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**Decreasing Size Of North Pacific Salmon (*Oncorhynchus* sp.):
Possible Causes And Consequences**

by

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ABSTRACT

As a consequence of wild stock management, artificial enhancement, and favorable ocean conditions, the abundance of North Pacific salmon (*Oncorhynchus* sp.) has nearly doubled during the period 1975-1993. As salmon population numbers have increased there has been growing evidence of regional decreases in average adult size. We found that five species of North Pacific salmon are decreasing in average body size on an ocean-wide scale. With the exception of chinook salmon populations in California and British Columbia, all populations and species of Pacific salmon examined were found to be decreasing at rates ranging from only detectable on a statistical level, to rates evident to fishery participants. Total salmon production (harvest) has 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 there is a limitation to the salmon-sustaining resources of the ocean. The increased ocean survivorship and expansion of enhancement programs in the late 1980s and early 1990s are probable factors in the ocean-wide reduced size of salmon. The reduction in body size may be contributing to the recent decline in abundance of Western Alaska chum salmon populations, where large adult body size is considered essential to survivorship. Among other size-related factors affecting reproductive success, reduced fecundity and egg size, and pressure from a selective gear type may be acting in combination to reduce survivorship of these populations and may represent the model portending the impact of reduced body size on other populations.

Abstract
6/CTrans

北洋鮭の大きさの縮小について

(*Oncorhynchus* sp.)

考えられる原因と結果

Brian S. Bigler and John H. Helle

ABSTRACT

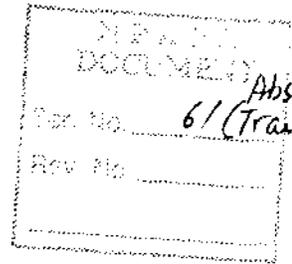
野生鮭の マネージメントの重大さに おいて、人工的に 増強し 又 海洋の好条件に おいて、1975-1993の間に 北海洋鮭の豊富さが2倍近くに なっております。 但し 平均して成長した数においては、増えているからサイズは小さくなっていると言う 実例が見られます。

我々の見た所では、カルフォルニアとカナダのブリテンユ コロンビアの マスノスケ 以外の北洋鮭の5種類の平均な実体は海洋全体に渡って、小さくなっている傾向です。

1925年から1989年間の全体の鮭の生産高は相互関係にある、環境のよさに有ると思われます。 しかしながら 漁獲量と平均サイズは 反比例して、海洋の鮭の資源に 限り有ることを示します。

1980年の終わりごろから1990年代にかけての、海洋資源の獲得と増強の プログラムはサイズの縮小の要因となっているかと思われます。 鮭のサイズの縮小の 与える影響としてアラスカのシロサケの数とサイズの減り方が実質的に生き残るための環 境が絶対必要かと思われます。 その他のサイズに関する影響としては 繁殖の成功、生 産力の減り方、卵のサイズ、さし網み漁などの、組み合った原因が 残存を阻み 又 鮭のサイズの縮小に関連していると思われます

Уменьшение размеров особей
тихоокеанского лосося (*Oncorhynchus*):
Возможные причины и следствия



Авторы: Брайен Биглер, Джон Хелль

За период 1975-1993 численность тихоокеанского лосося (*Oncorhynchus*) увеличилась почти вдвое вследствие использования и воспроизводства диких популяций, их искусственного усиления и благоприятного состояния океана. С увеличением численности популяций лосося, в данном регионе наблюдается всё более очевидное уменьшение средних показателей размеров взрослых особей. Нами установлено, что пять видов тихоокеанского лосося демонстрируют тенденцию к снижению средних размеров особей в общеокеанских масштабах. За исключением популяций чавычи (*Oncorhynchus tshawytscha*), обитающих в водах Калифорнии и Бриганской Колумбии, все обследованные популяции и виды тихоокеанского лосося терпят сокращение в размерах, масштаб которого варьируется от возможности его определения лишь на статистическом уровне, до очевидного уменьшения особей, отмеченного представителями рыболовецкого промысла. За период 1925-1989 общее воспроизводство лосося находилось, в основном, в зависимости от общих тенденций изменения окружающей среды, однако инверсионные (обратные) взаимоотношения между численностью популяции и средней величиной размера особей, наблюдаемые за период 1975-1993, указывают на ограниченность саморегулирующего механизма популяций лосося. Увеличение процента выживаемости, а также расширение программ искусственного усиления, произошедших во второй половине 80-ых и первой половине 90-ых годов, являются возможными факторами, влияющими на повсеместное уменьшение размеров особей лосося. Уменьшение размеров тела особей вероятно оказывает влияние и на недавнее снижение численности популяции кеты Западной Аляски (*Oncorhynchus keta*), где наличие крупных взрослых особей является особенно важным для выживаемости популяции. Наряду с другими факторам, оказывающими негативное влияние на успешную репродукцию, плодовитость, размер яиц, а также эволюционное воздействие применения селективных жаберных сетей, вероятно действуют в сочетании, снижая выживаемость таких популяций, и могут представлять собой модель, предвещающую воздействие сокращения размеров особей и на другие популяции.

(В сокращении)

INTRODUCTION

Advances in fisheries management, artificial enhancement, and favorable ocean conditions have more than doubled the number of salmon (*Oncorhynchus* sp.) produced in the North Pacific Ocean in the past twenty years (Fig. 1). There is a growing body of evidence, however, that coincident with population expansion, some North Pacific salmon populations are decreasing in average adult body size (length or weight).

