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CHIGNIK SALMON STUDIES:

EVIDENCE FOR MORPHOLOGICAL AND BEHAVIORAL RESPONSES BY JUVENILE SOCKEYE SALMON TO SIZE-BIASED PREDATION

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ABSTRACT

Effects of size-biased predation by juvenile coho salmon (*Oncorhynchus kisutch*) on the size and behavior of recently emerged sockeye fry (*O. nerka*) were examined in Chignik Lake, Alaska, during 1985-1988. Over 50% of coho within the 80-150 mm range consumed at least one juvenile sockeye salmon during the peak period (several weeks) of fry emergence. Coho salmon (58-162 mm) were capable of consuming juvenile sockeye up to about 45% of coho body length, but less than 10% of the sockeye consumed exceeded 35 mm. During 1985-1987, average lengths of recently emerged sockeye salmon consumed by coho salmon (30.1, 29.8 and 31.0 mm, respectively) were significantly ($p < 0.001$) shorter than those captured by fry emergence traps and beach seine hauls (31.7, 31.1 and 31.6 mm, respectively), indicating favorable survival of large versus small emerging sockeye. Recently emerged sockeye fry in Chignik Lake (30.5 mm, mean preserved measurement) were longer than fry from 26 of 30 sockeye stocks ($\bar{x} = 28.5$ mm) for which data were available, suggesting that size-biased predation may have influenced the body length of emerging sockeye at Chignik Lake. Sockeye fry also reduced predation by moving offshore where coho were less abundant; during peak emergence of sockeye fry from shoreline spawning areas in early June, sockeye fry were markedly less abundant (2 fry per beach seine set) than expected (up to 135 fry per set), based on rates of sockeye emergence and coho predation. Few (<8 fry per set) small sockeye (≤35 mm) were captured in all littoral areas during June and July, 1985-1988, whereas mid-size sockeye (36-45 mm, mostly age-0 fish) were present in small numbers beginning in late June ($\bar{x} = 10$ fish per set) and sockeye >45 mm (mostly age-1 and age-2 fish) were always abundant ($\bar{x} = 129$ fish per set). These data suggest that juvenile sockeye salmon returned to littoral areas after reaching sizes that were less vulnerable to predation.

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INTRODUCTION

Predation is generally believed to strongly influence population dynamics of prey species and may therefore influence the evolution of morphological and behavioral traits that reduce mortality of the prey (Sih 1987). Some antipredator traits observed in fishes include evasive or avoidance tactics such as schooling, habitat shifts, diel periodicity, spines, size, vigilance, camouflage, and chemical alarm reactions (Keenleyside 1979; Stein 1979). Individuals or populations that are most susceptible to predation generally show the strongest antipredator responses (Goodyear 1973; Seghers 1974a,b; Stein 1979; Werner et al. 1983).

Despite the number of studies concerning the effects of predation on juvenile Pacific salmon (e.g., Foerster 1968; Ruggerone and Rogers 1984, in review), few studies have examined antipredator tactics of salmon other than schooling, diel migration (Hartman et al. 1962; Levy 1987) and vigilance behavior (Patten 1977; Dill and Fraser 1984). Furthermore, few studies have examined antipredator behaviors of salmon that are population-specific.

In Chignik Lake, Alaska, sockeye salmon (*Oncorhynchus nerka*) may have evolved at least two characteristics in response to predation by juvenile coho salmon (*O. kisutch*). Predation occurs primarily near the littoral zone of the lake, where sockeye salmon emerge from spawning nests and coho are most abundant (Ruggerone 1989). Predation estimates during 1985 to 1987 indicated that juvenile coho (ages 1 and 2) consumed approximately 68, 24 and 78 million sockeye fry, respectively, representing about 59% of the sockeye fry each year (Ruggerone and Rogers, in review). The intense predation on emerging sockeye salmon in littoral areas of Chignik Lake and the possible selection of smaller fry by juvenile coho might have influenced traits such as larger size at the time of emergence or avoidance of habitats utilized most frequently by coho salmon.

The objectives of this investigation were to test for size-biased predation by juvenile coho salmon foraging on emerging sockeye fry in Chignik Lake and to compare the size and movement patterns of emerging sockeye fry in Chignik Lake relative to other sockeye populations. Size-biased predation by coho was tested by comparing lengths of fry consumed by coho in Chignik Lake with lengths of emerging fry. Movement patterns of recently emerged sockeye were examined by comparing beach seine catches of recently emerged fry on the sockeye spawning grounds with expected numbers of littoral area fry, based on rates of fry emergence and predation.

MATERIALS AND METHODS

STUDY AREA

Chignik Lake is the lower of two interconnected lakes on the Alaska Peninsula (56°16'N Lat., 158°50'W Long.). Situated between precipitous mountains, it is small (22 km^2), relatively deep

(64 m) and approximately 70% of the lake is >10 m deep. Breakup of ice on Chignik Lake generally occurs in March or April. Frequent and strong winds continually mix the water column. During May through July, water temperature ranges from 5-14°C, and water transparency (Secchi disk measurements) ranges from 1-4 m. Primary productivity is high relative to other sockeye producing lakes in Alaska (Burgner et al. 1969). Approximately 270,000 sockeye salmon spawn each fall (Ruggerone 1989), primarily along littoral areas that lack macrophytes or large rocks that could provide refuge for emerging sockeye fry. An estimated 76,000 coho spawn each year in the Chignik lakes system.

PREY SIZE SELECTION BY JUVENILE COHO

Juvenile coho salmon were sampled by beach seine (35 m long x 4 m maximum depth; 3 mm mesh) during 1985-1988. Twelve littoral areas, including sockeye spawning grounds, were sampled approximately every 10 days from mid-May to early August. The samples were enumerated by species, and random subsamples of coho (~10 fish) were taken at each station for length and stomach content analysis. The stomach cavity of coho was injected with 50% buffered formaldehyde to slow evacuation of prey, then all subsampled fish were preserved in 10% buffered formaldehyde.

