruction, bioenergetic/area swept, and bioenergetic/reconstruction methods. Data are smoothed by a moving average of three.

Table 3. Numbers (millions) of sockeye salmon fry consumed by coho salmon in Chignik Lake from 15 May to 5 August, 1985-1987. Estimates were based on the stomach evacuation rate (direct method) and bioenergetic methods for estimating daily consumption of sockeye per coho, and on the area swept by the beach seine (area method) and reconstruction methods for estimating coho abundance.

	Method				
Year	Direct/ area	Direct/ reconstruction	Bioenergetic/ area	Bioenergetic/ reconstruction	Average (± S.E.)
1985	69	93	50	61	68 ± 9
1986	7	39	7	44	24 ± 10
1987	42	114	40	116	78 ± 21

The percentage of the sockeye fry population consumed by coho may be estimated from the fry mortality estimates and initial fry abundance, which was estimated from the abundance of sockeye spawners in Chignik Lake, average fecundity, and an assumed egg to fry survival of 20% based on values in the literature (Foerster 1968; Mead and Woodall 1968; Drucker 1970; West and Mason 1987). Survival from egg to fry is highly variable but was believed to have been relatively high in Chignik Lake because of the excellent spawning gravel and the low environmental variability associated with the nests along the shoreline of the lake. Approximately 550, 591 and 410 million eggs were deposited by sockeye during 1984, 1985 and 1986, respectively, based on spawning densities of 268, 353 and 207 thousand sockeye (Conrad and Ruggerone 1985; Probasco et al. 1987) and estimates of fecundity calculated from fish length and age composition (Dahlberg and Phinney 1967; Phinney and Lechner 1969; Parr and Pedersen 1969; Wells and Parr 1971). The estimated average percentage of emerging sockeye fry consumed by coho was 59% during 1985-1987.

PREDATION EFFECTS ON SOCKEYE RUN SIZE

Relative production of adult sockeye returning to Chignik Lake has significantly declined by approximately 70% between brood years 1971-1976 and 1977-1982 (Fig. 10, $R^2 = 0.48$, $p < 0.05$, $n = 12$). In contrast, run size of adult coho during sockeye brood year t+2 has increased markedly ($R^2 = 0.27$, $p = 0.08$, $n = 12$) from 66,000 to 134,000 coho during 1971-1976 and 1977-1982, respectively.

DISCUSSION

Average seasonal predation rates (fry $coho^{-1}$ day^{-1}) of coho calculated from the bioenergetic model were similar to those calculated from the direct (stomach evacuation rate) method. However, differences in daily fry consumption were somewhat greater when daily values were compared in a paired analysis. Thus, the two methods for estimating prey consumption converged on a similar seasonal food consumption estimate but agreed less when estimating food consumption on a given day. As expected, the bioenergetic estimates were less variable than the direct estimates because the bioenergetic model described average trends between sampling periods of coho size. Nevertheless, differences in the seasonal food consumption estimates by the two methods were small