Comprehensive studies of reduced growth among Pacific salmon have been relatively few and limited to individual spawning populations or species. Kaeriyama (1989, In Press), Kaeriyama and Urawa (1992), Ishida et al. (1993) and Hayashizaki and Hitoshi (In Press) have documented decreases in average size of Asian chum salmon (*O. keta*) in recent years. Similarly, Helle and Hoffman (1994) have shown declines in average size of two North American chum salmon populations.

Ishida et al. (1993) found a depressed growth rate during the third year of life among both Japanese and Russian chum salmon, and concluded that density-dependent factors explain 35 percent of the resultant decrease in average size. The remaining 65 percent is attributable to other factors, including artificial enhancement and interactions with other salmon species. Beamish and Bouillon (1993) provide evidence that climate and marine environmental factors may be responsible for trends in salmon production. Selective fishing can also influence the size of spawners and thus genetically alter the size of adult returns (Ricker 1981).

Brodeur (1990) found that differences in food item selection between chinook (*O. tshawytscha*), coho (*O. kisutch*), pink (*O. gorbuscha*) and sockeye (*O. nerka*) salmon species are vague, and that these species feed opportunistically within a preferred range of prey organisms. Chum salmon are the most specialized among the genus and appear to select food items not commonly shared with other species. There is reliable evidence that North Pacific salmon variously coexist during portions of their ocean phase (Myers et al. 1990). Significant interactions among species could result in limitations of resources and the expression of density dependent reactions similar to that of chum salmon. Peterman (1984) and Rogers (1980) have discussed density-dependent decreases in adult body size among sockeye salmon from different stock origins coexisting at sea. Similar findings have been reported for pink salmon (Ricker et al. 1978; Foerster and Pritchard 1941), coho salmon (Ricker and Wickett 1980; van den Berghe and Gross 1989), and chinook salmon (Ricker 1980, 1981).

While various authors have reported decreasing salmon size in the recent past, there have been reports of both increasing and decreasing average body size on a regional level during this century. The mean size at maturity by age declined slightly during 1959-1978 for a population of chum salmon in Prince William Sound, Alaska (Helle 1989). Godfrey (1959a) found pink salmon of British Columbia increased in average weight from 1944 through 1958, and a similar increase in average weight among chum (Godfrey 1959b) from 1946 through 1958. Conversely, Ricker et al. (1978) summarized several

decades of decreasing average size among British Columbia pink salmon subsequent to the period reported by Godfrey, from 1951 through 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 1950's, but found differing results in a subsequent study (Ricker 1994).

Helle (1989) found that the mean size (length) of chum salmon spawners is positively related to the survival of their progeny. If this relationship applies in general to chum salmon and other species, the declining size trend could predict reduced survival rates for that species in the near future. We investigated whether other species of Pacific salmon manifest reduced growth or other evidence of density-dependent responses in population parameters, and examined size and age tendencies found in these populations. An analysis of limited ancillary data on fecundity and egg size is also presented.

Western Alaska

Yukon and Kuskokwim river drainages of Western Alaska have experienced declines in chum salmon abundance since 1990 (Buklis 1994) causing reductions of commercial and subsistence harvests during 1992, 1993 and 1994. Reductions in body size and the attendant decreased fecundity and egg size may equate to reduced size and survivorship of alevin and fry. We examined reductions in average adult body size of Western Alaska chum and chinook salmon since 1975, and the likelihood that reduced size is having an impact on population abundance.

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). Full analyses are confined to data characterizing the most recent 20 years (1975-1993). Body weight is a sensitive variable for assessing changes in average size based on the exponential change in mass that corresponds to a linear change in length of a fusiform shape. For salmon, the relation between body length and weight is approximately: $Weight = Length^3$, a one-unit change in length is expressed as a cubic change in weight.

Several authors reporting on density dependent changes in body size over time favor linear regression analysis (e.g., Ricker 1981, Kaeriyama 1989, Ishida et al. 1993). Many underlying assumptions to linear modeling are violated, however, when comparing trends over time. Fundamental to the generation of unbiased regression statistics is the assumption that error terms are random. Because salmon return to spawning rivers after one to several years at sea, those harvested in near-shore fisheries comprise portions of brood cohorts resulting from several spawning seasons. Size tendencies are shared within

each cohort, and between cohorts if size tendencies result from common environmental circumstances. It is not unusual for the year to year average size of salmon to follow cyclical patterns up or down for several seasons. Many depictions of these data demonstrate that deviations from a linear trend line are not random. Data that follow such patterns are autocorrelated and cannot be fit to a linear model without inefficient estimation of slope and underestimation of slope standard error. As a result, the risk of rejection of the null hypothesis, that slope is zero, is higher. The simple linear regression model with the random error terms following an autoregressive process is:

$$Y_t = \beta_0 + \beta_1 X_t + \varepsilon_t$$

$$\text{where: } \varepsilon_t = \rho\varepsilon_{t-1} + u_t$$

Each error term ε_t in this model consists of a fraction of the previous error term plus a disturbance term u_t .

Following the procedure of Neter et al. (1985), autocorrelation was tested, and unbiased regression parameters estimated. The slope, expressed as "b" throughout this document, of generated regressions is the calculated average annual change in the variable tested.

Data Sources

Except where noted, all data are based on summaries of commercial harvest information collected by State, Federal, and Provincial government agencies. Notable exceptions are those of comprehensive chum fecundity and egg size data from state and private hatcheries in Oregon and Alaska. Other unique data sources are identified when referenced. Where possible, data from relatively non-selective gear types (seine, troll) were used instead of selective gear types (gill net).

