

# Intra- and inter-specific competition and the reproductive success of sympatric Pacific salmon

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**Abstract:** Individual female Pacific salmon fight for breeding space with conspecific and heterospecific females. We evaluated the consequences of this competition on the reproductive success of sockeye (*Oncorhynchus nerka*), chum (*Oncorhynchus keta*), and pink salmon (*Oncorhynchus gorbuscha*) in the Weaver Creek spawning channel, British Columbia. We hypothesized that differences in body size, relative abundance, and spawning date would influence the magnitude of interspecific interactions. Reproductive success (survival rate of eggs to emigrating fry) of the most abundant species, sockeye, was strongly and inversely correlated with conspecific abundance but not with the abundance of the other, less abundant species. Chum reproductive success was inversely correlated with sockeye abundance but not with the abundance of the scarce and smaller pink. Surprisingly, pink reproductive success was not correlated with sockeye abundance and only marginally correlated with chum abundance despite the fact that pink are smaller and spawn earlier than sockeye. Thus, intra- and inter-specific competition can substantially affect salmon reproductive success, but the magnitude of the competitive effects may depend on relative abundance, size, spawning date, and microhabitat preferences.

**Résumé :** Les femelles du saumon du Pacifique se battent avec les femelles de leur propre espèce ou d'autres espèces pour l'obtention d'un espace de frai. Nous avons évalué les conséquences de cette compétition sur le succès de la reproduction du saumon rouge (*Oncorhynchus nerka*), du saumon kéta (*Oncorhynchus keta*) et du saumon rose (*Oncorhynchus gorbuscha*) du chenal de frai du ruisseau Weaver, en Colombie-Britannique. Nous avons formulé l'hypothèse que des écarts ayant trait à la taille corporelle, à l'abondance relative et à la date du frai devraient influencer sur l'importance des interactions interspécifiques. Le succès de la reproduction (taux de survie des oeufs jusqu'à l'alevin émergeant) de l'espèce la plus abondante, le saumon rouge, était fortement et inversement corrélé avec l'abondance des conspécifiques mais non avec l'abondance des individus des autres espèces, moins abondants. Le succès de la reproduction du saumon kéta était inversement corrélé avec l'abondance du saumon rouge mais non avec celle du saumon rose plus rare et plus petit. Au contraire des attentes, le succès de la reproduction du saumon rose n'était pas corrélé avec l'abondance du saumon rouge et ne l'était que très peu avec celle du saumon kéta, même si le saumon rose est plus petit et fraie plus tôt que le saumon rouge. Cette compétition intra et interspécifique peut modifier de façon appréciable le succès de la reproduction du saumon, mais l'importance des effets de la compétition peut être fonction de l'abondance relative, de la taille, de la date du frai et des préférences en matière de microhabitats.

[Traduit par la Rédaction]

## Introduction

Competition for limited resources is one of the fundamental forms of behavioral and ecological interaction among organisms. Competitive behavior is often observed in habitat choice, foraging, or direct aggression and interference. However, the fitness consequences of competition may be difficult to detect, owing to insufficient or inaccurate data or confounding influences of density-independent processes. Interspecific interactions, such as interference competition

for breeding space (e.g., Breitburg 1987; Hayes 1987), may also obscure intraspecific competitive effects. Interspecific competition may be particularly intense for closely related species that share overlapping preferences for spawning sites (e.g., Ming and Noakes 1984). Typically, interspecific competition is inferred from aggressive behavior between species, but the fitness consequences of this competition are rarely demonstrated (Gustafsson 1987). As Thornhill (1987) pointed out, "...in order to determine whether interspecific interactions may affect the evolution of species differences and species coexistence, it is necessary to document not only that such interactions do occur but also that they have consequences for fitness."

Salmonid fishes provide excellent opportunities to study competition and its effects on fitness. Competition on the spawning grounds is widely accepted as an important part of the behavioral ecology of female salmon (e.g., Keenleyside and Dupuis 1988; Foote 1990) and the dynamics of salmon populations (e.g., McNeil 1969). This competition is a consequence of high densities of spawning fish on spawning grounds, particularly for some of the semelparous *Oncorhynchus* spp. Female salmon select, prepare, and defend the

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nest or redd site without assistance from males. Females are highly territorial, and territory holders resist displacement (Schroder 1982; McPhee and Quinn 1998) until they approach death, although size does provide some advantage in territory acquisition (van den Berghe and Gross 1989; Foote 1990). Thus, arrival date on the spawning grounds and, to some extent, body size affect territory acquisition. However, the duration of the breeding period of the population almost invariably exceeds the life span of individual females. Consequently, fertilized eggs deposited by an early-arriving female may be displaced by the digging of females superimposing their redds over the redd of the previous territory holder after her death. Such redd superimposition has been documented in many salmonid species (e.g., Witzel and MacCrimmon 1983; Hayes 1987; Beard and Carline 1991) but is believed to be a particularly important density-dependent mortality factor for pink (*Oncorhynchus gorbuscha*) and chum salmon (*Oncorhynchus keta*) (McNeil 1969) and sockeye salmon (*Oncorhynchus nerka*) (Burgner et al. 1969). Large-bodied species should therefore affect the reproductive success of smaller-bodied species because larger females dig deeper redds (van den Berghe and Gross 1984; Kitano and Shimazaki 1995). In addition, early-spawning females should be more vulnerable to redd superimposition by conspecific (Essington et al. 1998; McPhee and Quinn 1998) and hetero-specific individuals (Hayes 1987).

