

A review of size trends among North Pacific salmon (*Oncorhynchus* spp.)

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Abstract: The abundance of North Pacific salmon (*Oncorhynchus* spp.) has nearly doubled during the period 1975–1993. As salmon population numbers have increased, there have been corresponding decreases in average adult size at return (maturity). As nearly all of the growth of Pacific salmon occurs in the ocean, the ocean plays an important role in determining salmon abundance. We found that 45 of 47 North Pacific salmon populations, comprising five species from North America and Asia, are decreasing in average body size. Total salmon production correlated well with environmental trends between 1925 and 1989, but the inverse relationship between population abundance and average size during the period 1975–1993 indicates that there is a limitation to the salmon-sustaining resources of the ocean. The increased ocean survivorship and expansion of enhancement programs in the 1980s and early 1990s are probable factors in the ocean-wide reduced size of salmon. If these trends continue, the productivity of salmon populations may decrease as fecundity, egg size, and age at maturity change in response.

Résumé : L'abondance des saumons du Pacifique nord (*Oncorhynchus* spp.) a presque doublé au cours de la période de 1975 à 1993. À mesure que la population de saumons a croissé, on a noté une diminution correspondante de la taille moyenne des adultes lors de la remonte (à maturité). Comme presque toute la période de croissance des saumons se déroule dans l'océan, ce dernier joue un rôle important dans l'abondance de ces poissons. Nous avons constaté une diminution de la taille corporelle moyenne chez 45 des 47 populations de ces saumons, qui comprennent cinq espèces de l'Amérique du Nord et de l'Asie. La production totale de saumons était assez bien corrélée avec les tendances environnementales de 1925 à 1989, mais la relation inverse entre l'abondance de la population et la taille moyenne observée de 1975 à 1993 indique l'existence d'une limitation des ressources de l'océan supportant le saumon. Le taux de survie accru dans l'océan et l'élargissement des programmes de mise en valeur au cours des années 1980 et au début des années 1990 sont des facteurs probables de la réduction de la taille du saumon observée dans toutes les parties de l'océan. Si ces tendances persistent, la productivité des populations de saumons pourrait diminuer en réponse aux changements de la fécondité, de la taille des oeufs et de l'âge du poisson à maturité.

[Traduit par la Rédaction]

Introduction

Advances in population management, artificial enhancement, and favorable ocean conditions have more than doubled the population of salmon (*Oncorhynchus* spp.) in the North Pacific Ocean over the past 20 years (Rogers 1994) (Fig. 1). There is a growing body of evidence, however, that some North Pacific salmon populations have decreased in average size at maturity as ocean abundance has increased.

Studies of reduced growth among Pacific salmon have been relatively few and limited to individual spawning populations or species. Kaeriyama (1989, 1996), Kaeriyama and Urawa (1992), Ishida et al. (1993), and Hayashizaki and Hitoshi (1996) have documented decreases in the average size of Asian chum salmon (*Oncorhynchus keta*) in recent years. Similarly, Helle and Hoffman (1995) have documented age-

specific declines in the average size of two North American chum salmon populations.

Because the ocean distributions of Pacific salmon populations overlap (Myers et al. 1990), significant trophic interaction among, and within, species could result in the expression of density-dependent growth if food is limiting. Some evidence exists for an inverse relationship between the growth of sockeye salmon (*Oncorhynchus nerka*) and the ocean abundance of that species (Rogers 1980; Peterman 1984). Similar findings have been reported for pink salmon (*Oncorhynchus gorbuscha*) (Foerster and Pritchard 1941; Davidson and Vaughan 1941; Ricker et al. 1978), coho salmon (*Oncorhynchus kisutch*) (Ricker and Wickett 1980; van den Berghe and Gross 1989), and chinook salmon (*Oncorhynchus tshawytscha*) (Ricker 1980, 1981). At least two hypotheses have been advanced that can explain declining body size: density-dependent growth, and selection of larger, older fish by selective fisheries.

While various authors have reported evidence that salmon size has decreased in the recent past, there is evidence of both increasing and decreasing average body size over longer periods. The age-specific size at maturity of chum salmon declined slightly from 1959 to 1978 in Prince William Sound, Alaska (Helle 1979). Godfrey (1959a) found that the average weight of British Columbia pink salmon increased from 1944 through 1958, and there was a similar increase in the average weight

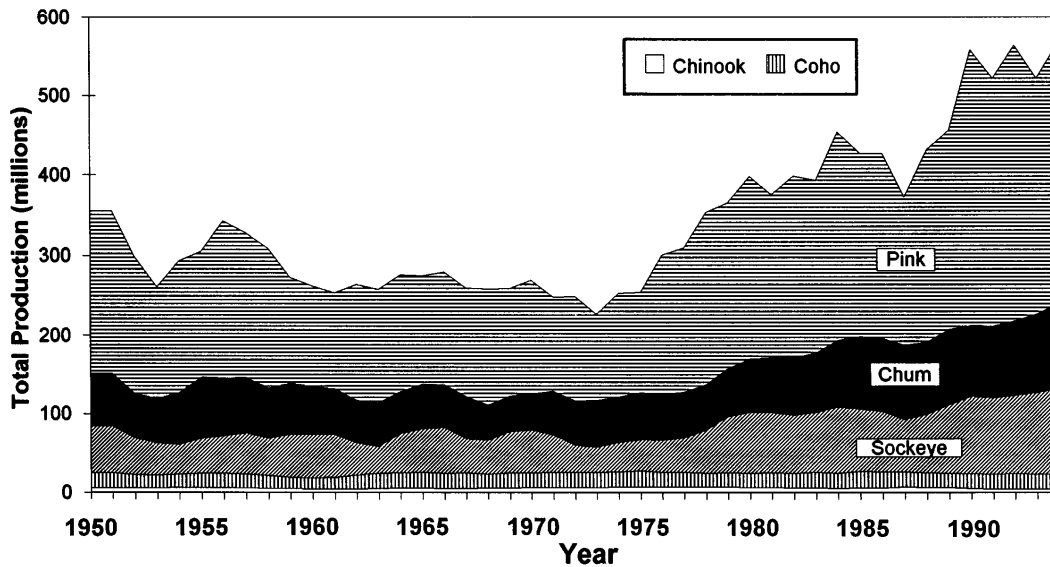
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Fig. 1. Total North Pacific Ocean salmon production, 1951–1994. Data from D. Rogers, Fisheries Research Institute, University of Washington, Seattle, WA 98195.



of chum salmon from 1946 through 1958 (Godfrey 1959b). Conversely, Ricker et al. (1978) found that the average size of British Columbia pink salmon decreased subsequent to the period reported by Godfrey (1951–1974). Ricker (1981) reported coincident changes in age and decreasing size among all Pacific salmon species intercepted in the commercial fisheries of British Columbia since the early 1950s, but found differing results in a subsequent study (Ricker 1994).