The Pacific Fishery Management Council Review of Fisheries summarizes dressed weight of troll-caught chinook and coho in California, Oregon, and Washington states, including monthly and seasonal summaries (Rod Kaiser, Oregon Department of Fish and Wildlife, 2040 Southeast Marine Science Drive, Newport, Oregon 97365, pers. comm.). These monthly data cover periods of the fishing season when harvests include "feeder" salmon, i.e., those not captured during the spawning migration. Accordingly, California, Oregon and Washington troll fishery data representing the month of August were selected for analysis for two reasons: 1) chinook average weights were highest during August, indicating a likelihood that they were captured during the spawning migration, and, 2) data are available for all years.

The Oregon Department of Fish and Wildlife (ODFW) maintains a data base for Columbia River salmon hatcheries and provided average size, fecundity, and average egg size data (John Leppink, Hatchery Data Coordinator, ODFW, PO Box 59, Portland, Oregon 97207, pers. comm.). The average size of salmon in Columbia River commercial harvests were available from published data (ODFW, 1993).

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

The Alaska Department of Fish and Game maintains extensive data archives of commercial harvest statistics. The agency provided average weight data for each species harvested in the near shore commercial fisheries under the following headings: 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, Alaska, 99802-5526, pers. comm.).

Private non-profit hatcheries operating under license in Alaska must report population data on an annual basis. These and other cited sources, provided average size, fecundity and egg size data (Steve McGee, Alaska Department of Fish and Game, P.O. Box 25526, Juneau, Alaska, 99802-5526, pers. comm.; Bruce Bachen, Northern Southeast Regional Aquaculture Association, 1308 Sawmill Creek Road, Sitka, Alaska, 99835, pers. comm.; Peter Rob, Sikusuiq Springs Hatchery, P.O. Box 1030, Kotzebue, Alaska, 99752, pers. comm.).

Using age-specific information, Helle and Hoffman (1994) demonstrated that decreases in average size for chum salmon populations is masked by an increasing number of older, larger, fish. This implies that, without age-specific data, changes in average size of a population may be more profound than that evidenced in aggregate. Age-specific size data covering the entire period under review is not generally available. Pink and coho salmon return at relatively uniform ages according to a two or three year life cycle, respectively, and age-specific analysis is not meaningful. Other species return to natal streams following one to several winters at sea, where density-dependent factors expressed by adult size are likely experienced. There were sufficient data among Yukon River fall and summer chum, Yukon River chinook, Cook Inlet sockeye and Kenai River (Cook Inlet) sockeye, to analyze age-specific information. Age is designated by European notation where two numerals that precede and follow a decimal point, respectively, indicate the observed number of fresh water and ocean annuli on the scales.

Western Alaska

Average length data for Western Alaska chum and chinook salmon were obtained from regional data summaries and state-wide reports by ADFG (333 Raspberry Road, Anchorage, Alaska 99518). The Yukon River supports both summer *O. keta* (Walbaum) and fall chum salmon *O. keta* (Walbaum) infra species *autumnalis* (Berg). Several characteristics including body size, body fat content, spawning distribution, and run timing differentiate summer and fall chum (Buklis and Barton 1984). Only summer chum salmon are found on the Kuskokwim River, and fall chum are not generally found south of the Western Alaska region. Length data are collected from salmon captured in gill nets operated in each fishery. Bagenal (1969), Beacham and Murray (1987), Helle (1989), and Fleming and Gross (1990) have shown that a decrease in average body size equates to a

smaller volume and decreasing egg numbers (fecundity). Although a direct relation with body size (weight) is assumed, characteristics such as fecundity and egg size are not measured among wild salmon populations in Western Alaska. Inferences are made from non-wild populations of Sikusuilaq Springs Chum Salmon Hatchery on the Noatak River near Kotzebue, and Hidden Falls and Medvejie hatcheries in southeast Alaska (Fig. 2).

RESULTS

A decreasing trend of body size is evident among all populations tested except for chinook salmon harvested in California and British Columbia (Table 1; Figs. 3-7). All other populations and species of Pacific salmon examined were found to be decreasing at rates ranging from only detectable on a statistical level, to rates evident to fishery participants.

Chinook Salmon

Chinook salmon migrate to sea after zero to two winters in fresh water, and return to spawn one to five winters later. The ocean-phase distribution of Asian chinook salmon is not as well documented as those of North American origin (Fig. 8A). Among nine populations of chinook salmon tested, the calculated average weights of troll chinook in California and British Columbia have increased in size 24.7 and 45.5 percent, respectively, between 1975 and 1993 (Table 1, Fig. 3). It is conspicuous, however, that every other population tested evidenced body size decreases ranging from 10.1 to 46.7 percent over the same period. In terms of average annual change in body weight (slope b), Oregon chinook have lost the least, 0.047 kg per year, while Kuskokwim River chinook have lost a calculated 0.162 kg of body weight each year (Table 1).

Age-specific length data collected from the Yukon River commercial fisheries corroborate the findings of average weight (Table 2, Fig. 9). All ocean age groups tested showed a relatively similar decreasing trend of approximately 3-5 percent of body length.

The average ocean age of Kuskokwim River chinook salmon has decreased as size has decreased, though the age of Yukon River chinook has been relatively unchanged over the period examined (Table 2, Fig. 9).

Coho Salmon

The majority of coho salmon are captured during the third or fourth year of life after spending two summers at sea (Fig. 8B). All populations tested showed decreased average body weight (Table 1, Fig. 4). The average annual change in weight among ten commercial fisheries from California to the Yukon River between 1975 and 1993, ranged from -0.012 to -0.059 kg/yr. Ricker (1994) found ambiguous results depending upon region and gear type among British Columbia coho from 1951 through 1992, except that coho harvested in seine fisheries declined in average size.