The shape of the spawner–recruit relationship often provides some insight into the mechanism of density dependence. An asymptotic (Beverton–Holt) spawner–recruit relationship reflects space limitation for spawning adults or offspring, while a dome-shaped (Ricker) spawner–recruit relationship reflects resource depletion by offspring. It is often difficult to distinguish these two models from a linear (density-independent) model or to distinguish between them based on empirical evidence for several reasons. First, the requisite long time series of data over a wide range of spawning population sizes are not common. Second, the number of females, their egg production, and the number of offspring must be accurately counted. Third, the importance of density-independent mortality factors such as flooding and freezing must be minimized.

In this study, we investigate the relative importance of intra- and inter-specific competition on the reproductive success of sockeye, chum, and pink salmon spawning in the Weaver Creek spawning channel (WCSC). The WCSC is a controlled-flow environment with ideal gravel and relatively uniform habitat, limiting the confounding influences of density-independent factors and habitat preference on recruitment. The three species of salmon differ in body size (pink being the smallest and chum the largest) and spawning date in this system (pink spawning somewhat earlier than chum and sockeye), two factors that we predicted would affect interspecific competition. The WCSC has recorded the number of returning females, fecundity, egg deposition, and fry production for over 30 years, allowing us to assess the extent of competitive interactions by fitting stock–recruit models and to identify whether density dependence occurs prior to or after egg deposition. We used these data to test whether less numerous species are primarily affected by the density of the most numerous species and whether larger-bodied and later-spawning species are least affected by inter-specific competition.

## Materials and methods

### Site description

The WCSC is located on Weaver Creek, a small tributary of the Harrison River, in the Fraser River system, British Columbia, approximately 100 km upstream from the mouth of the Fraser River and 2 km downstream of Harrison Lake. The WCSC was constructed in 1965 to augment sockeye production, which had been declining, apparently due to habitat degradation. It was operated and maintained by the International Pacific Salmon Fisheries Commission until 1985, after which it was operated by the Department of Fisheries and Oceans.

### Data collection

The channel, 2930 m long by 6.1 m wide, was designed to provide optimal conditions for survival of developing embryos and hatchling alevins prior to emergence as free-swimming fry (Rosberg et al. 1986). The channel is operated to receive a discharge of  $0.55 \text{ m}^3 \cdot \text{s}^{-1}$ , with a resulting mean depth of 0.25 m and mean velocity of  $0.4 \text{ m} \cdot \text{s}^{-1}$ . Spawning substrate consists of 1.2- to 10.2-cm-diameter gravel, approximately 40 cm deep. Periodic mechanical cleaning of the gravel and a settling pond upstream minimize siltation that might otherwise reduce water and oxygen flow to embryos in the gravel. Egg to fry survival in the spawning channel is approximately an order of magnitude greater than in Weaver Creek proper (Rosberg et al. 1986).

The number of spawning females of each species entering the spawning channel is controlled at a downstream weir to achieve an abundance of approximately 19 000 female sockeye plus approximately 2000 combined female chum and pink. Pink were present only during odd-numbered years. Sockeye are preferentially admitted into the spawning channel (relative to their abundance in the creek), and the ratio of pink to chum to sockeye averaged 2:5:32 over the odd-numbered years of the study. From 1965 to 1997 the number, species, and sex of returning fish were recorded. From 1975 to 1997, mean fecundity of sockeye and pink was also assessed by sampling 50 (sockeye) or 25 individuals (pink) each year. Prior to 1975, fecundity was estimated from regression of fecundity and standard length (Rosberg et al. 1986). For chum, fecundity was measured in 25 individuals each year from 1989 to 1997, and the mean value from this period (2793) was used for all other years. Mean female body size of carcasses and of fish sacrificed for fecundity estimates was measured from the posterior edge of the orbit of the eye to the hypural plate.

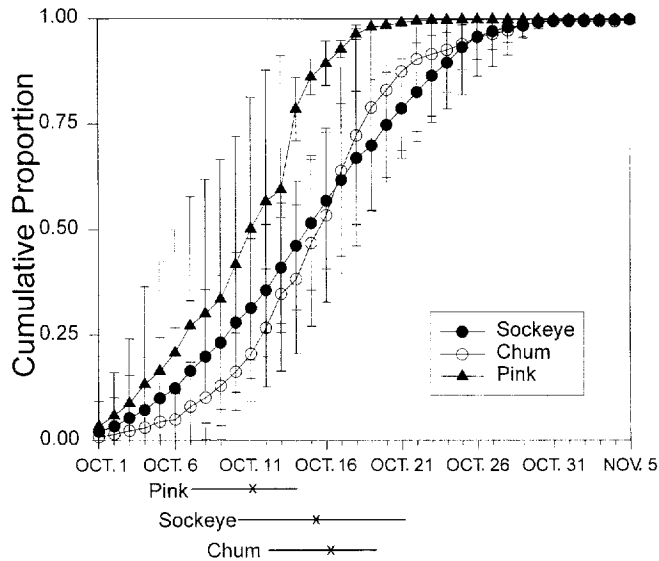
Total egg deposition for each species was calculated by estimating potential egg deposition (number of females times mean fecundity) and subtracting the number of eggs retained in females, estimated by inspection of female carcasses. Each carcass was classified as 100% spawned, 50% spawned, or 0% spawned, and the number of eggs retained by females was measured in a subsample of each category. Thus, total egg retention was equal to the egg retention in each category times the number of females in each category. For chum, data were not available on degree of spawning for 1965–1981, so potential egg deposition could not be adjusted for unspawned eggs for these years.

The number of fry produced in the channel was estimated by using a trap at the end of the channel. The trap sampled 5% of the fry migrating over a weir. The species composition of a subsample of the catch was determined each night and the nightly total was estimated from the weights of the catch and the weights of fry of each species. Because sockeye fry greatly outnumbered chum and pink fry, estimates of chum and pink fry abundance are less precise than those for sockeye.