Stomachs of coho were examined for frequency and size of sockeye salmon during 1985-1987. Fry and yearling sockeye salmon showing little or no loss of flesh were measured to the nearest 1 mm (fork length) at least 24 h after preservation, at which time post-mortem shrinkage of body length was considered complete (Rogers 1964). Standard length (S.L.) was measured for 18% of the sockeye and converted to fork length by the regression equation

$$\text{Fork length (mm)} = 0.73 + 1.09(\text{S.L.}),\quad n = 28,\ \text{S.E.R.} = 0.4\ \text{mm},\ R^2 = 0.98.$$

Preserved fish lengths were multiplied by 1.031 (sockeye fry) or 1.033 (coho) to transform them to live measurements.

Emerging sockeye fry were sampled with 30-40 traps placed on sockeye salmon spawning grounds in littoral areas of the lake during 1986-1988. The trap design was modified (cone-shaped rather than pyramid-shaped) from Collins (1975). A fry holding jar with a one-way trap was attached to the top of the cone and a 5-mm screen prevented predators from entering the holding jar. Each trap sampled 0.25 m^2 of habitat and from 6 to 12 traps were placed within the depths sampled by beach seine at each of the four major lake spawning habitats. The traps were sampled by boat approximately every 5 days from late May to late July. Sockeye fry were counted and, during 1987-1988, random samples of up to 30 fry from each location were preserved in formaldehyde for length measurements. Preserved weight of sockeye fry was calculated from fork length by the regression equation

$$\text{Sockeye wt} = -0.2359 + 0.0138(\text{length}),\ n = 90 \text{ fry},\ \text{S.E.R.} = 0.021 \text{ g},\ R^2 = 0.34.$$

Size-selectivity of coho salmon feeding on emerging sockeye was assessed by comparing fry lengths (≤35 mm) consumed by coho from May to July with those sampled in the emergent fry traps from May to July, 1987, and in beach seine hauls at the spawning grounds during mid- and late May (1985 and 1986). Lengths of age-0 sockeye fry captured by beach seine in May may be a reasonable representation of fry emerging throughout the summer because they experienced little growth before capture in the cold (5.5°C), unproductive water (Rogers 1973) and because a seasonal trend in mean length of emerging fry was not apparent in 1987 (regression, df = 10, F = 2.544, $p > 0.05$) or 1988 (df = 7, F = 0.101, $p > 0.05$).

SOCKEYE MOVEMENTS

Movement of emerging sockeye salmon was assessed by comparing beach seine catches of sockeye fry (≤35 mm) at the spawning areas (six sets every 10 days) with expected numbers of fry within a 500 m^2 area (i.e., the area swept by the beach seine). The algorithm for calculating the expected number of fry per beach seine haul was

$$\#\text{ fry per set} = (\#\text{ fry emerging}\cdot m^{-2}\cdot 24\text{ h}) \times (500\ m^2 \text{ per set}) \times (0.1 \text{ survival}).$$

This assessment assumed that sockeye fry were equally vulnerable to the beach seine and emergence, traps, and that fry emergence rates were equivalent in the adjacent areas sampled by the two gear types. The capture efficiency of the beach seine and emergence traps probably exceeded 70% (D.E. Rogers, Univ. Washington, Seattle WA 98195, pers. comm.; Collins 1975), suggesting that differences in gear efficiencies were not great. The assumed fry survival rate of 10% after emergence and the assumed residence time of 24 h were used to conservatively estimate the expected number of fry per beach seine set, thereby providing a minimum estimate of fry movement. For example, the expected number of fry-per-beach-seine-haul could be four times that estimated by the algorithm, based on the average mortality of emerging sockeye fry caused by coho predation (59% during 1985-1987), which probably is the major mortality source after emergence (Ruggerone 1989).

RESULTS

PREY SIZE SELECTION BY JUVENILE COHO

A total of 2,665 coho were examined for consumption of sockeye salmon during 1985-1987. Forty-eight to 74% of coho 80-150 mm consumed at least one sockeye during May-June compared to 12-38% during July and early August (Fig. 1), when fewer sockeye fry were emerging (Ruggerone 1989). Coho as small as 58 mm (live measure) consumed sockeye, although the frequency of consumption by small coho was considerably less than that of larger coho.

Over 90% of the juvenile sockeye consumed by coho salmon were ≤35 mm (Fig. 2). Juvenile sockeye consumed by 120-160 mm coho (geom. $\bar{x} = 34$ mm) were only slightly larger than sockeye consumed by 60-80 mm coho (geom. $\bar{x} = 30$ mm; Fig. 3). In contrast, the maximum length of sockeye consumed by coho increased rapidly with coho length. Maximum lengths of sockeye consumed by 67 mm and 162 mm coho were 32 mm and 78 mm, respectively. In general, coho were capable of consuming sockeye up to approximately 45% of their own fork length.

Coho salmon consumed sockeye fry that were significantly smaller than fry captured in emergence traps and beach seine hauls (Fig. 4; two factor ANOVA, $F = 194$, $p < 0.001$). Average fry lengths consumed by coho during 1985-1987 were 30.1, 29.8, and 31.0 mm, respectively, compared to average available fry lengths of 31.7, 31.1, and 31.6 mm, respectively. Lengths of emerging sockeye fry consumed by large coho salmon (≥105 mm) were slightly larger (30.5 mm) than those consumed by smaller coho (30.2 mm).