Chum Salmon

Chum salmon characteristically remain in fresh water about 30 days after fry emergence before beginning the migration to the sea, and return from two to five winters later. North American chum populations at sea tend to concentrate in the Gulf of Alaska, Aleutian Islands, and Bering Sea, and Asian chum concentrate in the Aleutian Island and Kamchatka regions with substantial overlaps with North American populations (Fig. 8C). Chum salmon among the eight populations examined have declined in average weight from 0.003 kg/yr for Yukon River summer chum between 1975 to 1993, to 0.075 kg/yr for Columbia River chum (Table 1; Fig. 5).

Age-specific data of Yukon River fall and summer chum show that, as the average chum salmon size decreased, the average age at maturity increased. The average length of each age group of summer and fall chum decreased in relative uniformity, between 2 and 4 percent (Table 2, Fig. 10). Summer chum age increased from 3.03 to 3.77 yr, while fall chum increased from 2.92 to 3.42 yr.

Pink Salmon

Pink salmon follow a two year life cycle, migrating to sea for one winter. The ocean phase of this species is spent well out to sea until immediately before the spawning migration (Fig. 8D), avoiding capture in the inshore troll fisheries (Ricker 1994). Average weight of North American pink salmon populations have decreased at a relatively uniform rate of approximately 0.020 kg/yr, or about 20 percent from 1975 to 1993 (Table 1; Fig. 6). A notable circumstance is that of British Columbia where average body size of some populations has reduced 40 percent, a full kilogram lighter, since first studied in the 1950's (Ricker 1994).

Sockeye Salmon

The sockeye salmon life cycle includes age groups from zero to three freshwater winters and one to four winters at sea where they distribute widely (Fig. 8E). Though all sockeye salmon populations tested showed decreasing trends in average weight, three of the five populations indicated statistically insignificant fit ($P > 0.05$) to a linear model (Table 1; Fig. 7). Sockeye harvested from Kodiak Island and Cook Inlet from 1975 to 1993 have decreased an average of 0.027 kg/yr, or 16.8 and 11.5 percent, respectively.

Age-specific measurements of sockeye salmon body length in the Cook Inlet gill net fishery and Kenai River escapement samples show similar tendencies in declining length, although each population is sampled independently (Table 2; Fig. 11). The average ocean age of these sockeye salmon increased approximately 7 percent over the period tested (Table 2).

Fecundity and Egg Size

Fecundity and egg size data normally collected from hatchery populations are well suited for comparison with wild salmon stocks. Sikusuilq Springs hatchery on the Noatak River in northwest Alaska has produced fall chum salmon since 1982. Hidden Falls and Medvejie hatcheries in southeast Alaska have produced summer chum within the last ten years. The Port San Juan Hatchery in Prince William Sound, Alaska, provided 14 years of average fecundity information, and summary data for coho salmon was obtained combining several Columbia River, Washington, hatcheries. A tendency for diminished fecundity is evident among all of these populations (Fig. 12). Chum salmon fecundity and egg size data demonstrate that, for both fall and summer chum salmon, fecundity is related positively to body size, and egg size is positively related to fecundity. Fall chum egg size measured volumetrically (Sikusuilq Springs) and summer chum egg size measured by weight (Hidden Falls) show a significant decrease in egg size with decreasing fecundity (Fig. 13).

Commercial Fishing

Temporal, spatial, or selective removal according to physical characteristics, can cause abnormal tendencies in physical characteristics of an exploited population. Fleischman (ADFG, 333 Raspberry Road, Anchorage, Alaska 99518 pers. comm.) has modified the methods of McCombie and Fry (1962) and Ishida (1969) to estimate selectivity curves for 15.2 cm (6 in.) and 20.4 cm (8 in.) stretched mesh (Fig. 14), the two gill net sizes operated in the Yukon and Kuskokwim River commercial fisheries. Commercial gill nets capture fish of a wide size distribution; 15.2 cm mesh peaks in efficiency among fall chum of approximately 565-620 mm and summer chum of approximately 570-640 mm body length (Fig. 14). This mesh size, however, continues to capture larger (older) fish disproportionately to the upper limits of the species size distribution.

CONCLUSIONS

Students of fisheries science learn that Pacific salmon population abundance is related to spawner abundance. The model described by spawner-recruitment relationships is typically confounded by other factors, but generally yields a positive slope and first derivative when spawning populations are relatively small and the resultant progeny thrives on abundant resources. As the population abundance increases, the spawner/recruitment ratio diminishes to less than replacement and population numbers decline as limited resources are consumed. Naturally occurring salmon populations are thus held in check and their numbers defined by resource limitations. With the discovery of the spawner-recruitment relationship, management of Pacific salmon has generally followed a philosophy of recruitment maximization at optimum spawner density. 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 salmon population numbers have expanded, there has been a coincident decrease in average adult size, and variable changes in average age at spawning.

The average ocean age of Kuskokwim River chinook salmon has decreased, and the age of Yukon River chinook has been relatively unchanged over the period examined. Reduction in average age coincident with average weight of British Columbia chinook was also reported by Ricker (1981) and is likely a result of differential exposure to mortality during the ocean phase. Western Alaska chinook salmon are known to distribute within the Bering Sea during the ocean phase, but there are insufficient data to draw conclusions of overlap with other populations. Comprehensive estimates of chinook salmon bycatch by vessels operating in both Alaska and Russian waters of the Bering Sea do not exist, though these removals are presumably inconsequential. Within the U.S. Exclusive Economic Zone, the interception of less than 50,000 chinook per year (National Marine Fisheries Service, Juneau, Alaska 99801, pers. comm.) is not a source of significant removal such that an influence on average size or age can be hypothesized.