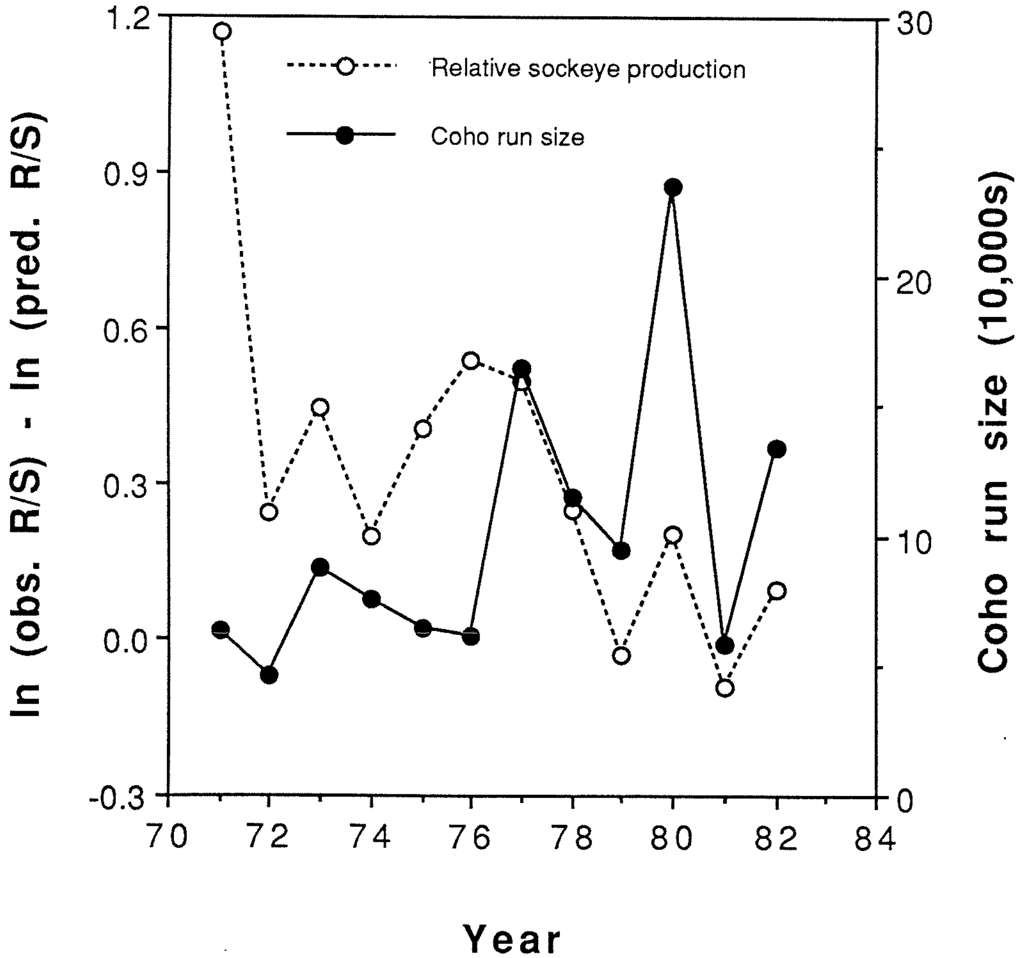

Figure 10. Comparison of relative production of adult sockeye salmon, ln (observed R/S) - ln (expected R/S), with run size of adult coho salmon during year, t-2. Expected return per sockeye spawner was based on the estimated Ricker recruitment curve for years 1922-1982.

given the complexity of fish energetics, food processing and assimilation (Kapoor et al. 1975; Brett 1983; Ruggerone 1989a; Smith 1989). The general agreement between the two methods tends to validate each estimate.

Few studies have compared independently derived estimates of fish food consumption. Beauchamp et al. (in prep) reported that bioenergetic and field-derived estimates of seasonal consumption rates by juvenile sockeye salmon in Lake Washington and Lake Dalnee were similar. Rice and Cochran (1984) demonstrated that total food consumption by largemouth bass (*Micropterus salmoides*), based on a similar bioenergetic model, was within 8.5% of direct field estimates during spring and summer. However, daily food consumption estimates based on the field estimates often deviated markedly from the bioenergetic estimates because the latter method averaged food consumption over time, as in the present study of coho salmon.

The greatest source of error in estimating numbers of sockeye consumed by coho was probably the estimates of coho abundance. The area swept method probably underestimated coho abundance because of net avoidance. Furthermore, catches of coho in 1986 declined 80% after a severe flood in mid-June, presumably because of reduced seine efficiency during the exceptionally high water in the lake. In contrast, the reconstruction of coho abundance from adult run size suggested large numbers of juvenile coho in Chignik Lake during each year. The average of the area swept and reconstruction estimates were judged to provide a reasonable estimate of coho abundance for the purpose of estimating the magnitude of predation.

The large number of sockeye salmon fry consumed by juvenile coho in Chignik Lake during 1985-1987 indicates that coho salmon may be an important factor in the life history of Chignik Lake sockeye salmon. Predation rates by coho increased during peak emergence of sockeye fry in early June, then declined as emergence slowed from nests along the lake shoreline (Ruggerone 1989a). Few sockeye greater than 35 mm were consumed by coho (Ruggerone 1989a). Recently emerged sockeye salmon in Chignik Lake moved offshore where coho were less abundant, possibly an adaptation to reduce predation. Sockeye length at emergence was also larger than most sockeye populations and large size may reduce predation by the size-limited coho.

Emerging sockeye fry appear to be especially vulnerable to predators in Chignik Lake relative to larger, older sockeye parr and smolt. While preyed upon by coho salmon, recently emerged sockeye are also consumed by Dolly Varden char, chinook salmon, coastrange sculpin (*Cottus aleuticus*), and Bonaparte gulls (*Larus philadelphia*), although gulls and char may take an occasional sockeye yearling or smolt. Char appear to be important predators on sockeye because of their great abundance (~43 char per set) and moderate numbers of fry consumed per individual (~0.7 fry/char, Ruggerone 1989a). However, many of the anadromous char are at sea during the period of fry emergence and few char returning to Chignik Lake in late July or August consumed sockeye salmon. Also, predation by char is highly variable in that only a few individuals in a sample typically consumed sockeye. Roos (1959, 1960, 1965) concluded that char were less significant predators on sockeye than were coho, although Burgner and Marshall (1974) reported that char, primarily from Chignik River, contained more sockeye than did coho during 1970-1971. Neither of these studies considered the slow gastric evacuation rates of Dolly Varden char (Armstrong and Blackett 1966) relative to coho salmon (Ruggerone 1989b). Thus, coho salmon appear to be the most significant predator on sockeye salmon in Chignik Lake, although other predators, especially char, contribute to the mortality juvenile sockeye in freshwater. Relatively little predation is believed to occur on sockeye yearlings or smolts.