### Data analysis

To compare the timing of spawning for each species, we calculated the cumulative proportion of females entering the channel

**Fig. 1.** Temporal pattern of channel entry for female sockeye, chum, and pink salmon. Data points represent the mean ( $\pm$ SD) cumulative proportion of the total run entering the channel on each day, averaged over 5 years. Lines at the bottom indicate the peak entry period, and X indicates the 50% entry date for each species



each day, averaged across years (1993–1997), and used two parameters to describe these data. The first was the date at which 50% of the annual total number of females had entered the channel (median entry date). The second was the peak entry period, defined by the dates when 25–75% of the annual total entered the channel. These dates will closely approximate the peak spawning dates because most female salmon spawn within 1–3 days of entry onto spawning grounds (Schroder 1982; Quinn and Foote 1994; McPhee and Quinn 1998). Ideally, we would evaluate the entry date of each species for each year to determine how interannual variation in entry date affects interspecific competition, but the limited data on channel entry (1993–1997) preclude this analysis.

To evaluate whether each species exhibited density-dependent reproductive success, we fit three stock–recruit curves for each species (Ricker 1975). The general form of the stock–recruit curves was

$$(1) \quad R = f(P)e^V$$

where  $R$  is the number of fry produced,  $P$  is the number of females, and  $V$  is an error term that is normally distributed with mean 0 and variance  $\sigma^2$ , i.e., we assumed lognormal errors. The stock–recruit function,  $f(P)$ , was either a linear (density independent), Beverton–Holt (density dependent, saturation curve), or Ricker curve (density dependent, dome-shaped curve).

Linear:

$$(2a) \quad f(P) = \alpha P$$

Beverton–Holt:

$$(2b) \quad f(P) = \frac{1}{\alpha + \beta P^{-1}}$$

Ricker:

$$(2c) \quad f(P) = \alpha P \exp(-\beta P).$$

Best-fitting model parameters were those that minimized the negative log-likelihood of the residuals. Instead of including  $\sigma^2$  as a

free parameter, we calculated the likelihood profile by estimating  $\sigma^2$  from the model (Hilborn and Mangel 1997). To determine whether there was significant density-dependent reductions in reproductive success, we compared the likelihoods of the linear model with that of the Beverton–Holt or the Ricker model. For this analysis, we recognized that both the Ricker and Beverton–Holt models could be reduced to the linear model by setting one parameter to zero ( $\alpha$  in the Beverton–Holt model,  $\beta$  in the Ricker model). Thus, the linear models were nested within the Beverton–Holt or Ricker models, allowing us to compare models using the likelihood ratio (Hilborn and Mangel 1997). For this test, the more complex model (Beverton–Holt or Ricker) provided a significantly better fit to the data than the linear model if the ratio of likelihoods exceeded 7.25 (or equivalently, if the difference in negative log likelihoods exceeded 1.98).

For those species that exhibited density-dependent reproductive success, we evaluated whether density dependence occurred primarily by affecting the behavior of mature females or by affecting the survivorship of deposited eggs. We first determined whether the proportion of females that were 100% spawned was correlated with female abundance. We then evaluated whether the postdeposition reproductive success (fry produced per deposited egg) was correlated with female abundance. For all analyses, we used simple linear regression to identify significant correlations. We used standard diagnostics of residuals to evaluate whether the assumptions of normality and linearity were met (Draper and Smith 1981).

To evaluate the effect of heterospecifics on reproductive success, we determined whether the total reproductive success of each species was correlated with heterospecific abundance. Total reproductive success was defined as the ratio of fry produced to potential egg deposition. We used stepwise multiple regression to identify significant correlations between total reproductive success and conspecific and heterospecific abundances. Although we were not specifically interested in the effect of conspecifics in this analysis, it was necessary to include this parameter as a covariate. We set  $\alpha$  for entry and removal from the model equal to 0.05. When we identified a significant correlation, we identified whether density-dependent reduction in reproductive success occurred prior to or after egg deposition by determining whether the proportion of females that spawned and (or) the postdeposition reproductive success were correlated with heterospecific abundance.

## Results

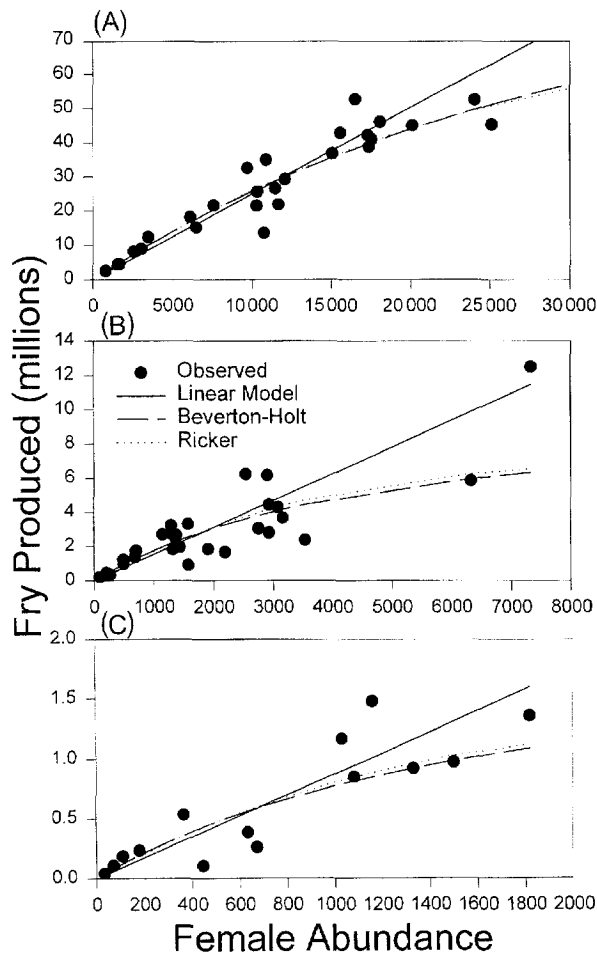
Pink entered the channel earliest in each year and had the earliest 50% entry date (October 11). Timing of returns was similar between chum and sockeye, with sockeye having a slightly earlier median entry date (October 15) than chum (October 16). However, sockeye had longer peak entry period (11 days) than pink and chum (both 7 days). Consequently, peak entry period for sockeye broadly overlapped with the peak period of pink and chum and overlapped the 50% entry date of both species (Fig. 1). Moreover, the peak entry period of sockeye extended later than that of pink and chum. Peak entry periods of pink and chum overlapped by 3 days, yet did not overlap with the other species' 50% entry date. These differences were consistent across years, except for 1994 when sockeye 50% entry date occurred 5 days later than chum 50% entry date.