The changes in both average size and age we found for Western Alaska chum salmon follow those of Japanese and Russian stocks reported by Ishida et al. (1993), and two north American populations reported by Helle and Hoffman (1994). In those cases, reduced size was attributed to density dependent pressures. Chum experience reduced food availability during periods of large population numbers, and reduced growth delays the onset of the spawning migration.

Sockeye salmon sampled from two locations indicate an increase in average ocean age as average size has decreased. As with chum salmon, these results are explainable by density dependent pressures reducing the available food supply and retarding the spawning size and age.

In the only other document known to these authors describing a concurrent reduction in average size among several salmon species, Ricker (1981) attributed this phenomenon to commercial fishing pressures, discounting environmental influences. It is highly unlikely that commercial fishing pressures throughout the North Pacific species range are acting simultaneously to account for the decreasing size among all salmon species. The use of gill nets in Western Alaska riverine fisheries, however, may contribute to the reduced average size of chum and chinook salmon. We found that gill nets operated in these fisheries capture larger fish disproportionately to that of smaller fish. Selectivity of Yukon River gill nets was cited by Buklis (1982) to explain a reduced percentage of males and smaller adult body size among summer chum escapements compared with commercial harvest. We also found a disproportionate selection for larger (older) Yukon River chinook salmon by 15.2 cm and 20.4 cm mesh gill nets, but the population has not shown reductions in abundance. The skewness in these selectivity curves is likely attributable to the development of a kype (protruding upper and lower jaws) and enlargement of teeth during the spawning migration that entangle in the mesh. Irrespective of the underlying explanation, the selective removal of larger chum and

chinook salmon by gill nets must be viewed with concern; particularly during periods of depressed body size caused by factors independent of influences during the freshwater phase.

Environmental Influences

Changes in population parameters on an ocean-wide scale are likely caused by common events during the ocean phase where the influences would necessarily be on a massive scale. Beamish and Bouillon (1993) found that long-term patterns of the Aleutian Low pressure system, a weather system extending throughout the southern Bering Sea and north Pacific Ocean, correlates well with fluctuations in salmon abundance and the production of copepod food items. Hare and Francis (1994) report similar environmental changes that correlate with the nearly doubled production of North Pacific salmon. The inverse relationship between population abundance and average body size during the same period, however, indicates there is a limitation to the salmon-sustaining resources of the ocean.

Beamish and Bouillon (1993) state that their environmental data extends until 1989, and that in the subsequent four years before publication the weather systems in the North Pacific tended toward less productive conditions. Hare and Francis (1994) also found moderating trends in environmental indicators toward the latter part of the 1980s, suggesting the movement into a period of reduced ecological production. With the limited data available, it is not possible to postulate what this trend, if it continues, will mean to the salmon populations of the North Pacific Ocean.

Implications of Reduced Body Size

If smaller North Pacific salmon were the sole consequence of reduced average size, this would likely be of curious note to fishery managers and scientists, and of more serious significance to the commercial fishing industry. Reduction in body size, however, equates to reductions in potential reproductive success and the decline in abundance of Western Alaska chum salmon may be evidence of this principle.

Life history theory predicts that large body size is a premium among salmon populations that migrate over long distances to spawn and return to the ocean as smolt. Beacham et al. (1988) conclude that salmon body shape is heavily influenced by local selective forces in large and small rivers. Large rivers usually provide more variety of spawning habitats, over geographically distant areas, than do small rivers. Beacham and Murray (1987) found those chum salmon spawning in large rivers in British Columbia adapt larger heads, thicker caudal peduncles, and larger fins than those spawning in smaller rivers. Deleterious effects of reduced average size among salmon will likely first be evident in populations where large body size is an important adaptation. Rivers of Western Alaska are relatively long and slow-moving, with high annual silt loads. Larger adult size aids a prolonged upriver migration, as large fry size aids in the downriver

migration. It is likely that a larger body size in fall chum salmon is an adaptation to the relatively long migration in the rivers of Western Alaska.

Results from the present study, and others, indicate that density dependent factors are currently working to decrease the average size of chum salmon throughout the range of the species, and that the reductions in body size of Western Alaska chum salmon may be a significant factor contributing to the regional decline in population abundance. 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) have shown that small eggs in turn produce smaller alevin and fry that, in turn, inherit a diminished probability of survival.

Healey and Heard (1984) found that egg numbers and adult body length is positively correlated in chinook. They concluded that there is substantial variation in fecundity between populations as an 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 advantages in numbers and vitality of sexual products (egg size, sperm motility). Foerester and Pritchard (1941) have shown that sockeye and pink salmon follow principles between fecundity and body size similar to that of other species. There is no reason to doubt that properties of fecundity, egg size and subsequent growth previously described for chum salmon are at work on other salmon as well.

Enhanced pink salmon have virtually replaced wild stocks within Prince William Sound, Alaska, as have enhanced coho on the Columbia River in Washington state. Pink salmon fecundity data collected from the Port San Juan Hatchery in Prince William Sound, and Columbia River coho data based on several hatchery sites, also demonstrate declining fecundity over the past several years. Although direct comparison with size data is not possible, we accept that the coincident decrease in both size and fecundity is comparable to the relationship shown for chum salmon. Salmon returns to Prince William Sound and Columbia River hatcheries have been substantially below expectations for the 1991 through 1993 seasons, despite ample fry releases. Reduced returns from these releases indicate significant ocean-phase mortality and the source of that mortality is currently under investigation.