As growth rates decrease, many life history traits that affect population productivity also decrease (Forbes and Peterman 1994). Reduction in fecundity and egg size, increases in mean age at reproduction, or the ability to migrate upstream and spawn with optimal success all influence population productivity and therefore harvest rates. Helle (1989), for example, found that the mean size (length) of chum salmon spawners is positively related to the survival of their progeny. If this relationship applies more generally, declines in size could reduce survival. We present a survey of reported associations between growth rate and other density-related population responses in Pacific salmon. We also examine temporal trends in size and age and review data on fecundity and egg size.

Materials and methods

A variety of state, provincial, and federal governmental agencies in North America provided average weight and other data for five Pacific salmon species to test for trends in average size (Fig. 2). Additional summary data were available from published reports (Ishida et al. 1993; Welch and Noakes 1993). Pacific salmon abundance nearly doubled in the period 1975–1993 compared with that in the period 1950–1975 (Fig. 1). Analyses are confined to data characterizing the years 1975–1993.

Several authors reporting on temporal changes in body size favor linear regression analysis (e.g., Ricker 1981; Kaeriyama 1989; Ishida et al. 1993). Fundamental to the generation of unbiased regression statistics is the assumption that error terms are random. Because salmon return to spawning rivers after 1 to several years at sea, those harvested in nearshore fisheries comprise portions of brood cohorts resulting from several spawning seasons. Though not true in every

case, it is not unusual for the year to year average size of salmon to follow cyclical, nonrandom patterns over time. Data that follow such patterns are often autocorrelated and do not always fit a linear regression model without inefficient estimation of slope and underestimation of slope standard error (J. Pella, National Marine Fisheries Service, 11 305 Glacier Highway, Juneau, AL 99801, personal communication). As a result, the risk of rejecting the null hypothesis (that slope is zero) is higher. The simple linear regression model with the random error terms following an autoregressive process is $Y_t = \beta_0 + \beta_1 X_t + \varepsilon_t$, where $\varepsilon_t = \rho \varepsilon_{t-1} + u_t$. Each error term ε_t in this model consists of a fraction of the previous error term $\rho \varepsilon_{t-1}$ plus a disturbance term u_t .

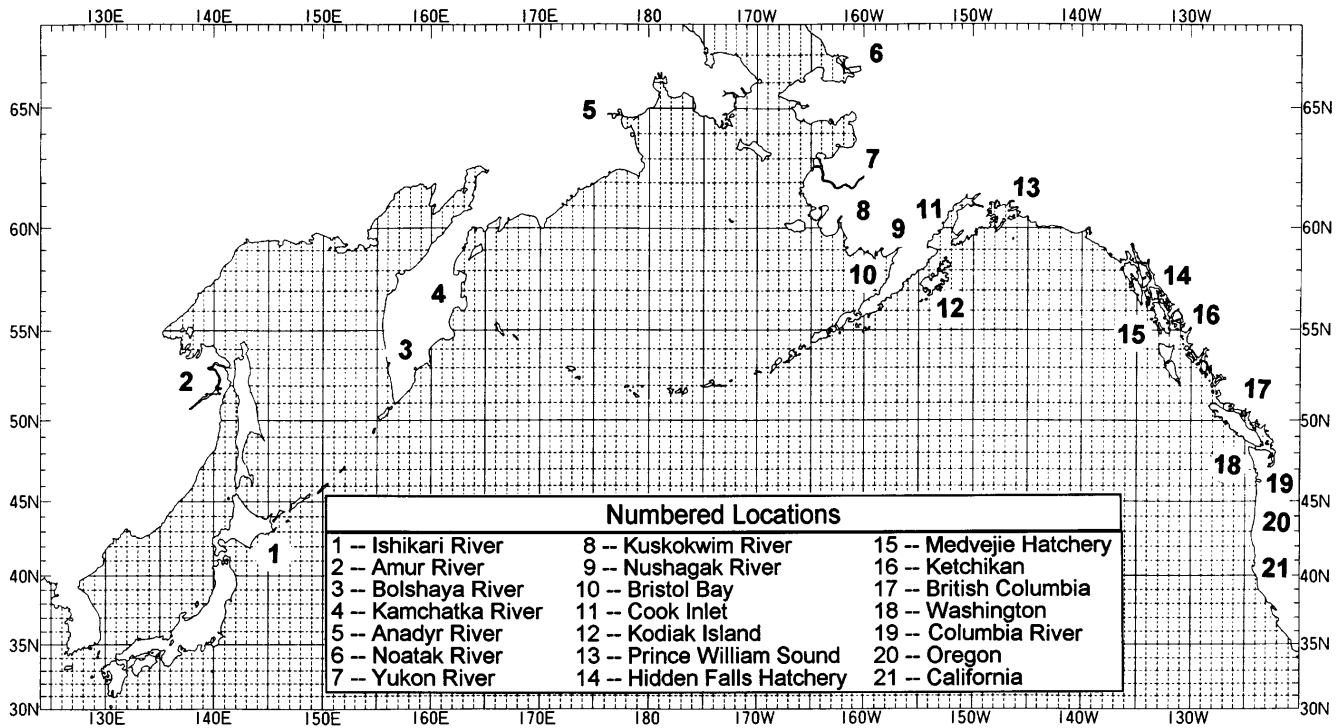
Autocorrelation was tested following the procedure of Neter et al. (1985) to calculate unbiased regression statistics. The slope of generated regressions, expressed as b throughout this document, is the calculated average annual change in the variable tested.

Data sources

Size-at-return data (weight or length) are based on summaries of commercial harvest information collected by state and federal government agencies, and data summaries from the Pacific Biological Station, Nanaimo, British Columbia (Welch and Noakes 1993), and the University of Washington (Rogers 1994). Chum salmon fecundity and egg size data were supplied by state and private hatcheries in Oregon and Alaska. Other unique data sources are identified when referenced. Where possible, data from less selective fishing gear (seine, troll) were used.

The Pacific Fishery Management Council Review of Fisheries summarizes data on dressed weight of troll-caught chinook and coho in the states of California, Oregon, and Washington (Rod Kaiser, Oregon Department of Fish and Wildlife, 2040 Southeast Marine Science Drive, Newport, OR 97365, personal communication). California, Oregon, and Washington troll fishery data for the month of August were selected for analysis because chinook average weights were highest during August, indicating that mature salmon comprised the highest proportion of the catch, and because data are available for all years.