Data on mean female size were available for 1993, 1995, and 1997 for pink and for 1989–1997 for sockeye and chum (except for 1994 when no data were available for chum). During these years, pink had the smallest mean size (430 mm), with annual means ranging from 424 to 437 mm. Sockeye were larger than pink, with a mean size of 502 mm and annual

Table 1. Number of returning salmon females, egg deposition, and fry production in the WCSC, 1965–1995.

Year	Sockeye				Chum				Pink			
	Females	Potential egg deposition (millions)	Actual egg deposition (millions)	No. of fry (millions)	Females	Potential egg deposition (millions)	Actual egg deposition (millions)	No. of fry (millions)	Females	Potential egg deposition (millions)	Actual egg deposition (millions)	No. of fry (millions)
1965	2 986	11.90	11.44	9.00	487	1.36	na	0.98	32	0.07	0.06	0.04
1966	3 424	14.75	14.13	12.39	92	0.26	na	0.23				
1967	1 631	6.85	6.08	4.50	202	0.56	na	0.47	70	0.16	0.14	0.11
1968	784	3.18	2.95	2.56	1138	3.18	na	2.70				
1969	9 671	37.59	36.33	32.62	1286	3.59	na	3.23	108	0.22	0.21	0.19
1970	2 519	10.75	9.89	8.19	482	1.35	na	1.24				
1971	1 520	6.35	6.29	4.51	696	1.94	na	1.76	178	0.36	0.35	0.24
1972	6 418	25.61	25.29	15.21	7333	20.48	na	12.51				
1973	10 857	46.64	45.74	35.05	3077	8.59	na	4.29	364	0.70	0.69	0.54
1974	15 044	67.28	59.21	36.85	2893	8.08	na	6.18				
1975	10 287	43.79	41.64	25.68	2532	7.07	na	6.24	633	1.28	1.23	0.39
1976	16 525	69.11	65.09	52.75	6322	17.66	na	5.86				
1977	19 172	83.32	77.72	19.52	2486	6.94	na	1.65	600	1.28	1.19	0.28
1978	17 527	76.68	75.15	40.98	3535	9.87	na	2.39				
1979	11 424	48.85	47.90	26.67	2753	7.69	na	3.06	444	0.81	0.79	0.11
1980	24 043	96.99	94.72	52.60	1905	5.32	na	1.87				
1981	10 244	42.10	41.56	21.62	2928	8.18	na	2.81	671	1.31	1.30	0.26
1982	30 983	130.50	122.60	56.05	3160	8.83	8.13	3.67				
1983	12 037	52.19	51.19	29.31	2927	8.18	8.04	4.43	1030	1.86	1.85	1.17
1984	25 098	101.35	97.51	45.40	2186	6.11	5.96	1.69				
1985	11 362	47.61	45.37	18.88	2812	7.85	7.81	1.98	2297	4.63	4.60	0.92
1986	24 375	94.53	80.57	19.14	333	0.93	0.72	0.23				
1987	18 281	80.99	77.65	33.77	509	1.42	1.38	0.77	660	1.32	1.29	0.81
1988	14 192	57.73	56.63	20.44	404	1.13	1.07	0.58				
1989	7 527	27.97	27.65	21.66	1570	4.48	4.40	0.93	1326	2.37	2.34	0.92
1990	6 061	21.76	21.59	18.22	1426	3.87	3.82	1.97				
1991	15 563	56.66	55.70	42.90	263	0.70	0.68	0.36	1156	1.80	1.78	1.48
1992	18 080	64.81	63.91	46.09	681	1.76	1.73	1.39				
1993	17 354	62.41	61.66	38.82	1366	3.46	3.40	2.67	1823	2.77	2.73	1.36
1994	17 301	67.79	67.36	42.22	1297	3.59	3.48	2.74				
1995	11 486	32.73	31.68	21.96	1360	4.14	3.93	2.50	1077	1.77	1.60	0.85
1996	20 120	68.53	67.83	45.05	1315	3.88	3.835	1.85				
1997	10 700	38.44	32.03	13.70	1567	4.74	4.707	3.31	1497	2.29	2.24	0.97
Mean	12 867	51.45	49.15	27.71	1919	5.37	3.94	2.68	821	1.47	1.43	0.62

**Fig. 2.** Best-fitting stock–recruit curves fit to (A) sockeye, (B) chum, and (C) pink salmon data. For each species, a linear (density independent), Beverton–Holt (density dependent), and Ricker (density dependent) curve were fit to the data. See Table 2 for parameter estimates.



means ranging from 483 to 518 mm. Chum had the largest mean length, 587 mm, ranging from 558 to 610 mm.