Recently emerged sockeye fry at Chignik Lake were longer than fry from 26 of 30 sockeye stocks for which data were available (Table 1). Only sockeye from Karluk River (31.4 mm), upper Pitt River (30.0-32.3 mm), and Weaver Creek (31 mm) were longer than fry at Chignik Lake (30.5 mm). Average fry length of the 29 sockeye stocks was 28.5 mm (±0.3 S.E.), excluding the smaller kokanee sockeye salmon (24.3 mm). Latitude does not appear to strongly affect mean fry length, as similar size ranges were measured in Alaska and British Columbia. Average weight of Chignik fry (185 mg) was slightly greater than other sockeye populations (175 mg), but the mean condition factor (k_D) of Chignik fry (1.87) was lower than that of other populations (1.95 ± 0.8 S.D.). Yolk was not visible by external inspection in approximately 90% of the emerging sockeye fry in Chignik Lake during 1987 and 1988.

SOCKEYE MOVEMENTS

Recently emerged sockeye fry were abundant on the spawning grounds during mid-May but were markedly less abundant than expected from late May through July (Fig. 5). During peak emergence of sockeye in June ($2.7\ \text{fry} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$, Ruggerone 1989), only 2 fry, on average, were

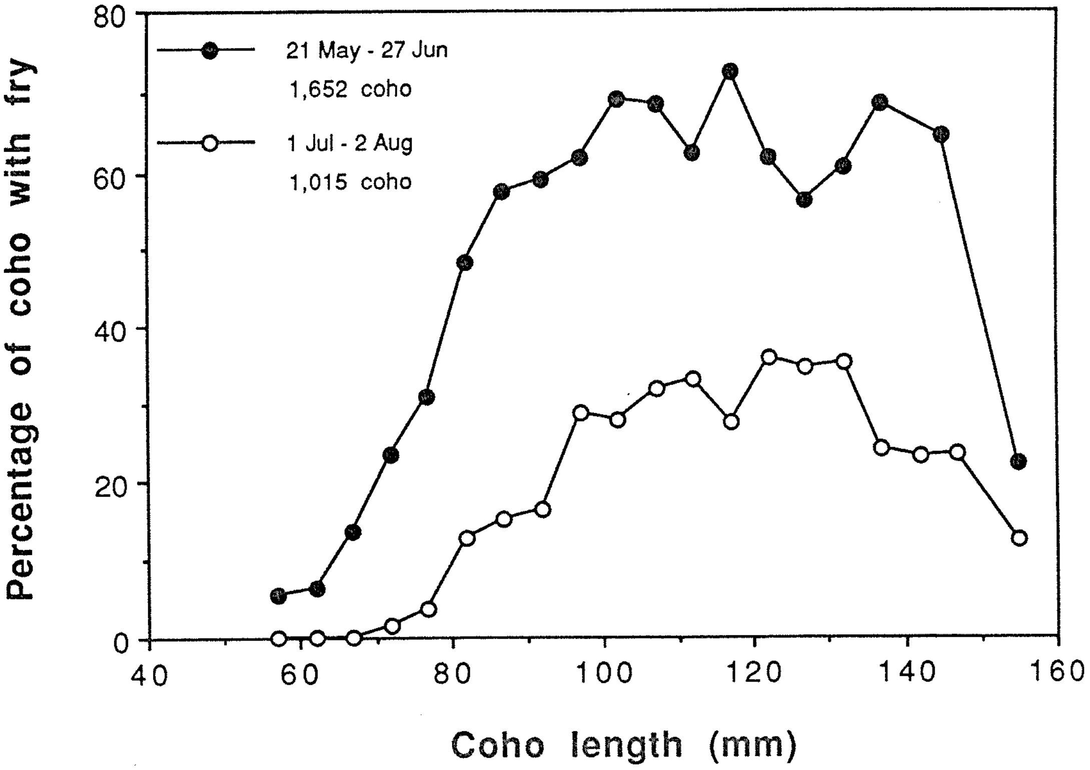

Figure 1. Percentage of coho salmon, by 5-mm length categories, that consumed sockeye salmon fry during spring (May 21-June 27) and summer (July 1-August 2).

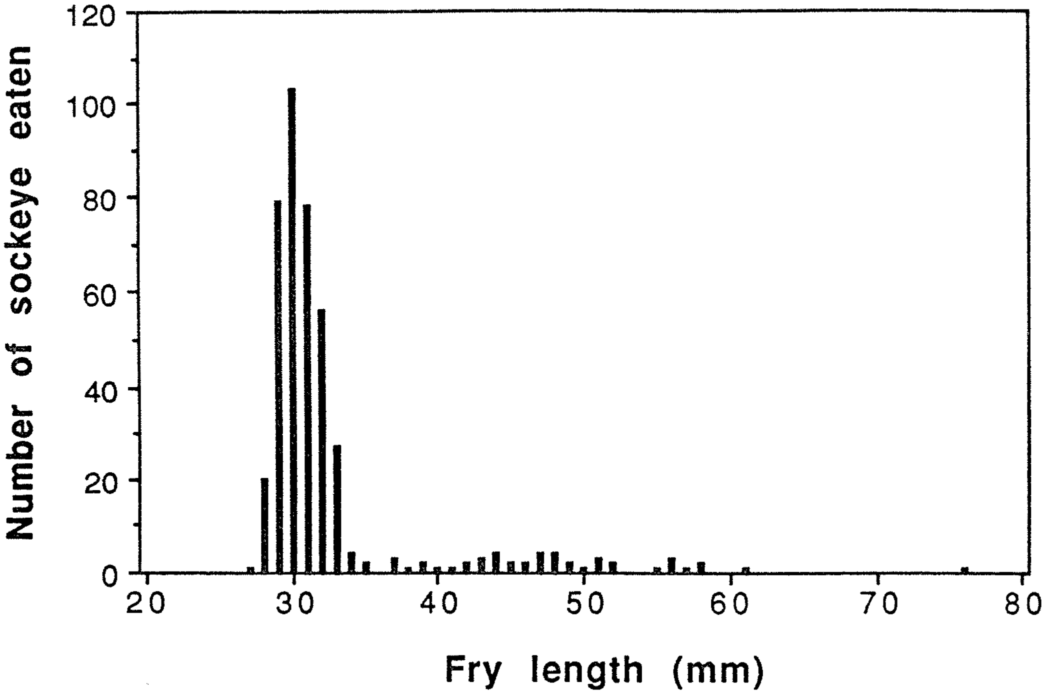

Figure 2. Length frequency distribution of juvenile sockeye salmon consumed by coho salmon during 1985-1987.