The Oregon Department of Fish and Wildlife (ODFW) provided data on average size at return, fecundity, and egg size for Columbia River salmon returning to hatcheries (John Leppink, Hatchery Data

Fig. 2. Locations of salmon populations tested for changes in average weight, length, age, or ancillary information.

Coordinator, ODFW, P.O. Box 59, Portland, OR 97207, personal communication). The average sizes of salmon in Columbia River commercial harvests were taken from published data (Oregon Department of Fish and Wildlife 1993).

Welch and Noakes (1993) reported average size data for all salmon species in British Columbia. Ricker (1994) reported a comprehensive analysis of these data.

The Alaska Department of Fish and Game provided average weight data for each species harvested in the following nearshore commercial fisheries: Kotzebue Sound, Yukon River, Kuskokwim River, Bristol Bay, Kodiak Island, Cook Inlet, and Ketchikan (Herman Savikko, Alaska Department of Fish and Game, P.O. Box 25526, Juneau, AL 99802-5526, personal communication).

Several hatcheries in Alaska provided average size, fecundity, and egg size data (Steve McGee, Alaska Department of Fish and Game, P.O. Box 25526, Juneau, AL 99802-5526, personal communication; Bruce Bachen, Northern Southeast Regional Aquaculture Association, 1308 Sawmill Creek Road, Sitka, AL 99835, personal communication; Peter Rob, Sikusuilq Springs Hatchery, P.O. Box 1030, Kotzebue, AL 99752, personal communication). Sikusuilq Springs Hatchery on the Noatak River in northwest Alaska has produced fall chum salmon since 1982. Hidden Falls and Medveje hatcheries in southeast Alaska provided fecundity data collected since 1986 and 1988, respectively. The Port San Juan Hatchery in Prince William Sound, Alaska, provided 14 years of average fecundity information.

Decreases in average size for chum salmon populations can be confounded by variability in age at return. An increasing number of older, larger fish (Helle and Hoffman 1995) will tend to mask the overall decrease in average body size. Age-specific size data covering the period under review are not generally available. Pink salmon return at 2 years of age and coho salmon generally return at age 3; however, there is probably little likelihood that variation in age at return will be confounded with variation in growth rate because these species always spend only one summer (two winters) at sea. Chinook, sockeye, and chum salmon return to natal streams following one to several winters at sea. There are sufficient data to examine changes in age-specific growth rates for chinook from the Yukon, Kuskokwim,

and Kenai rivers, Yukon River fall and summer chum, and Bristol Bay and Kenai River sockeye.

A decrease in average body size results in a smaller volume and decreasing fecundity (Bagenal 1969; Beacham and Murray 1987; Helle 1989; Fleming and Gross 1990). Although a direct relation with body size (weight) is assumed, fecundity and egg size are not regularly measured for wild salmon populations in western Alaska. Data from Columbia River coho, Sikusuilq Springs (Noatak River; Kotzebue, Alaska) chum and Hidden Falls and Medveje (southeast Alaska) chum, and Prince William Sound pink salmon hatchery populations are available (Fig. 2).

Results

Among five species of Pacific salmon, 45 of 47 populations tested decreased in mean size between 1975 and 1993 (Table 1, Figs. 3–7). Only California and British Columbia chinook salmon failed to show an inverse association between size and time.

Chinook salmon

Chinook salmon migrate to sea after spending up to two winters in fresh water; they then return to spawn zero to five winters later. Among nine populations of chinook salmon tested, the calculated average weights of chinook in California and British Columbia increased 25 and 45%, respectively, between 1975 and 1993 (Table 1, Fig. 3). Body size decreased in all other populations tested, from 10 to 47%. The decline in body weight was least for Oregon chinook (0.047 kg/year) and greatest for Kuskokwim River chinook (0.162 kg/year) (Table 1).

Age-specific length data collected with the Yukon River commercial fisheries and Kenai River sport fishery corroborate

Table 1. Trends in mean weight (kg) of North Pacific salmon populations.