The inverse relationship between relative production of adult sockeye salmon and coho run size suggests that predation by juvenile coho on sockeye fry in Chignik Lake may affect returns of adult sockeye. This is not surprising given the magnitude of predation during 1985-1987. However, two other factors may also have reduced returns of Chignik Lake sockeye in recent years. First, interceptions of sockeye salmon[4] during July and August in the Shumagin Islands, 200 km west of Chignik, have increased 160% during 1983-1988 (220,000 fish yr^{-1}) relative to 1977-1982 (84,000 fish yr^{-1}, A. Shaul, ADFG, pers. comm.). The origin of sockeye harvested in the Shumagin Islands during July and August is unknown, although preliminary analysis of age composition in 1985 and 1987 suggested that most of these fish were returning to Cook Inlet and Kodiak Island rather than Chignik (McCullough 1987). Further analysis and research is needed to quantify the stock composition of the Shumagin Islands sockeye catch.

Density-dependent growth of juvenile sockeye also may have reduced adult sockeye returns to Chignik Lake. Narver (1966) and Burgner and Marshall (1974) reported that

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[4]ADFG assumes that 80% of Cape Igvak interceptions, 215 km east of Chignik and 80% of Stepovak Bay interceptions, 150 km west of Chignik, belong to Chignik and Black lakes. These interception estimates have been included in the run data sets for Chignik and Black lakes.

many age-0 sockeye migrated from Black Lake to Chignik Lake during mid-July to mid-August, apparently because of crowding. Adult sockeye returns to Black Lake have doubled in recent years (0.9 million fish and 2.0 million fish during brood years 1971-1986 and 1977-1982, respectively), suggesting that more Black Lake sockeye have migrated to Chignik Lake in recent years than in the past. Growth and survival of Chignik Lake fry could have been reduced by the immigration of the slightly older and larger Black Lake fry. However, Parr (1972) could not demonstrate a negative relationship between growth of age-0 sockeye and abundance of sockeye (all ages) and other planktivorous fishes during a 10-yr period, although he suggested that density dependence may have been masked by the prolonged emergence of Chignik Lake fry. Furthermore, it may be argued that the favorable conditions that produced large sockeye returns to Black Lake and other Alaskan lake systems in recent years should have also produced strong returns to Chignik Lake. Further investigation is needed to determine whether large migrations of sockeye from Black Lake to Chignik Lake influence growth and survival of Chignik Lake sockeye.

The large number of sockeye fry consumed by coho during 1985-1987 and the potential effects of coho predation on sockeye returns suggest that a reduction in coho abundance at Chignik could enhance sockeye abundance. However, eradication of the coho population is not reasonable because greater abundance of emerging sockeye fry in Chignik lake, as a result of coho eradication, could reduce growth (Narver 1966; Parr 1972) and marine survival (Hyatt and Stockner 1985; Koenings and Burkett 1987) of sockeye salmon. Furthermore, indirect effects of predation on prey populations are complicated and removal of a predator population could lead to unexpected negative effects (Hubbs 1940; Kerfoot and Sih 1987).

Coho abundance in the Chignik lakes could be controlled by a harvest management plan similar to the current plan for sockeye salmon. Presently, harvest management of coho consists of 2-3 day fishery closures each week. This type of management leads to a relatively constant rate of exploitation, which allows more coho to spawn during years of greater coho run size. For example, the estimated average run size of coho during 1973-1978 and 1979-1988 was 66,000 and 170,000 coho, respectively, and the corresponding average escapement was 40,000 and 97,000 coho (Ruggerone 1989a). A fixed spawning population of coho would stabilize the coho/sockeye spawning ratio (sockeye escapement is relatively fixed) and reduce the potential of low in-lake sockeye survival during years of growing coho population size. Without a weir or hydroacoustic equipment to estimate coho escapement, a harvest strategy might consist of fishing for 5-6 days per week when coho are abundant but only 3-4 days per week when they are scarce. Additional research is needed to determine a spawning escapement range for coho salmon based on predation by juvenile coho on sockeye fry and on density-dependent growth of juvenile sockeye in Chignik Lake.

The present harvest practices of Chignik fishermen may have also influenced the apparently large number of juvenile coho in Chignik Lake relative to Black Lake. The mid-point of the coho run is approximately 1 September, yet only 35% of the catch occurred after this date, resulting in a disproportionately large escapement during the second half of the run. If early arriving coho spawn in Black Lake and late coho spawn in Chignik Lake, as do sockeye (Conrad 1983), then the current tendency for fishermen to stop fishing in early September may allow the Chignik Lake stock of coho to rapidly increase. Thus, reduced fishing of late arriving coho and the mid-summer emigration of age-0 and age-1 coho from Black Lake to Chignik Lake (Burgner and Marshall 1974) may have contributed to the great abundance and intense predation of coho on sockeye fry in Chignik Lake in recent years.

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