Average size data extending farther than several decades are rare. Ricker (1994) reported several cycles of increasing and decreasing size tendencies among British Columbia sockeye back to 1912. Welch (Pacific Biological Station, Nanaimo, British Columbia, Canada V9R 5K6, pers. comm.) has found evidence of long-term density dependent changes in average size among British Columbia pink salmon. Such fluctuations likely occurred as a consequence of relatively natural population pressures independent of influences from enhancement programs. The remarkable expansion of salmon enhancement programs in the North Pacific since 1975, however, preclude simple comparison of the changes in average size documented here with anything that has

occurred previously. That artificially propagated salmon enjoy several survival advantages over wild populations is well documented. 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 will have to be recognized to assure optimal common management of salmon.

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Table 1. Trends in mean weight (kg) of selected North Pacific salmon populations. Column headings are as follows: n = number of years considered; r = correlation coefficient; b = regression slope (average annual change in weight); 1975 and 1993 are values computed from available data. (* = P<0.05; ** = P<0.01)

CHINOOK					Calculated Weight Percent		
Region	Area	n	r	b	1975	1993	Change
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 R.	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 R.	19	-0.761**	-0.162	9.27	6.35	-31.50
	Yukon R.	19	-0.670**	-0.102	10.43	8.60	-17.55

COHO					Calculated Weight Percent		
Region	Area	n	r	b	1975	1993	Change
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 R.	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 R.	19	-0.560*	-0.018	3.40	3.07	-9.71
	Yukon R.	17	-0.374	-0.012	3.21	2.99	-6.85

CHUM					Calculated Weight Percent		
Region	Area	n	r	b	1975	1993	Change
Washington	Columbia R.	18	-0.564*	-0.075	6.12	4.84	-20.92
British Columbia	Seine/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 R.	19	-0.460*	-0.013	3.26	3.02	-7.36
	(Summer) Yukon R.	16	-0.144	-0.003	3.22	3.17	-1.55
	(Fall) Yukon R.	16	-0.765**	-0.030	3.59	3.02	-15.88
	(Fall) Kotzebue Sound	19	-0.545*	-0.018	4.13	3.80	-7.99

From Ishida et al. (1993)					Calculated Weight Percent		
Region	Area	n	r	b	1970	1988	Change
Russia	Anadyr R.	11	-0.720*	-0.083	4.69	3.20	-31.77
	Kamchatka R.	16	-0.650**	-0.029	3.88	3.35	-13.66
	Bolshaya R.	15	-0.502	-0.039	4.02	3.33	-17.16
	(Summer) Amur R.	16	-0.546*	-0.016	2.66	2.37	-10.90
	(Fall) Amur R.	18	-0.627**	-0.048	4.89	4.03	-17.59
Japan	Ishikari R.	16	-0.646**	-0.048	3.72	2.85	-23.39

Table 1. Trends in mean weight (kg) of selected North Pacific salmon populations. Column headings are as follows: n = number of years considered; r = correlation coefficient; b = regression slope (average annual change in weight); 1975 and 1993 are values computed from available data. (* = P<0.05; ** = P<0.01) (Continued)

PINK		n	r	b	Calculated Weight Percent		
Region	Area				1975	1993	Change
British Columbia	Seine/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 Wm. Snd.	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		n	r	b	Calculated Weight Percent		
Region	Area				1975	1993	Change
British Columbia	Seine/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

Table 2. Trends in age-specific mean length (mm) and average age (yr) of selected North Pacific salmon populations. Column headings are as follows: n = number of years considered; r = correlation coefficient; b = regression slope (average annual change in weight); 1975 and 1993 are values computed from available data. (* = P<0.05; ** = P<0.01)

Chinook

Length Population	Age Group	n	r	b	Calculated Length		Percent Change
					1979	1993	
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

Age Population	Age Group	n	r	b	Calculated Age		Percent Change
					1975	1993	
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

Chum

Length Population	Age Group	n	r	b	Calculated Length		Percent Change
					1979	1993	
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 Population	Age Group	n	r	b	Calculated Age		Percent Change
					1975	1993	
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	Not Calculated		
Anadyr River ¹	Ocean Age	11	0.265	0.014	3.16	3.41	6.01
Kamchatka River ¹	Ocean Age	16	0.665 **	0.025	3.15	3.60	10.84
Bolshaya River ¹	Ocean Age	15	0.611 *	0.039	2.96	3.66	17.68
Amur River ¹ (Summer)	Ocean Age	16	0.817**	0.027	2.80	3.28	12.63
Amur River ¹ (Fall)	Ocean Age	18	0.823 **	0.024	2.80	3.23	11.32
Ishikari River ¹	Ocean Age	16	0.574 *	0.028	2.31	2.82	15.41

1) Based on Ishida et al. (1993)

Table 2. Trends in age-specific mean length (mm) and average age (yr) of selected North Pacific salmon populations. Column headings are as follows: n = number of years considered; r = correlation coefficient; b = regression slope (average annual change in weight); 1975 and 1993 are values computed from available data. (* = P<0.05; ** = P<0.01) (Continued)

SOCKEYE							
Length Population	Age Group	n	r	b	Calculated Length		Percent Change
					1975	1993	
Kenai River (Escapement)							
	2-Ocean	18	-0.450	-1.18	504.9	483.7	-4.20
	3-Ocean	18	-0.663**	-1.86	596.1	562.6	-5.62
Cook Inlet (Fishery)							
	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 Population	Age Group	n	r	b	Calculated Age		Percent Change
					1975	1993	
Kenai River (Escapement)							
	Ocean	19	0.333	0.013	2.59	2.78	7.34
Cook Inlet (Fishery)							
	Ocean	19	0.420	0.010	2.61	2.79	6.90