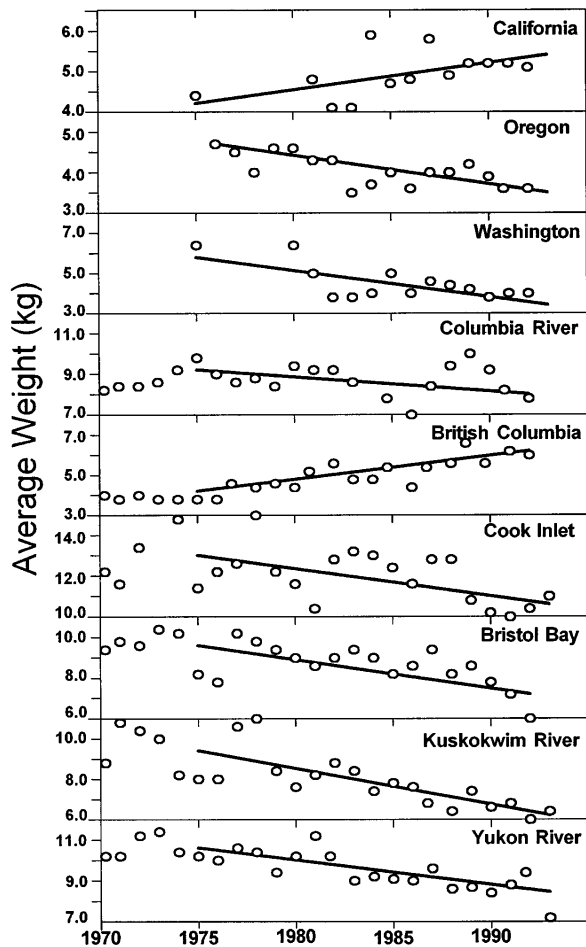
Region	Area or fishery	<i>n</i>	<i>r</i>	<i>b</i>	Calculated weight		% change
					1975	1993	
Chinook							
California	Troll fishery	12	0.439	0.058	4.21	5.25	24.70
Oregon	Troll fishery	17	-0.627**	-0.047	4.61	3.76	-18.44
Washington	Troll fishery	14	-0.747**	-0.161	6.21	3.31	-46.70
	Columbia River	18	-0.568*	-0.054	9.16	8.19	-10.09
British Columbia	Troll fishery	18	0.761**	0.105	4.15	6.04	45.54
Alaska	Cook Inlet	19	-0.566*	-0.106	12.82	10.91	-14.90
	Bristol Bay	19	-0.637**	-0.136	9.59	7.14	-25.55
	Kuskokwim River	19	-0.761**	-0.162	9.27	6.35	-31.50
	Yukon River	19	-0.670**	-0.102	10.43	8.60	-17.55
Coho							
California	Troll fishery	12	-0.316	-0.024	3.17	2.74	-13.56
Oregon	Troll fishery	17	-0.588*	-0.043	2.84	2.07	-27.11
Washington	Troll fishery	14	-0.693**	-0.044	2.56	1.77	-30.86
	Columbia River	18	-0.737**	-0.059	3.90	2.83	-27.44
British Columbia	Troll fishery	18	-0.600**	-0.035	3.15	2.52	-20.00
Alaska	Kodiak	19	-0.500*	-0.025	4.01	3.57	-10.97
	Bristol Bay	19	-0.378	-0.017	3.46	3.16	-8.67
	Kuskokwim River	19	-0.560*	-0.018	3.40	3.07	-9.71
	Yukon River	17	-0.374	-0.012	3.21	2.99	-6.85
Chum							
Washington	Columbia River	18	-0.564*	-0.075	6.12	4.84	-20.92
British Columbia	Seine or gill net	18	-0.521*	-0.046	5.45	4.63	-15.05
Alaska	Ketchikan	19	-0.570*	-0.035	4.50	3.87	-14.00
	Cook Inlet	19	-0.627**	-0.029	3.64	3.10	-14.84
	Kodiak	19	-0.637**	-0.036	3.92	3.28	-16.33
	Bristol Bay	19	-0.280	-0.005	3.00	2.91	-3.00
	Kuskokwim River	19	-0.460*	-0.013	3.26	3.02	-7.36
	Yukon River (summer)	16	-0.144	-0.003	3.22	3.17	-1.55
	Yukon River (fall)	16	-0.765**	-0.030	3.59	3.02	-15.88
	Kotzebue Sound (fall)	19	-0.545*	-0.018	4.13	3.80	-7.99
Russia	Anadyr River	11	-0.720*	-0.083	4.69	3.20	-31.77
	Kamchatka River	16	-0.650**	-0.029	3.88	3.35	-13.66
	Bolshaya River	15	-0.502	-0.039	4.02	3.33	-17.16
	Amur River (summer)	16	-0.546*	-0.016	2.66	2.37	-10.90
	Amur River (fall)	18	-0.627**	-0.048	4.89	4.03	-17.59
Japan	Ishikari River	16	-0.646**	-0.048	3.72	2.85	-23.39
Pink							
British Columbia	Seine or gill net	18	-0.505*	-0.030	1.97	1.43	-27.41
Alaska	Ketchikan	19	-0.710**	-0.030	1.89	1.36	-28.04
	Prince William Sound	15	-0.529*	-0.015	1.64	1.37	-16.46
	Cook Inlet	19	-0.760**	-0.020	1.73	1.37	-20.81
	Kodiak	19	-0.722**	-0.021	1.82	1.45	-20.33
	Bristol Bay	19	-0.676**	-0.020	1.91	1.56	-18.32
Sockeye							
British Columbia	Seine or gill net	18	-0.039	-0.002	2.58	2.55	-1.16
Alaska	Ketchikan	19	-0.315	-0.008	2.77	2.64	-4.69
	Cook Inlet	19	-0.474*	-0.027	3.05	2.70	-11.48
	Kodiak	19	-0.665**	-0.027	2.85	2.37	-16.84
	Bristol Bay	19	-0.136	-0.003	2.71	2.66	-1.85

Note: *n*, number of years; *r*, correlation coefficient; *b*, regression slope (average annual change in weight). Predicted values for 1975 and 1993 are based on linear regression, and were used to calculate the percent change. Data for chum salmon from Russia and Japan are taken from Ishida et al. (1993), and predicted values are for the years 1970 and 1988.

* $P < 0.05$

** $P < 0.01$.

Fig. 3. Mean weight of chinook salmon sampled from nine North American commercial fisheries.



these findings (Table 2, Fig. 8). All age groups tested decreased by approximately 3–5% of body length.

The mean age at return of Kuskokwim River chinook salmon decreased over the period 1975–1993, while the age of Yukon River chinook remained essentially unchanged and Kenai River chinook increased in mean age over the period examined (Table 2, Fig. 8).

Coho salmon

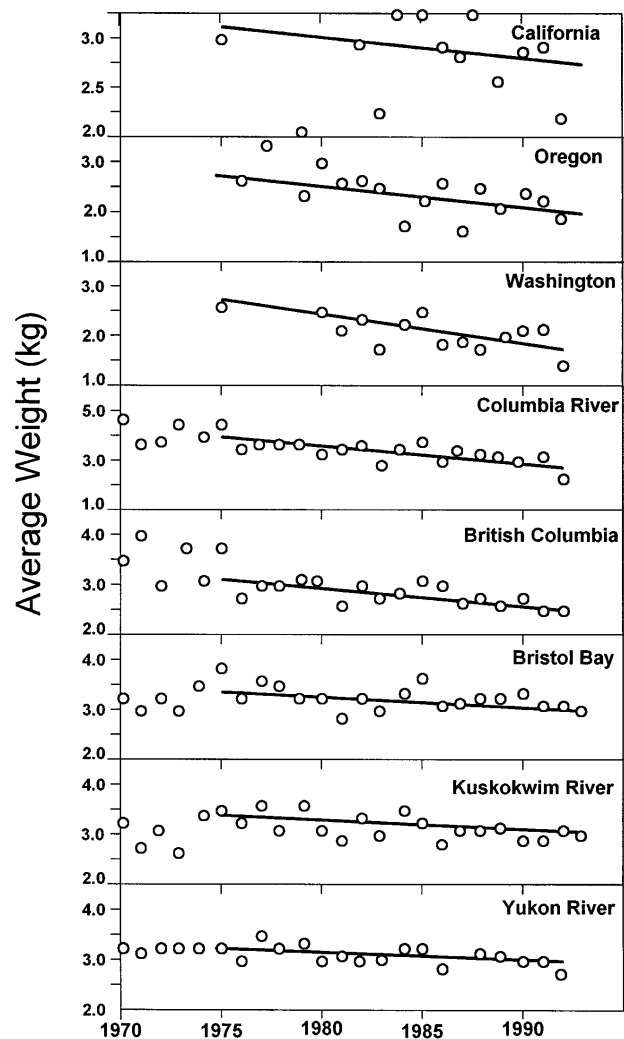
The majority of coho salmon are captured during their third or fourth year of life after spending two winters, or one summer, at sea. All populations tested showed decreased average body weight ranging from -0.012 to -0.059 kg/year (Table 1, Fig. 4).