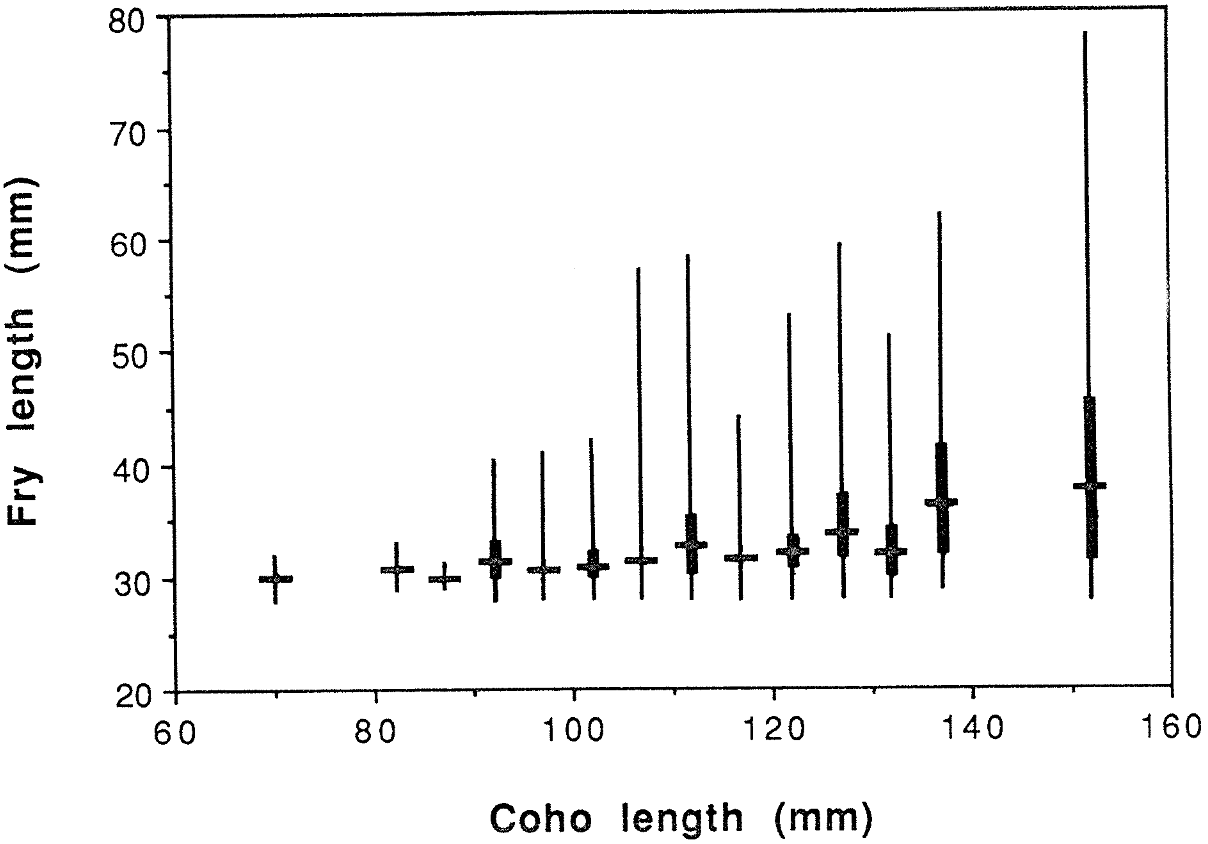

Figure 3. Geometric mean, 95% confidence interval and range of fry lengths consumed by coho salmon within 5 mm length categories.