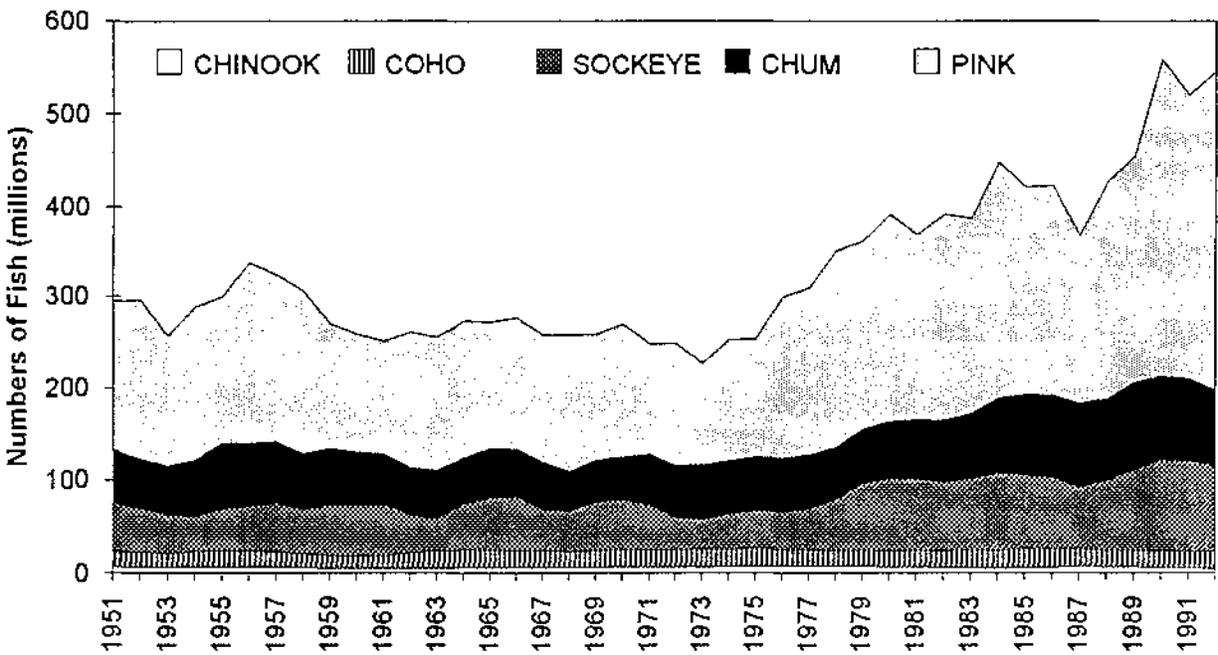


Figure 1. Total North Pacific salmon production (harvest and escapement), 1951-1992. Unpublished data from D. Rogers, Fisheries Research Institute, University of Washington, WH-10, Seattle, Washington