Chum salmon

Chum salmon characteristically migrate to sea soon after fry emergence, and return from two to five winters later. Chum salmon among the 10 populations examined declined in average weight from 0.003 kg/year for Yukon River summer chum to 0.075 kg/year for Columbia River chum (Table 1, Fig. 5).

Age-specific data for Yukon River fall and summer chum show that as average size at age decreased, the mean age at return increased. The average lengths of each age group of

Fig. 4. Mean weight of coho salmon sampled from eight North American commercial fisheries.



summer and fall chum decreased similarly, at rates of 2–4% over 1975–1993 (Table 3, Fig. 9). Summer chum age increased from 3.0 to 3.8 years, while fall chum increased from 2.9 to 3.4 years.

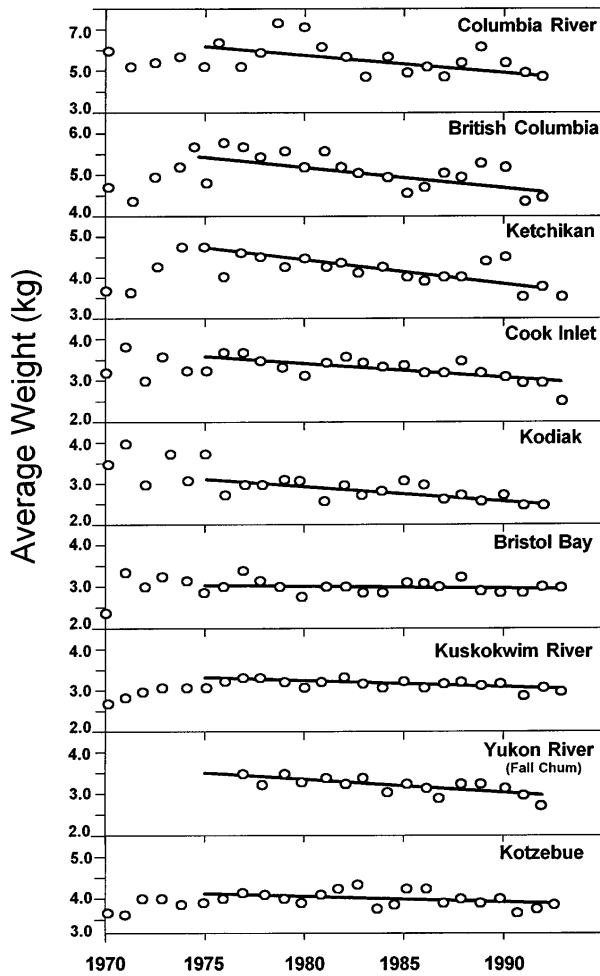
Pink salmon

Pink salmon follow a 2-year life cycle, spending one winter at sea. The average weights of North American pink salmon populations have decreased at a relatively uniform rate of approximately 0.020 kg/year, or about 20% from 1975 to 1993 (Table 1, Fig. 6). The decline is most notable in British Columbia where the declining trend has continued since the early 1950s (Ricker et al. 1978); currently British Columbia pink salmon are approximately 1 kg (40%) smaller than in the 1950s (Ricker 1994).

Sockeye salmon

The sockeye salmon life history is very plastic, with fish spending from zero to three winters in fresh water and one to four winters at sea. Though regression slopes are uniformly negative, only two of five sockeye salmon populations tested

Fig. 5. Mean weight of chum salmon sampled from nine North American commercial fisheries.



showed statistically significant ($P < 0.05$) declines (Table 1, Fig. 7). Sockeye salmon harvested from Kodiak Island and Cook Inlet decreased by 0.027 kg/year (16.8 and 11.5%, respectively) from 1975 to 1993.

Age-specific length measurements for sockeye salmon caught in the Cook Inlet and Bristol Bay gill-net fisheries show similar tendencies in declining length and weight, respectively (Table 4, Fig. 10). The average ocean age of these sockeye salmon gradually increased as growth rates declined and a smaller proportion of young fish returned with time (Table 4).

Fecundity and egg size

Fecundity and egg size data collected from hatchery populations are well suited for basic comparison with wild salmon stocks. Fecundity declined among all hatchery populations tested (Fig. 11). The egg sizes of coho salmon and fall and summer chum showed a significant decrease with decreasing fecundity (Fig. 12).

Discussion

Maximization of natural production and advances in artificial enhancement techniques have assisted in the near doubling of salmon harvests over the past two decades. As North Pacific

Fig. 6. Mean weight of pink salmon sampled from six North American commercial fisheries.

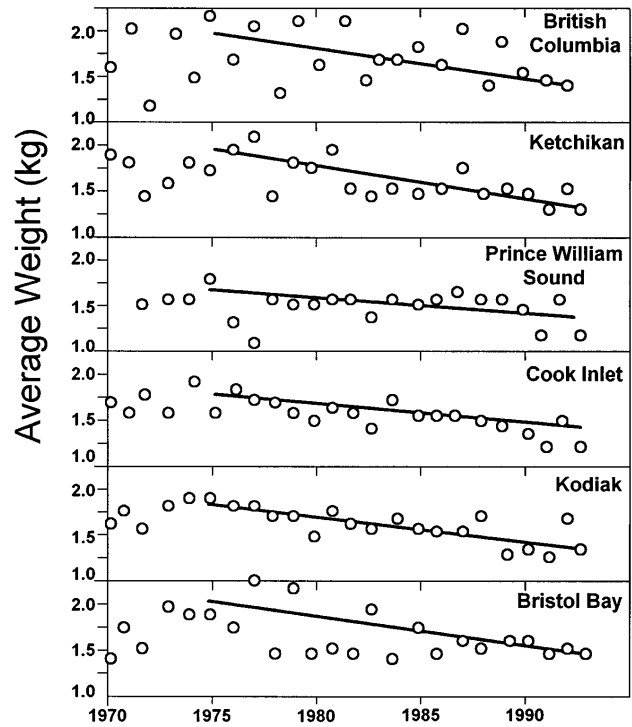
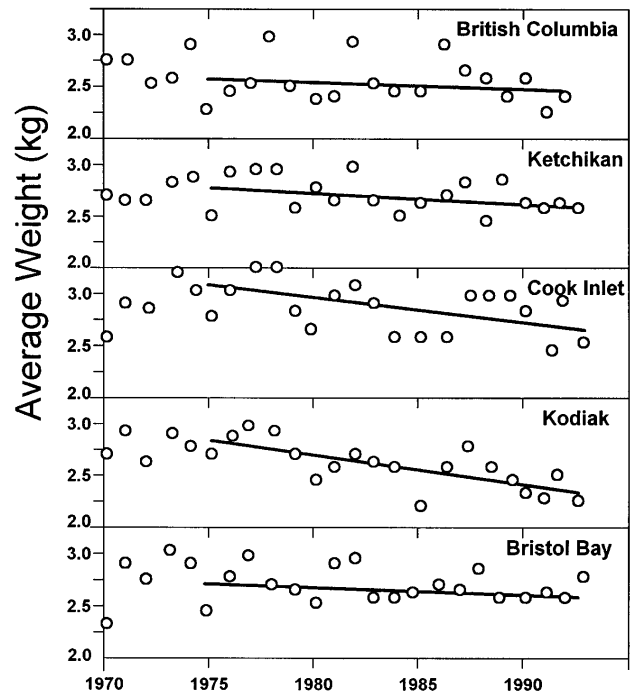