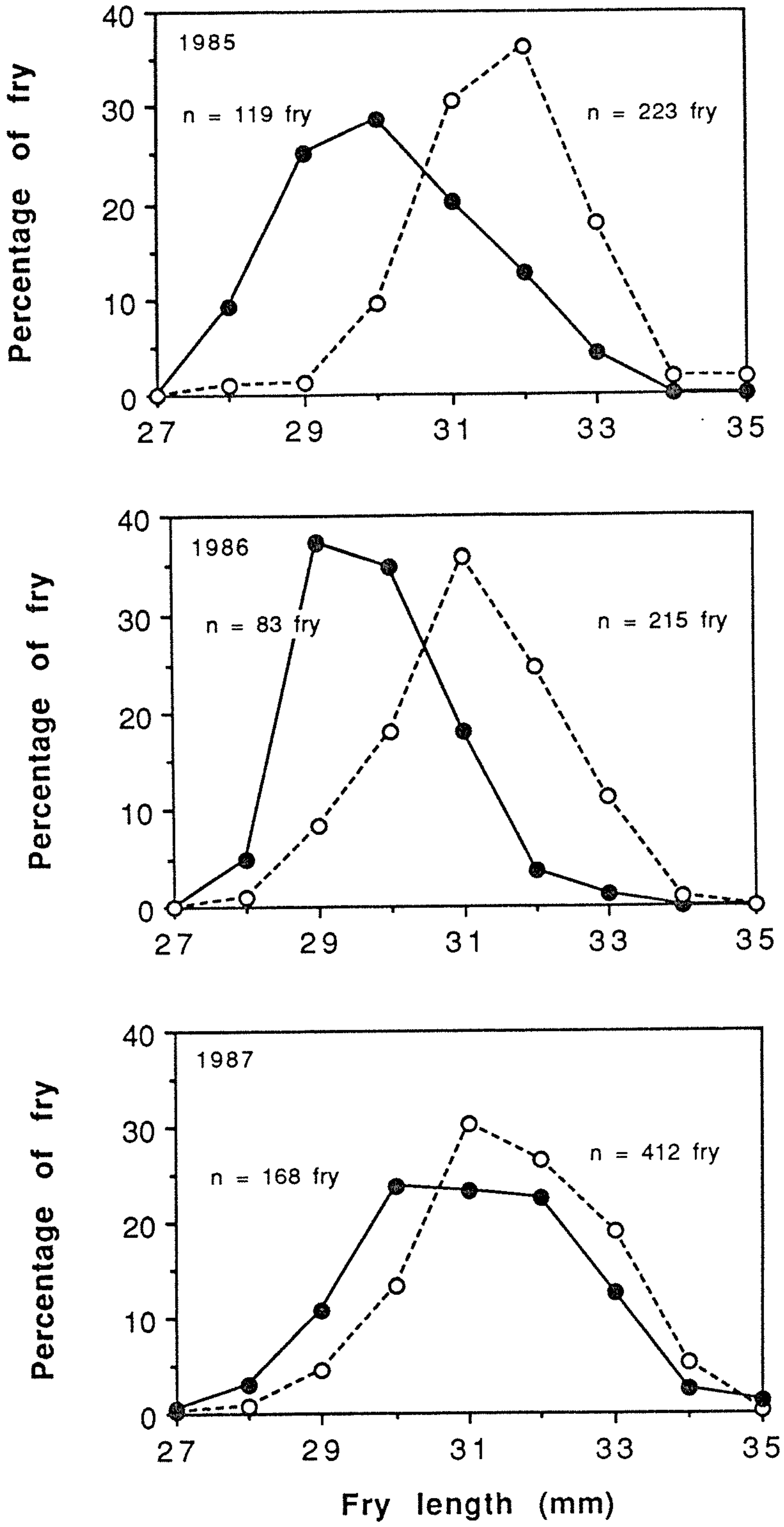

Figure 4. Comparison of sockeye fry lengths consumed by coho salmon (●) with lengths of emerging sockeye salmon captured by fry emergence traps and beach seine hauls (o) during 1985-1987.

Table 1. Average fork length (preserved, ± S.E.), wet weight and condition factor (k_D) of recently emerged sockeye salmon fry from stocks in Washington, British Columbia and Alaska.

Location	Length (mm)	Weight (mg)	Condition factor (k_D)*	n	Source
Karluk R., AK	31.4	257	2.02	NA	1
Upper Pitt R., B.C.	30.0 ± 0.03	228 ± 1	2.04	580	2
	32.3			20	3
Weaver Cr, Harrison Lk, B.C.	31.0	NA	NA	20	3
Chignik Lk, AK	30.5 ± 0.05	185 ± 0.7	1.87	789	4
Pitt R., B.C.	30.5 ± 0.06	236 ± 2	2.03	>200	2
Pitt R. A.S.C., B.C.	29.9 ± 0.07	226 ± 2	2.04	>160	2
Chilko R., B.C.	29.3 ± 0.07	190 ± 2	1.96	380	2
Gates R. A.S.C., Anderson Lk, B.C.	29.2 ± 0.07	181 ± 1	1.94	540	2
Newhalen R., Lk Iliamna, AK	29.1 ± 0.03	NA	NA	1,987	5
Cabin Bay, Lk Nerka, AK	29.1 0.32	220	2.07	29	6
Little R., Shuswap Lk, B.C.	28.7 ± 0.13	166 ± 3	1.91	120	2
Weaver Cr A.S.C., B.C.	28.6 ± 0.05	186 ± 1	2.00	580	2
Fulton R., Babine Lk, B.C.	28.6	153	1.87	daily	7
Early Thumb R., Karluk Lk, AK	28.2 - 29.1	132 - 176	1.87	NA	1
Lk Aleknagik, AK	28.4 ± 0.75	NA	NA	NA	8
Horsefly R., Quesnel Lk, B.C.	28.3 ± 0.10	158 ± 3	1.91	300	2
Late Thumb R., Karluk Lk, AK	28.2 - 28.5	176 - 184	2.00	NA	1
Cultus Lk, B.C.	28.2	NA	NA	20	3
Adams R., Shuswap Lk, B.C.	28.2 ± 0.06	150 ± 1	1.88	300	2
Fulton R. A.S.C., B.C.	28.2	NA	NA	450	9
Pinkut Cr, Babine Lk, B.C.	28.1	145	1.87	daily	7
Little Wenatchee R., WA	26 - 30	NA	NA	NA	10
Lower Shuswap R., B.C.	27.8 ± 0.15	137 ± 3	1.85	20	2
Gulkana R. S.I.B., Copper R., AK	27.3 - 27.7	NA	NA	NA	11
Nadina R. A.S.C., Francois Lk, B.C.	27.5 ± 0.05	150 ± 1.5	1.93	598	2
Anvil Bay, Lk Nerka, AK	27.4 ± 0.12	163	1.99	138	6
Cedar R., Lk Washington, WA	26.0 - 27.9	147 - 193	2.05	daily	12
Conuma R., Vancouver Island, B.C.	27.4 ± 0.23	115 ± 6.0	1.77	40; 10	13
Bear Cr, Tustumena Lk, AK	26.8 ± 0.15	132 ± 2	1.90	57	14
		139		43,411	15
Glacier Flats, Tustumena Lk, AK	NA	170	NA	983	15
Banks Lk, WA	24.3 ± 0.05	104 ± 1.2	1.94	258	16
Great Central Lk, B.C.	23.5	156	NA	NA	17,18

$^*k_D = \dfrac{10\sqrt[3]{\text{wt. (mg)}}}{\text{length (mm)}}$, (Bams 1970); A.S.C. - Artificial spawning channel; S.I.B. - Streamside incubation box.