Female sockeye abundance varied greatly, from 784 in 1968 to 30 983 in 1982 (Table 1). Sockeye fry production was similarly variable, ranging from 2.56 million in 1968 to 52.75 million in 1976. Abundance of female chum and pink also varied greatly, ranging from 92 to 7333 (chum) and from 32 to 2297 (pink) (Table 1). Fry production ranged from 0.23 to 12.51 million for chum and from 0.04 to 1.17 million for pink.

A large flood occurred in 1977 and an outbreak of infectious haematopoietic necrosis virus occurred from 1985 to 1988 (Traxler and Rankin 1989). Because reproductive success was markedly reduced during these years owing to density-independent effects, data from these years were not used for any analyses (which estimate density-dependent processes). For sockeye, the Beverton–Holt and Ricker models both provided a significantly better fit to the data than the linear model (Fig. 2), with a likelihood ratio of 190 for the Beverton–Holt/linear comparison and 176 for the Ricker/linear comparison (Table 2). Both of these ratios greatly exceeded the critical value of 7.25 needed for statistical signifi-

cance at the 0.05 level. Assuming a uniform, noninformative prior probability for each model (i.e., each model was equally likely, a priori), then the best-fitting Beverton–Holt model was only 1.08 times as likely as the best-fitting Ricker model based on the ratio of likelihoods. The similarity in the likelihoods of these two models is also indicated by the similarity in the shapes of the two curves (Fig. 2). Thus, there was strong evidence for density-dependent reproductive success for sockeye, but we could not ascertain whether the Beverton–Holt or the Ricker model best described this density dependence.

There was also some evidence for density-dependent reproductive success for chum (Fig. 2). Both the Ricker and Beverton–Holt models fit the data significantly better than the linear model, with a likelihood ratio of 26.2 for the Beverton–Holt/linear comparison and 12.9 for the Ricker/linear comparison (Table 2). The Beverton–Holt model was 2.0 times as likely as the Ricker model, but both model fits were strongly influenced by two high-leverage data points, corresponding to chum abundances of 6322 and 7333 (Fig. 2). Excluding either of these points resulted in large changes in the model fits because there were few data points within that range of female abundances. Thus, the evidence for density-dependent reproductive success was equivocal.

There was no evidence of density-dependent reproductive success for pink. Neither the Beverton–Holt model (likelihood ratio = 2.6) nor the Ricker model (likelihood ratio = 2.17) provided a significantly better fit to the data than the linear model (Table 2). These likelihood ratios were substantially smaller than those calculated from the sockeye and chum data.

Because sockeye showed evidence for density-dependent reproductive success, we evaluated at what life stage density dependence took place. There was no relationship between the total number of females and mean fecundity ( $F_{1,31} < 0.001$ ,  $P = 0.99$ ) (data not shown) or the proportion of females that spawned ( $F_{1,31} = 0.362$ ,  $P = 0.552$ ) (Fig. 3). However, there was a strong negative correlation between postdeposition reproductive success and the abundance of spawning females ( $R^2 = 0.34$ ,  $F_{1,26} = 14.848$ ,  $P < 0.001$ ) (Fig. 3). Thus, density-dependent reduction in reproductive success occurred after fertilization and was manifest by reduced survivorship of deposited eggs. The slope of this relationship was  $-1.06 \times 10^{-5}$ , indicating a 10% decline in postdeposition reproductive success with every 10 000 sockeye females. Although proportional data are often transformed to meet the assumption of normality, residual analyses indicated that no transformation was needed.

The three species exhibited different responses to heterospecific abundances. Stepwise multiple regression of sockeye total reproductive success against sockeye, chum, and pink abundance indicated that only conspecific abundance affected sockeye reproductive success ( $R^2 = 0.28$ ,  $F_{1,26} = 11.46$ ,  $P = 0.002$ ). In other words, there was no evidence of competitive effects of pink or chum on sockeye reproductive success. Chum reproductive success was best predicted by a model that included only sockeye abundance ( $R^2 = 0.285$ ,  $F_{1,26} = 13.7$ ,  $P = 0.008$ ) (Fig. 4). The slope of this relationship was slightly steeper than that observed for the intraspecific density-dependent effects on sockeye (slope =  $-1.73 \times 10^{-5}$ ), but the standard errors of these parameter estimates overlapped broadly. Chum abundance was not a

**Table 2.** Parameter estimates and negative log-likelihoods ( $L$ ) of best-fitting stock–recruit models for each salmon species.

Species	Linear		Beverton–Holt			Ricker		
	$\alpha$	$L$	$\alpha$	$\beta$	$L$	$\alpha$	$\beta$	$L$
Sockeye	$2.5 \times 10^{-3}$	-1.7	$6.9 \times 10^{-3}$	318	-6.98*	$3.2 \times 10^{-3}$	$1.7 \times 10^{-5}$	-6.90*
Chum	$1.6 \times 10^{-3}$	15.39	$9.4 \times 10^{-2}$	466	12.56*	$1.9 \times 10^{-3}$	$1.1 \times 10^{-4}$	13.26*
Pink	$8.8 \times 10^{-4}$	10.63	$4.6 \times 10^{-1}$	828	10.64	$1.1 \times 10^{-3}$	$3.3 \times 10^{-4}$	10.82

**Note:** Recruits expressed as millions of fry produced. An asterisk denotes a significantly better fit than the linear model ( $\alpha = 0.05$ ).

good predictor of chum total reproductive success when sockeye abundance was included in the model, suggesting that there was little intraspecific effect on chum reproductive success. There was no correlation between the proportion of chum females that spawned and sockeye abundance ( $R^2 = 0.00$ ) (Fig. 4). We did not regress postdeposition reproductive success versus sockeye abundance because removal of data points from the infectious haematopoietic necrosis virus years left only nine data points and insufficient statistical power. However, because there was little evidence that sockeye affected chum by reducing their egg deposition, we can infer that sockeye most likely affected chum by reducing the postdeposition reproductive success.