Fig. 7. Mean weight of sockeye salmon sampled from five North American commercial fisheries.



salmon population numbers have expanded, there has been a coincident decrease in average adult size and an increase in average age at maturity.

The changes in both average size and age for western

Table 2. Trends in age-specific mean length (mm) and average age (years) of selected North Pacific chinook salmon populations.

Population	Age group	n	r	b	Calculated values			% change
					1975	1979	1993	
Length								
Yukon River	3-ocean	14	-0.658*	-2.16		789.9	759.7	-3.82
	4-ocean	14	-0.485	-1.74		885.0	860.7	-2.75
	5-ocean	13	-0.508	-4.11		965.5	912.1	-5.53
Kenai River	3-ocean	17	-0.444	-4.25	905.0		828.5	-8.50
	4-ocean	17	-0.742**	-6.52	1102.5		985.0	-10.70
	5-ocean	17	-0.545*	-5.88	1169.4		1063.6	-9.00
Age								
Yukon River	Ocean age	19	0.078	0.002	3.69		3.77	2.17
Kuskokwim River	Ocean age	19	-0.821**	-0.049	3.64		2.76	-24.18
Kenai River	Ocean age	16	-0.731**	-0.039	3.30		4.00	20.90

Note: n, number of years considered; r, correlation coefficient; b, regression slope (average annual change in weight). The calculated values (lengths for the length section of the table, and ages for the age section of the table) were computed from available data.

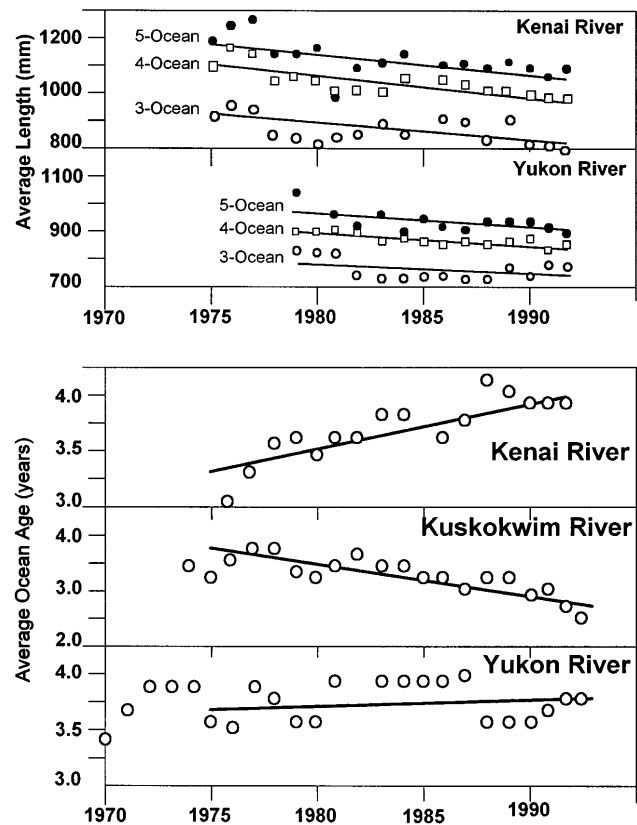
*P < 0.05.

**P < 0.01.

Alaska chum salmon mirror those for Japanese and Russian stocks reported by Ishida et al. (1993), and for two other North American populations reported by Helle and Hoffman (1995). Ishida et al. (1993) observed a depressed growth rate during the third year of life among both Japanese and Russian chum salmon and concluded that density-dependent factors explained 35% of the resultant decrease in average size. The remaining 65% was attributable to other factors, including artificial enhancement and interactions with other salmon species. Helle (1979) showed that reduced growth of Prince William Sound chum salmon during the second year at sea delayed the onset of maturity. Chum experience reduced food availability during periods of large population numbers, and reduced growth delays the onset of sexual maturation. Although pink salmon have maintained a fixed 2-year age at return, the declines in mean size have been even larger than for chum salmon. Similar changes are evident for other salmon species, although the evidence for widespread declines in growth rate is not as consistent as for pink and chum salmon. Sockeye salmon sampled from two locations in Alaska also exhibited an increase in average ocean age as average size decreased. The results for the average age of chinook salmon examined here are ambiguous. The mean age of Kuskokwim River chinook has decreased, the age of Yukon River chinook has been relatively unchanged, and Kenai River chinook have increased in age over the period examined. Reduction in average age coincident with average weight of British Columbia chinook was also reported by Ricker (1981) and is probably a result of differential exposure to mortality during the ocean residence. Comprehensive estimates of chinook salmon by-catch by vessels operating in both Alaskan and Russian waters of the Bering Sea are not available. Within the U.S. Exclusive Economic Zone in the Bering Sea the annual interception of chinook salmon is approximately 50 000 fish/year (G. Trumble, National Marine Fisheries Service, Juneau, AL 99801, personal communication). This level of removal is probably too small to influence estimates of average size or age.

Each of the above cases of decreasing size with time may be the result of increasing salmon abundance causing a reduction in the available food supply through density-dependent interaction and retarding size and age. Brodeur (1990) found

Fig. 8. Change in average length and age among chinook salmon from the Kuskokwim, Yukon, and Kenai rivers.



significant dietary overlap between chinook, coho, pink, and sockeye salmon, and that these species appear to feed opportunistically on a broad range of prey organisms. Chum salmon appear to be the most specialized and select food items not commonly shared with other species. Ricker (1981), on the other hand, attributed the decline in growth of British Columbia salmon to size-selective fisheries acting to select against rapid growth and discounted the possibility of environmental or density-dependent factors playing a major role. The use of

Table 3. Trends in age-specific mean length (mm) and average age (years) of selected North Pacific chum salmon populations.