Sources: (1) L. White, ADF&G, Kodiak AK 99615, pers. comm., range of daily means; (2) R. Kent, Dept. Fish. and Oceans, New Westminister B.C. V3L5B3, pers. comm.; (3) Mead and Woodall 1968; (4) Chignik Lake average for 1987 and 1988; (5) Fisheries Research Institute, Seattle WA 98195, unpublished data, 1985; (6) Burgner 1962, lake trap samples before major growth; (7) West 1978, mean of 9-14 yrs, live wt.; (8) Rogers, 1973, mean ± S.D. for 10 yrs, beach seine samples before major growth; (9) McDonald, 1969; (10) Mullan 1986, range; (11) Roberson and Holder 1987, streamside incubation boxes; (12) Stober and Hamalainen 1979, range of daily means; (13) T. Quinn, Univ. Washington, Seattle WA 98195, pers. comm., no rearing lake available; (14) J. Koenings, ADF&G, Soldotna AK 99669, pers. comm.; (15) Kyle 1988; (16) Stober et al. 1979, beach spawning kokanee sockeye; (17) Barraclough and Robinson 1972; (18) LeBrasseur et al. 1978.

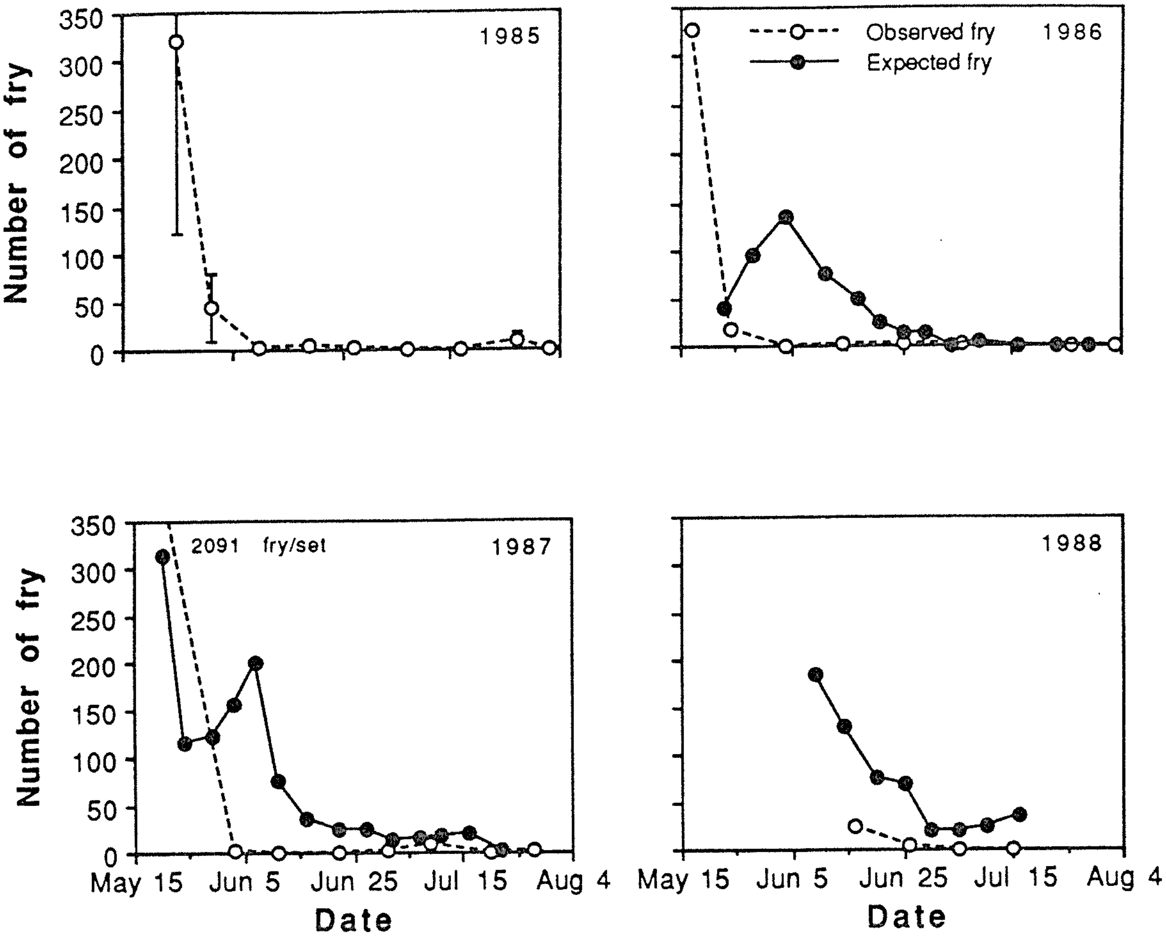

Figure 5. Comparison of expected (●) and actual (o) numbers of sockeye salmon fry (≤35 mm) captured per beach seine set on the sockeye salmon spawning grounds during spring and summer, 1985-1987. Expected numbers of fry were calculated as follows:

$$\#\ \text{fry}\cdot\text{set}^{-1} = (\#\ \text{fry emerging}\cdot\text{m}^{-2}\cdot 24\ \text{h}^{-1}) \times (500\ \text{m}^{2}\cdot\text{set}^{-1}) \times (0.1\ \text{survival}).$$

captured in a 500 m^2 sweep of the beach seine compared to the expected 135 fry. Catches of sockeye fry (≤35 mm) in all littoral areas of Chignik Lake averaged <8 fish per set during June and July, 1985-1988, whereas mid-size sockeye (36-45 mm, mostly age-0 fish) were present in small numbers ($\bar{x}$ =10 fish per set) beginning in late June, and sockeye >45 mm (mostly age-1 and age-2 fish) were relatively abundant ($\bar{x}$ = 129 fish per set) in littoral areas from mid-May to early August (Fig. 6).