Total reproductive success of pink was best predicted by a model that included only chum female abundance ( $R^2 = 0.31$ ,  $F_{1,15} = 8.2$ ,  $P = 0.012$ ) (Fig. 5). This reduction was not attributable to a reduction in the proportion of spawning females, as there was no relationship between this parameter and chum abundance ( $F_{1,14} = 0.827$ ,  $P = 0.379$ ) (Fig. 5B). However, there was a significant reduction in postdeposition reproductive success attributable to chum abundance ( $R^2 = 0.34$ ,  $F_{1,15} = 9.27$ ,  $P = 0.008$ ) (Fig. 5C). The slope of this line was steep (slope =  $-1.44 \times 10^{-4}$ ) and was nearly an order of magnitude larger than the effect of sockeye on sockeye and chum postdeposition reproductive success. Further, the 95% confidence interval for the slope ( $-1.87 \times 10^{-4}$ ,  $-0.93 \times 10^{-4}$ ) did not overlap with the 95% confidence interval of the slopes of the sockeye postdeposition reproductive success versus sockeye spawner abundance ( $-1.34 \times 10^{-5}$ ,  $-0.79 \times 10^{-5}$ ) or the chum–sockeye regression ( $-2.19 \times 10^{-5}$ ,  $-0.13 \times 10^{-5}$ ).

## Discussion

Based on species-specific patterns of relative abundance, body size, and timing of salmon in WCSC, we predicted that sockeye (the most numerous species) would experience the greatest intraspecific competition whereas pink (the smallest, scarcest, and earliest spawning species) would experience the greatest interspecific competition. Because of their relative abundance, pink should have little effect on the reproductive success of either chum or sockeye whereas sockeye should have the greatest effect on heterospecific reproductive success. Chum, being the largest species, should not be affected by the smaller, earlier-spawning, and generally scarce pink. Chum should also be too scarce to display intraspecific effects, but they might be affected by sockeye, which were much more abundant but are smaller and spawn slightly earlier than chum.

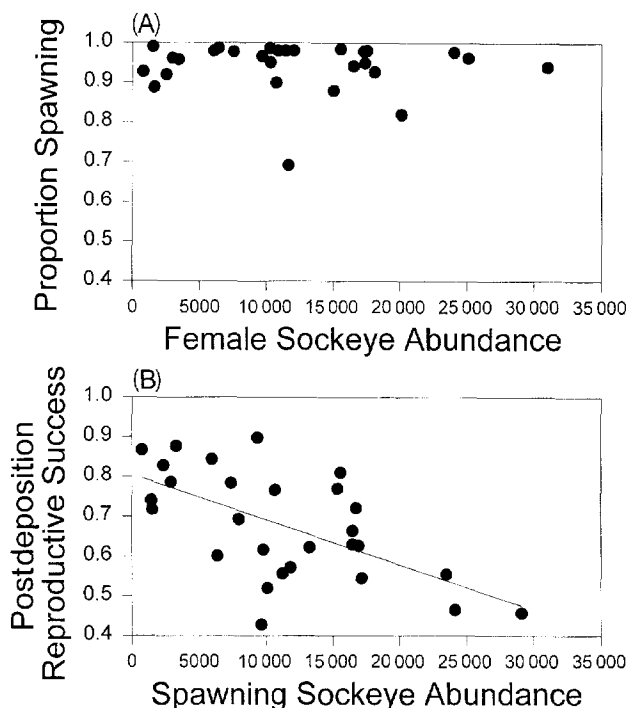
Consistent with the predictions, sockeye were the only species to experience any intraspecific competition, and they were not affected by heterospecifics. The Ricker and

Beverton–Holt spawner–recruit models were three orders of magnitude more likely than the linear model, clearly indicating that reproductive success was reduced at high densities. Further, linear regression predicted that mean sockeye reproductive success is reduced 50% at high spawner densities. As predicted, pink had no effect on the reproductive success of sockeye or chum, most likely because they were too small, too scarce, and spawn too early to dig up many redds of the other species. Chum, despite being larger than sockeye, were affected by them, presumably because sockeye were very numerous and the timing of spawning overlapped. Chum recruitment was slightly correlated with conspecific abundance, but this correlation vanished after accounting for the effects of sockeye. The lack of significant density dependence likely reflects the fact that chum abundance was, on average, one sixth that of sockeye.

Contrary to our expectations, pink were unaffected by the abundance of sockeye ( $F_{1,15} = 0.847$ ,  $P = 0.372$ ). Because of their early spawning date and small size, we expected pink to be highly susceptible to redd superimposition and experience large reductions in reproductive success as a function of sockeye and, to a lesser extent, chum abundance. However, there was no correlation between pink reproductive success and sockeye abundance. There are several plausible explanations for this result. One possibility is that our statistical power was too small to detect significant effects. Pink were only present during odd-numbered years; thus, there were only half as many observations as for the other species. However, this explanation seems unlikely. Because WCSC is operated to provide ideal physical habitat, variation in reproductive success due to abiotic factors is minimal. Moreover, there was a fourfold range in sockeye abundance, providing a more than adequate range to detect significant correlations. Thus, the lack of statistical significance likely reflects an absence of ecologically significant effects.