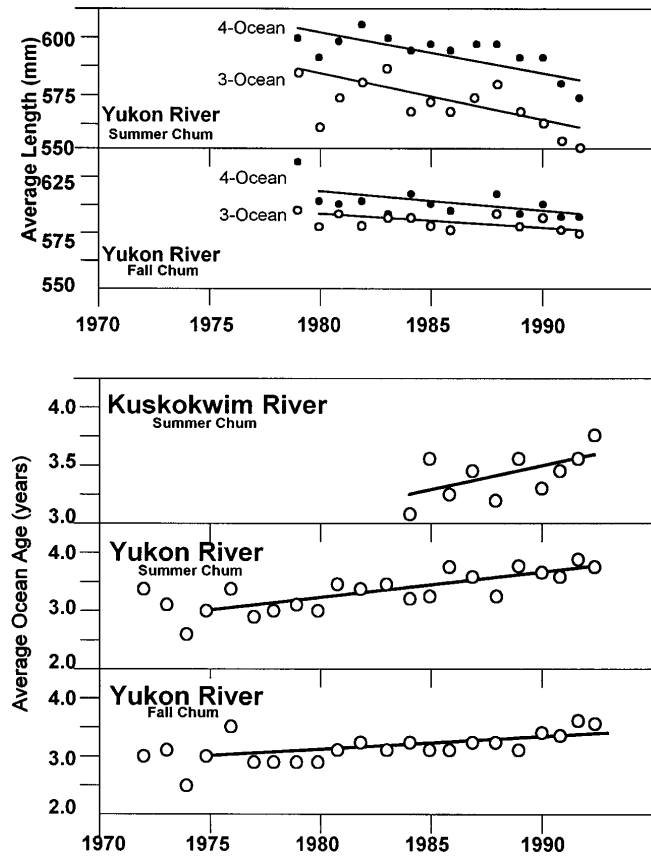
Population	Age group	n	r	b	Calculated values			% change
					1975	1979	1993	
Length								
Yukon River (summer)	0.3	14	-0.587*	-1.19		580.4	563.7	-2.88
	0.4	14	-0.782**	-1.82		605.1	579.6	-4.21
Yukon River (fall)	0.3	13	-0.534*	-0.71		598.1	588.1	-1.67
	0.4	13	-0.704**	-1.18		619.1	602.6	-2.67
Age								
Yukon River (summer)	Ocean age	19	0.805**	0.041	3.03		3.77	18.36
Yukon River (fall)	Ocean age	19	0.629**	0.028	2.92		3.42	12.76
Kuskokwim River (summer)	Ocean age	10	0.453	0.033	nc		nc	nc
Anadyr River	Ocean age	11	0.265	0.014	3.16		3.41	6.01
Kamchatka River	Ocean age	16	0.665**	0.025	3.15		3.60	10.84
Bolshaya River	Ocean age	15	0.611*	0.039	2.96		3.66	17.68
Amur River (summer)	Ocean age	16	0.817**	0.027	2.80		3.28	12.63
Amur River (fall)	Ocean age	18	0.823**	0.024	2.80		3.23	11.32
Ishikari River	Ocean age	16	0.574*	0.028	2.31		2.82	15.41

Note: n, number of years considered; r, correlation coefficient; b, regression slope (average annual change in weight); nc, not calculated. The calculated values (lengths for the length section of the table, and ages for the age section of the table) were computed from available data. Data for the Anadyr, Kamchatka, Boshaya, Amur, and Ishikari rivers are from Ishida et al. (1993).

*P < 0.05.

**P < 0.01.

Fig. 9. Change in average length and age among chum salmon from the Kuskokwim and Yukon rivers.



selective gear types in nearshore harvests may contribute to the reduced average size of salmon through a genetic response, but it is highly unlikely that commercial fishing pressures through-

out the North Pacific species range are acting simultaneously to account for the decreasing size among all species. Another possibility is that the increases in salmon abundance over the last two decades could be the result of reduced mortality on slower growing members of a cohort; in this case, changes in survival act to increase the proportion of small, slow-growing fish contributing to the fishery, thereby lowering the average size at age, even if growth rates do not change.

Environmental influences

Changes in population parameters that are coincident on an oceanwide scale are probably caused by common events during the ocean phase. Beamish and Bouillon (1993) found that long-term changes in the intensity of the Aleutian low pressure system, a weather system extending throughout the southern Bering Sea and North Pacific Ocean, correlate well with fluctuations in salmon abundance and the production of copepods. The inverse relationship between population abundance and average body size during the same period, however, suggests that there may be a limitation to the salmon-sustaining resources of the ocean.

Implications of reduced body size

Reduction in body size may result in reduced reproductive success (Helle 1989; review by Forbes and Peterman 1994). Life history theory predicts that large body size is a premium among salmon populations that migrate over long distances to spawn and enter the ocean as smolt. Beacham et al. (1988) and Beacham and Murray (1987) conclude that salmon body shape is heavily influenced by local selective forces in large and small rivers. Chum salmon spawning in large rivers in British Columbia adapt larger heads, thicker caudal peduncles, and larger fins than those spawning in smaller rivers. Healey and Heard (1984) found that egg numbers and adult body length are positively correlated in chinook. They concluded that there is substantial variation in fecundity between populations as an

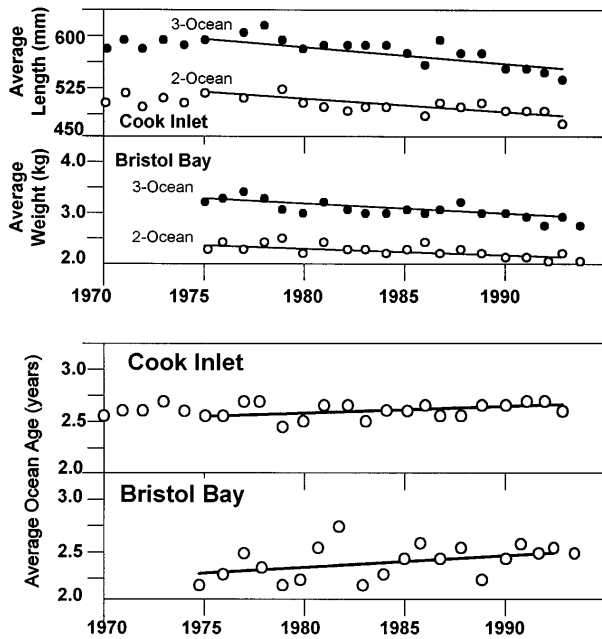
Table 4. Trends in age-specific mean length (mm), weight (kg), and average age (years) of selected North Pacific sockeye salmon populations.