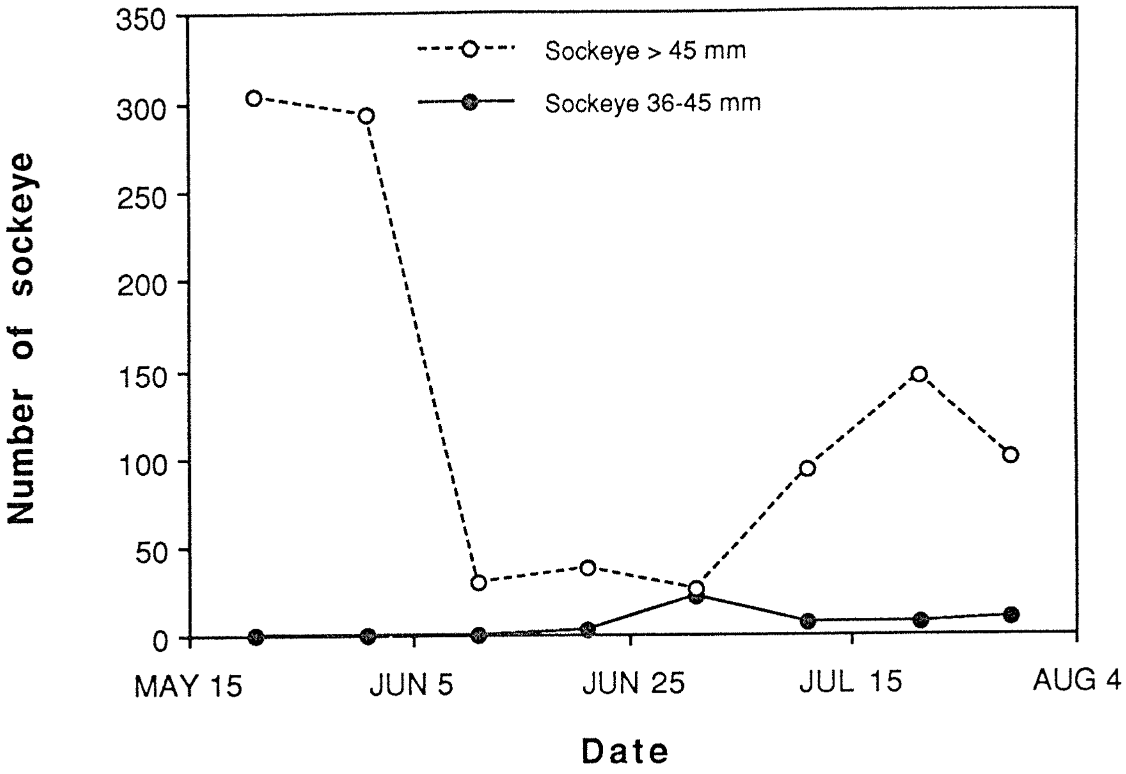

Figure 6. Numbers of large (>45 mm) and mid-size (36-45 mm) sockeye salmon captured per beach seine haul during 1985-1987.

DISCUSSION

PREY SIZE SELECTION BY JUVENILE COHO

Selection of smaller sockeye fry by coho salmon in this field study supports the findings of Parker (1971) and Hargreaves and LeBrasseur (1986), who reported that young coho in saltwater aquaria and in net pens consumed the smallest available salmon. A major difference in the present study is that the lengths of emerging sockeye salmon (31.5 mm, live measure) and the ratio of sockeye/predator length (28.8% of coho length) was markedly less than those studies utilizing pink (55.2 mm, 44% of coho length, Parker 1971) and chum salmon (~52 mm, ~43-44% of coho length; Hargreaves and LeBrasseur 1986). The ratios of prey/predator length utilized by the previous studies were close to the maximum (i.e., ~50%) observed in this and other field studies; therefore selection of smaller pink and chum salmon by coho was not surprising. The present study demonstrated that juvenile coho salmon will consume the smaller individuals among a population of newly emerged sockeye fry even though the fry are considerably smaller than the maximum size potentially consumed by coho. Net-pen studies (Ruggerone 1989) involving juvenile coho salmon (105-120 mm) and sockeye fry (29-45 mm) from Chignik Lake also indicated that predation rates declined rapidly at fry lengths ≥32 mm, which is the length of large sockeye fry emerging from the spawning grounds in Chignik Lake.

Hargreaves and LeBrasseur (1986) hypothesized that coho feeding on recently emerged salmon fry would initially select the largest fry, then gradually shift to smaller fish as the prey grew and approached the maximum size that coho could capture, handle, or consume. This hypothesis was based, in part, on optimality models and observations that fish predators may select the largest prey available when the predators are substantially larger than the prey (Ivlev 1961; Werner 1974; Werner and Hall 1974). For example, Ivlev reported that pike and perch preferentially selected the largest available fish, which were approximately 2% and 25% of the predator's weight, respectively. Contrary to this hypothesis, the large size group of coho in Chignik Lake (105-160 mm) continued to consume proportionately more of the smaller sockeye, which were approximately 26% of coho body length or <1% of coho weight. Presumably, capture success, handling time, and/or attack rate of coho reduced the consumption of larger fry. Arctic char (*Salvelinus alpinus*) appeared to consume sockeye smolts (17% of char length) randomly with respect to size (Ruggerone and Rogers 1984). Further research is needed to determine the size ratio of prey/predator and other characteristics at which piscivorous fishes switch from small to large prey (Nilsson 1978).

At least three factors must be present before coho could influence the evolution of larger fry at the time of emergence in Chignik Lake. First, intense predation by coho must differentially reduce the survival of small versus large sockeye fry. Second, fry size at emergence must have a significant heritable component. Third, negative effects of producing larger fry size such as reduced fecundity must be insufficient to override the fitness benefits of larger fry size. The intense predation (Ruggerone and Rogers, in review) and the selection of smaller sockeye fry by coho in Chignik Lake indicate that coho are capable of reducing the survival of small versus large fry. Significant predation by juvenile coho probably occurred historically based on large harvests of adult coho with little effort during the early 1900s (up to 100,000 fish, INPFC 1979). The influence of coho on the evolution of emerging fry size may be considerable because predation occurs before environmental factors in the lake affect the growth of sockeye salmon and because salmonid size is believed to have a large heritable component (Ricker 1972, Ricker et al. 1978, Gjedrem 1983, Gall and Huang 1988). Thus, unless factors favoring greater fecundity select against large fry size, size-biased predation by coho should influence the evolution of large sockeye size at emergence.