One explanation for the absence of a negative interaction between pink and sockeye is that there are isolating mechanisms that reduce interspecific interactions. For example, differences in habitat preferences may give rise to spatial segregation of spawning sites. Because these species differ in mean body size and egg size, their optimal spawning habitats may also differ. Fukushima and Smoker (1998) reported that pink and sockeye exhibited only small differences in microhabitat preferences, yet spawned in very different areas of Lake Creek, Alaska. Alternatively, size-mediated aggression between females may result in spatial segregation of redd sites. Territoriality in spawning salmonids, especially females, is common and territorial disputes are typically won by larger females (Foote 1990), especially if neither is in possession of the territory. Further, the sockeye females were always more abundant than pink females, even early in the spawning period when pink channel entries were at their

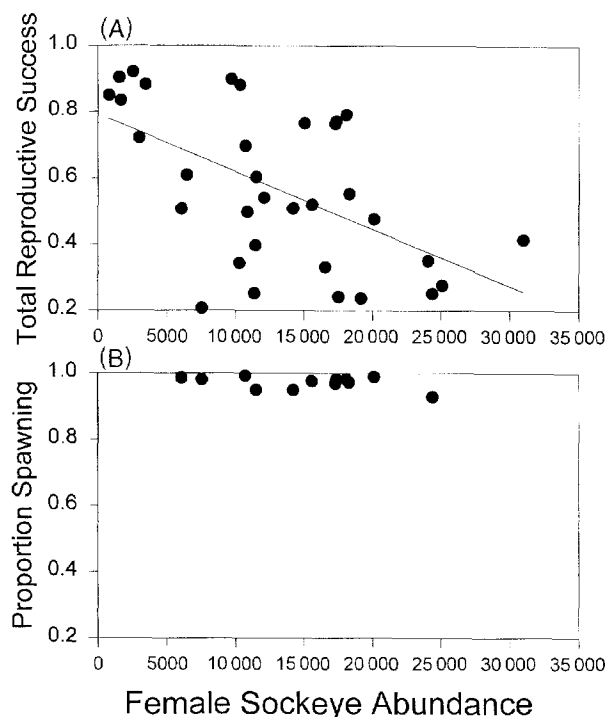
**Fig. 3.** Effect of female sockeye salmon abundance on the (A) proportion of sockeye females that spawned and (B) postdeposition reproductive success (fry produced per deposited eggs). There was a significant reduction in postdeposition reproductive success with increasing sockeye abundance but no effect of sockeye abundance on the proportion of females that spawned.



peak. Thus, all three species might seek the same habitat, but the larger chum and sockeye might displace pink into less desirable habitat. Because these habitats are less likely to be used by later-spawning chum or sockeye, they are less susceptible to redd superimposition.

Both hypotheses predict nonrandom distributions of the species throughout the channel. Although designed to provide uniformly suitable habitat, the channel cannot be homogeneous. There are edges and a thalweg in the channel, and there are deeper, slower sections associated with its 180° bends and low, in-channel structures built to increase oxygenation, in addition to the long stretches of more uniform depth typical of most of the channel. It was beyond the scope of this study to document the spatial distribution of the species, but behavioral observations of hundreds of courting pairs of salmon have indicated that pink and chum tend to build redds in the vicinity of conspecifics and that interspecific aggression among females is common (Quinn 1999). Those spatial distribution data are consistent with both hypotheses whereas the aggression data are more consistent with the second hypothesis. Under the first hypothesis, reproductive success of all species would be similar, whereas under the second, the average reproductive success of pink might be lower than that of the other species if they were forced to use inferior habitat. Although there were differences in total reproductive success between pink (mean = 0.51), sockeye (mean = 0.61), and chum (mean = 0.57), these differences were not significant (ANOVA of arcsine square root transformed data,  $F_{1,63} = 2.6$ ,  $P = 0.11$ ). More-

**Fig. 4.** Effect of female sockeye salmon abundance on (A) chum salmon total reproductive success and (B) proportion of female chum that were 100% spawned. There was a significant reduction between chum total reproductive success and sockeye abundance but no effect of sockeye on the proportion of chum that spawned.

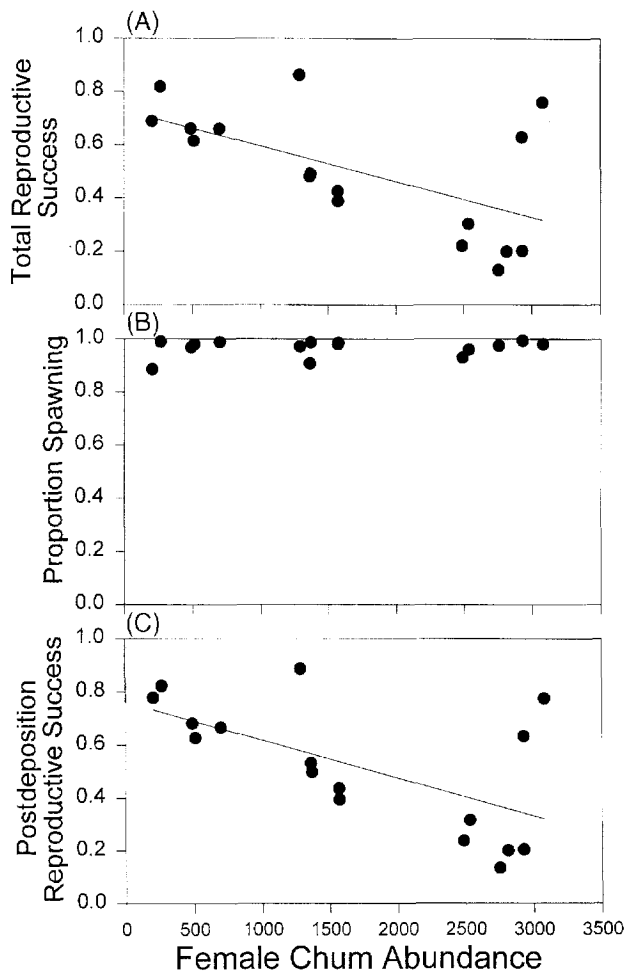


over, Fukushima and Smoker (1998) found no evidence that pink redd site selection was influenced by sockeye abundance. Thus, the hypothesis that differences in body size resulted in habitat segregation appears unlikely.