Population	Age group	n	r	b	Calculated values		% change
					1975	1993	
Weight							
Bristol Bay	2-ocean	20	-0.671**	-0.013	2.41	2.18	-23.00
	3-ocean	20	-0.663**	-0.018	3.25	2.94	-31.60
Length							
Cook Inlet	2-ocean	17	-0.675**	-1.85	522.0	488.7	-6.38
	3-ocean	17	-0.780**	-2.47	596.4	552.0	-7.44
Age							
Bristol Bay	Ocean	20	0.296	0.009	2.34	2.48	14.21
Cook Inlet	Ocean	19	0.420	0.010	2.61	2.79	6.90

Note: n, number of years considered; r, correlation coefficient; b, regression slope (average annual change in weight). The calculated values (weight, length, and age for the weight, length, and age sections of the table, respectively) were computed from available data.

**P < 0.01.

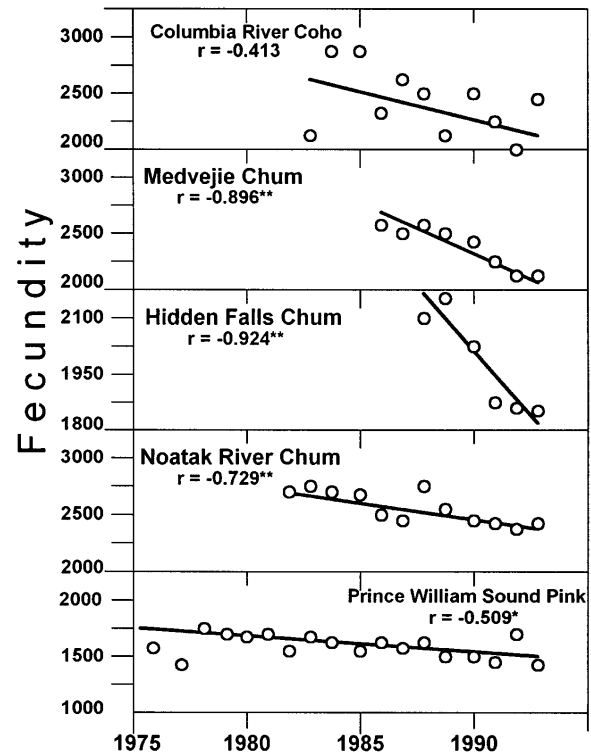
Fig. 10. Change in average weight, length, and age among Bristol Bay and Cook Inlet sockeye salmon.



adaptation to specific spawning and habitat conditions. Healey (1982) demonstrated the importance of size for the survival of small salmon, a principle that is presumed true for larger salmon as well.

The reproductive value of size is attributable to physical strength and longevity on the spawning ground, as well as to advantages in the numbers and vitality of sexual products (egg size, sperm motility). Foerster and Pritchard (1941) showed that sockeye and pink salmon follow principles governing the relationship between fecundity and body size similar to those of other species. Specifically, decreased body size and the attendant reductions in fecundity and egg size equate to greatly reduced abundance and survivorship of the progeny. Beacham and Murray (1987) showed that small eggs produce smaller alevin and fry that in turn inherit a diminished probability of survival. The effects of reduced average size among salmon

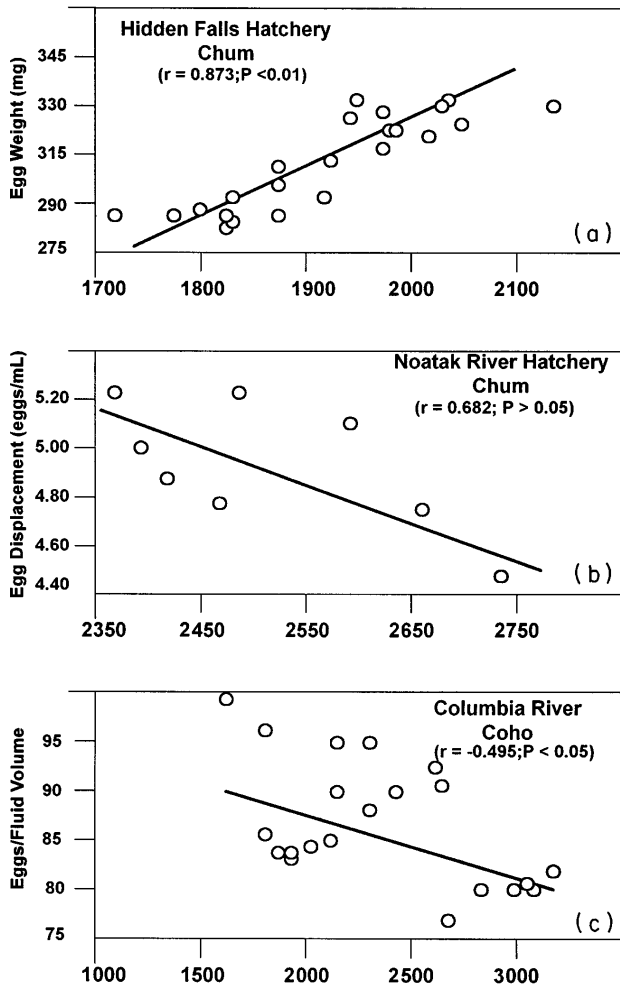
Fig. 11. Mean fecundity of hatchery coho, chum, and pink salmon, 1982–1993.



may first be evident in populations in which large body size is an important adaptation.

Average size data extending for more than several decades are rare. Ricker (1994) reported several cycles of increasing and decreasing size tendencies among British Columbia sockeye back to 1912. Welch and Morris (1994) found evidence of long-term density-dependent changes in average size among British Columbia pink salmon for the period 1927–1993. Such fluctuations probably occurred because of natural population pressures independent of influences from enhancement programs. The remarkable expansion of Pacific salmon enhancement programs since 1975, however, precludes simple comparison of the changes in average size documented here

Fig. 12. Relationship between egg size and fecundity in summer chum (a), fall chum (b), and coho (c) salmon, based on data from hatcheries in Alaska and Washington state.



with anything that has occurred previously. Artificially propagated salmon enjoy several survival advantages over wild populations, such as feeding to attain optimal fry size and abundance independent of environmental influence. Consequently, deleterious effects of reductions in average adult size will very likely appear first, and be most pronounced, among wild populations. As programs for the artificial propagation of Pacific salmon expand and the technology improves, the allocation of increasingly limited ocean resources may need to be recognized to assure optimal common management of salmon.

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