Average fork length of Chignik sockeye salmon near the time of emergence was longer than most other sockeye stocks. Only fry from the Pitt River system, Karluk River, and Weaver Creek were longer. The large fry size at Karluk River and Weaver Creek may be related to their upstream migration, rather than the typical downstream migration of sockeye fry. Fry at Chilko and Little rivers also migrate upstream and were above average length at the time of emergence. In comparison, fry in Chignik Lake emerge from gravel along the lake shoreline and are not subjected to strong currents. The reason for large fry in the Pitt River system is not known.

Chignik Lake sockeye have greater absolute fecundity and similar length-specific fecundity (4,040 eggs per 566 mm female [mid-eye to tail fork], Phinney and Lechner 1969) relative to most sockeye (Rounsefell 1957; Foerster 1968; Manzer and Miki 1986; Burgner, in press; D.E. Rogers, University of Washington, Seattle WA 98195, unpublished data). This suggests that Chignik sockeye suffer little reduction in fecundity associated with production of longer fry, which have greater swimming stamina (Bams 1966) and presumably greater burst speed (Taylor and McPhail 1985). The absence of the expected inverse relationship between fecundity and fry length may be explained by the lower mean condition factor (k_D) of Chignik fry (1.87) relative to other sockeye populations (1.95). The relatively low condition factor of Chignik fry may be related to the absorption of yolk, which was visibly absent from approximately 90% of the emerging fry.

This study supports the "safe harbor" hypothesis (Shine 1978, 1989), which states that optimal egg or fry sizes should be determined by the relative survival rates of eggs and free-living juveniles. If the egg stage is a "safe harbor" (as in salmon that bury their eggs in gravel), but juvenile life is relatively hazardous, selection should favor an increase in egg or fry size and thus a decrease in the duration of the high-risk juvenile phase. In Chignik Lake, the large size of fry at emergence reduced the probability of capture by coho before the fry move to offshore areas where coho were less abundant (Ruggerone and Rogers, in review).

SOCKEYE MOVEMENTS

Sockeye fry were significantly more abundant on the shoreline spawning grounds of Chignik Lake during mid-May, prior to the apparent peak emergence of sockeye (Ruggerone 1989), than during June and July. The abundance of fry on the spawning grounds during mid-May could be related to the scarcity of coho during May (19 coho per set, n = 23) versus June (86 coho per set, n = 59). In May, coho were never abundant in beach seine sets that captured numerous sockeye fry. Apparently, many coho overwintered in the outlet of the lake or in limnetic areas, then dispersed to littoral areas in late May and early June, when emergence of sockeye fry increased.

Comparison of beach seine and fry trap catches of emerging sockeye fry indicated that fry rapidly moved away from the shoreline of Chignik Lake during June and July. Many fry inhabited offshore waters based on tow net and hydroacoustic surveys (Narver 1966; Marshall et al. 1974; Ruggerone 1989). The offshore movement of sockeye fry may be a response to the onshore movement of piscivorous coho salmon and the lack of refuges (e.g., large rocks or macrophytes) in the littoral zone of Chignik Lake. Many sockeye salmon exceeding 45 mm reentered the littoral zone, which could be a response to reduced predation on these larger fish and to a greater food supply, especially insects, in the shallow water (Reeves 1968; Rogers 1979).

In many lakes, recently emerged sockeye fry disperse from the spawning grounds and rear nearshore during spring. This pattern occurs in lakes of the Bristol Bay Basin (Hartman et al. 1962; Pella 1968; Rogers 1973; Newcome 1976; D.E. Rogers, Univ. Washington, Seattle WA 98195, pers. comm.), Cook Inlet (J. Koenings, ADF&G, Soldotna AK 99669, pers. comm.), Kodiak Island, the Alaska Peninsula (Ruggerone 1989), and interior areas of British Columbia (McDonald 1969; Goodlad et al. 1974). Densities of newly emerged sockeye fry in the littoral zone of these lakes may be great, as indicated by the 10-yr geometric mean catch of 192 age-0 fry per beach seine set (same net size as present study) at Lake Aleknagik, Alaska (Rogers 1973), a lake without coho or other abundant piscivores in the littoral zone. Some sockeye fry populations inhabit both littoral and limnetic areas during spring; older sockeye generally rear in both littoral and limnetic areas. In contrast, sockeye fry in coastal lakes of British Columbia, including Cultus Lake and Great Central Lake, develop primarily in limnetic areas during spring (Goodlad et al. 1974; K. Hyatt, Dept. Fisheries and Oceans, Nanaimo, B.C. V9R 5K6, pers. comm.).

Many factors may influence the distribution and behavior of recently emerged sockeye fry, including ice cover, temperature, food availability, competitors, and predators. For example, fry populations that primarily inhabit littoral areas during spring (e.g., Alaskan and interior British Columbia stocks) occupy lakes that freeze during winter. Presumably, these fry occupy littoral areas in spring because food is more abundant and water is warmer than in offshore areas (Rogers 1979). Sockeye fry in Chignik Lake appear to be an exception to the occurrence of fry in the littoral zones of lakes that freeze. In Chignik Lake, the behavior of newly emerged sockeye fry appears to reflect a balance between the risks of predation and low food availability: they move to limnetic areas when risk of predation in the littoral area is great. As juvenile sockeye grow and the risk of predation declines, many juveniles reenter the littoral zone.

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