Even with rather long and very accurate data sets, it was difficult to distinguish between Ricker and Beverton–Holt patterns of density dependence. That is, it was unclear whether fewer (Ricker) or the same (Beverton–Holt) number of recruits were produced at high densities as were produced at intermediate adult densities. This partly reflects the limitations of these data; the number of females entering the channel is controlled to avoid overcrowding, so we do not have fry production data for very high spawner abundances. However, it is interesting that we failed to find evidence to support a dome-shaped spawner–recruit relationship over an asymptotic curve despite a 40-fold range of sockeye spawner abundance. This suggests that if density dependence is of the Ricker type, it is only severe enough to cause a dome-shaped spawner–recruit curve at very high spawner abundances.

The importance of intra- and inter-specific competition in Pacific salmon species will vary from site to site and from year to year according to the relative abundance of salmon and the amount of suitable habitat available. Even so, this study under controlled conditions indicates the potential for interspecific competition among sockeye and chum. It also suggests that the fitness consequences of the competition observed in Weaver Creek result primarily from redd superimposition. The mechanisms and potential for interspecific competition identified in Weaver Creek should generalize to

**Fig. 5.** Effect of female chum salmon abundance on (A) pink salmon total reproductive success, (B) proportion of female pink that were 100% spawned, and (C) pink postdeposition reproductive success. Total reproductive success and postdeposition reproductive success were reduced at increasing chum abundances, but the proportion spawning was unaffected by chum abundance.



other natural situations, provided the spawning habitat and densities are not too artificial. Female salmon density at WCSC averaged  $0.83 \text{ female}\cdot\text{m}^{-2}$  during 1965–1997. This density exceeds the  $0.5 \text{ female}\cdot\text{m}^{-2}$  that Burgner et al. (1969) concluded was the general carrying capacity for Bristol Bay stream spawning areas. However, the WCSC density is not unprecedented for wild populations. Densities of  $0.7$  and  $0.8 \text{ female}\cdot\text{m}^{-2}$  were documented by Quinn and Foote (1994) and McPhee and Quinn (1998), respectively, in two sockeye populations in Alaska. Fleming and Gross (1989) documented female coho salmon (*Oncorhynchus kisutch*) density in 11 northwestern streams and reported a mean density in suitable spawning habitat of  $0.72 \text{ female}\cdot\text{m}^{-2}$ . Thus, the processes operating in the channel may be comparable with those in other areas of high-quality habitat and high salmon densities.

The survival rates from egg deposition to emergence were considerably higher than typical survival rates in natural channels. Rosberg et al. (1986) reported that egg to fry survival rates in the spawning channel are approximately an order of magnitude greater in Weaver Creek proper. Foerster (1968) reviewed survival to emergence studies on sockeye

and concluded that 10% survival was typical (versus 57–69% in this study). Survival to emergence of chum averaged 14% in the Fraser River (Beacham and Starr 1982), 22% prior to logging in Carnation Creek (Scrivener and Brownlee 1989), and 5.6% in Hooknose Creek (Hunter 1959). Heard (1991) concluded that "...survival of pink salmon from egg to alevin, even in highly productive streams, commonly reaches only 10–20%...." Presumably, the lower survival rates in natural systems, compared with the WCSC, result from such factors as floods that scour the gravel and damage or dislodge embryos (McNeil 1966; Seegrist and Gard 1972; Thorne and Ames 1987), poor circulation from low flow and small substrate size (Chapman 1988), low dissolved oxygen (McNeil 1966), and predation (Hunter 1959; Phillips and Claire 1966), all of which are minimized in the WCSC. Although these factors affect the survival of embryos in natural systems, they do not preclude the effects of competition. Rather, they are additional effects and also serve to mask the effects of competition by introducing variability into data sets.

We believe that interspecific competition among adults can be an important factor in salmon population dynamics in the many cases of sympatric spawning. Spawning date may dictate the direction of asymmetric competitive effects by facilitating disturbance of one species' redds by species spawning afterward. However, these effects may be mitigated by differences in habitat use. The Pacific salmon species have ranges that overlap broadly but do not coincide (Groot and Margolis 1991), presumably for a variety of reasons. Within the area of overlap, few streams support all species. Some patterns of habitat use are clearly related to the species-specific feeding and migration patterns of juveniles, e.g., the affinity of sockeye for streams flowing into lakes and coho for streams with pools and complex channel structure (Groot and Margolis 1991). In other cases, salmon body size or swimming performance may be matched to the depth and velocity of the river. At a still finer scale, patterns of microhabitat preference (e.g., depth, velocity, substrate, cover) may segregate the species. It is unclear to what extent this segregation reflects past competition and present preferences.

In summary, competitive interactions had profound effects on the population-level reproductive success of sympatric salmonids. In the WCSC, sockeye and chum reproductive success was reduced by 50% in response to variations in sockeye abundance. However, the magnitude of interspecific effects may depend on relative body size, spawning date, and habitat use patterns within the spawning grounds as a whole. Interspecific competition by adults probably has very important effects on the dynamics and evolution of salmon populations, although these effects are hard to document owing to the many other factors affecting habitat use by adults and survival to emergence of their progeny.

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