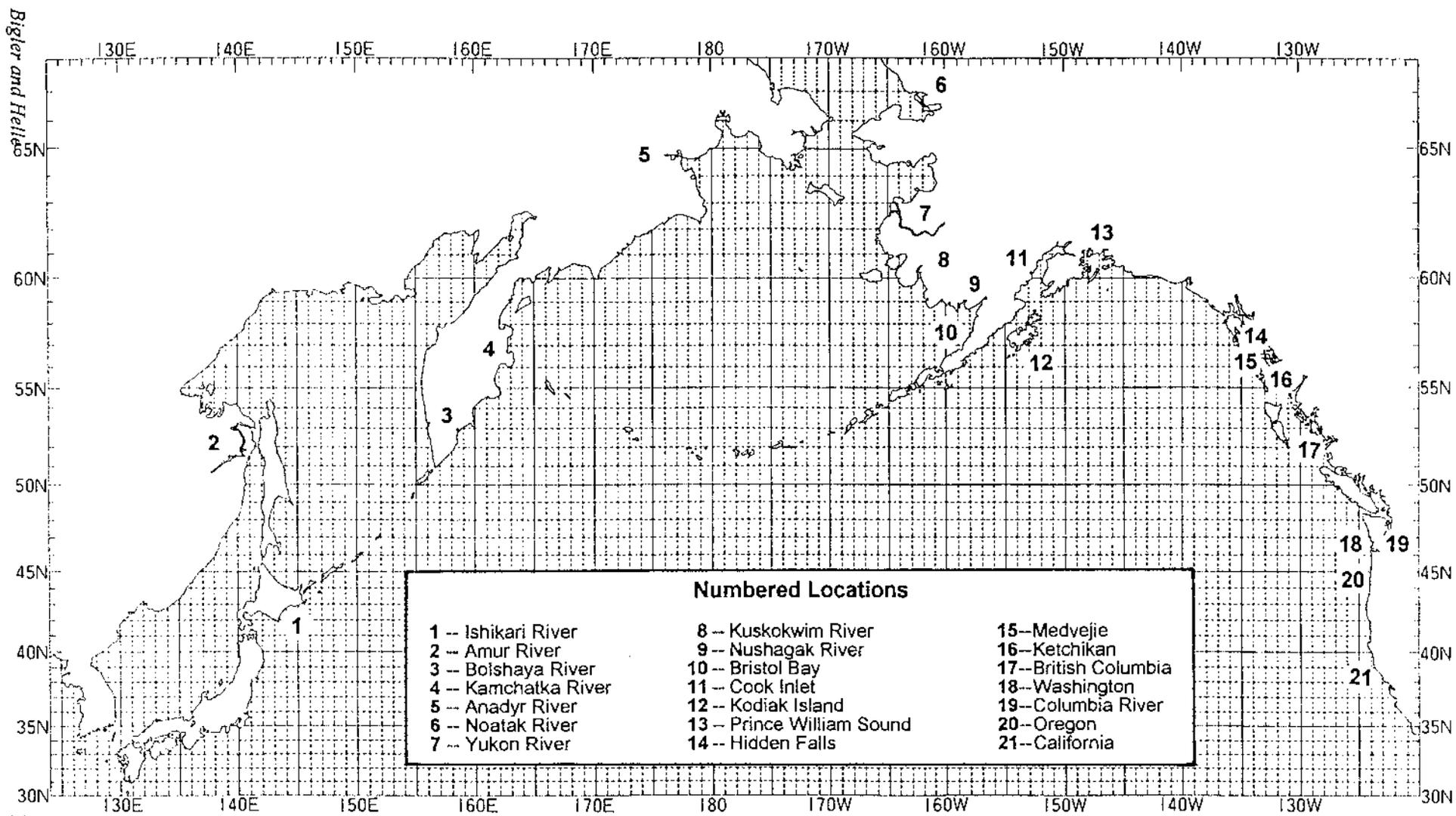


Figure 2. Locations of salmon populations tested for changes in average weight, length, age, or ancillary information.

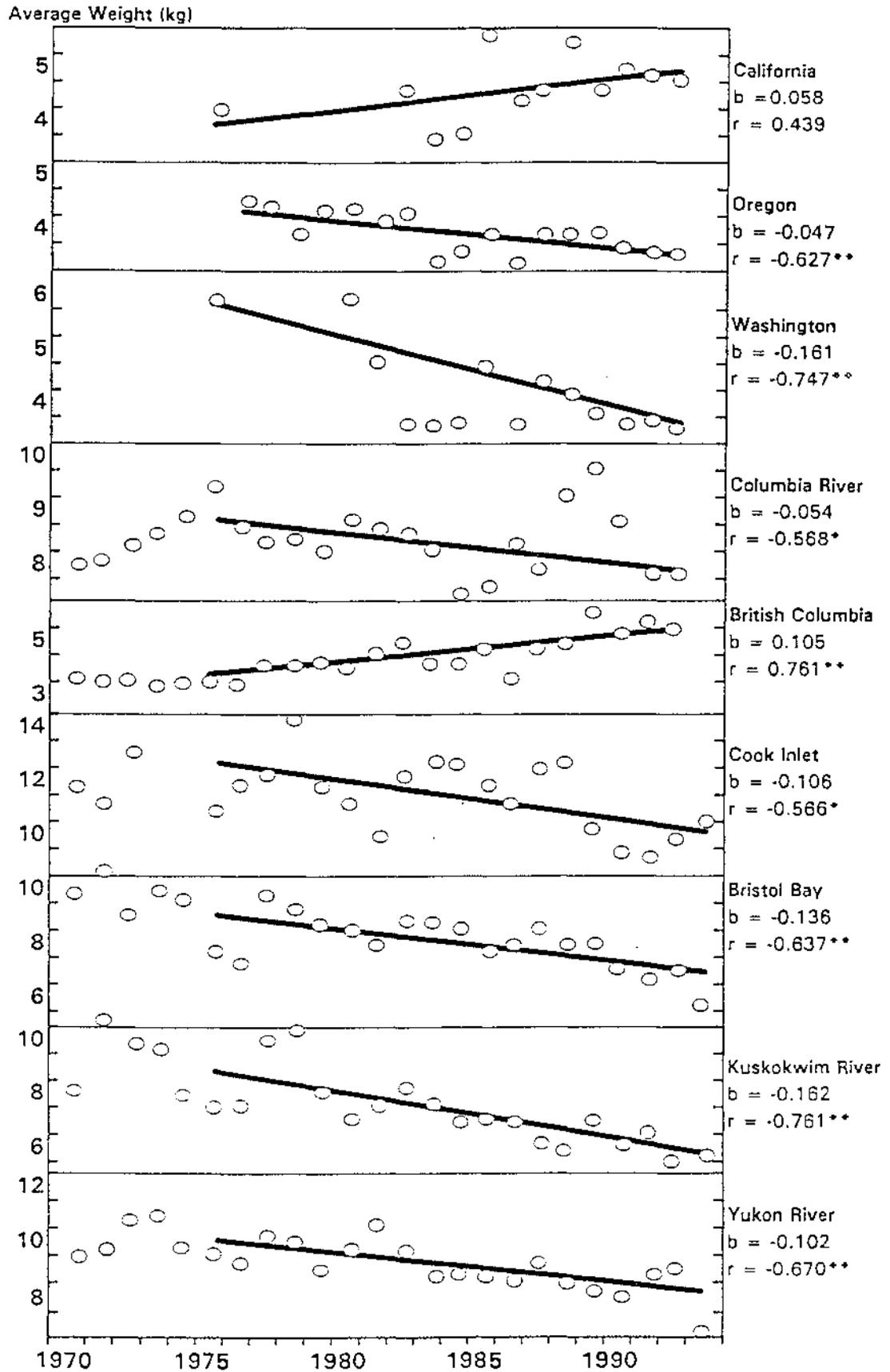


Figure 3. Mean weight, in kilograms, of chinook salmon sampled from nine North American commercial fisheries. See text for data sources. (* = $P < 0.05$; ** = $P < 0.01$)

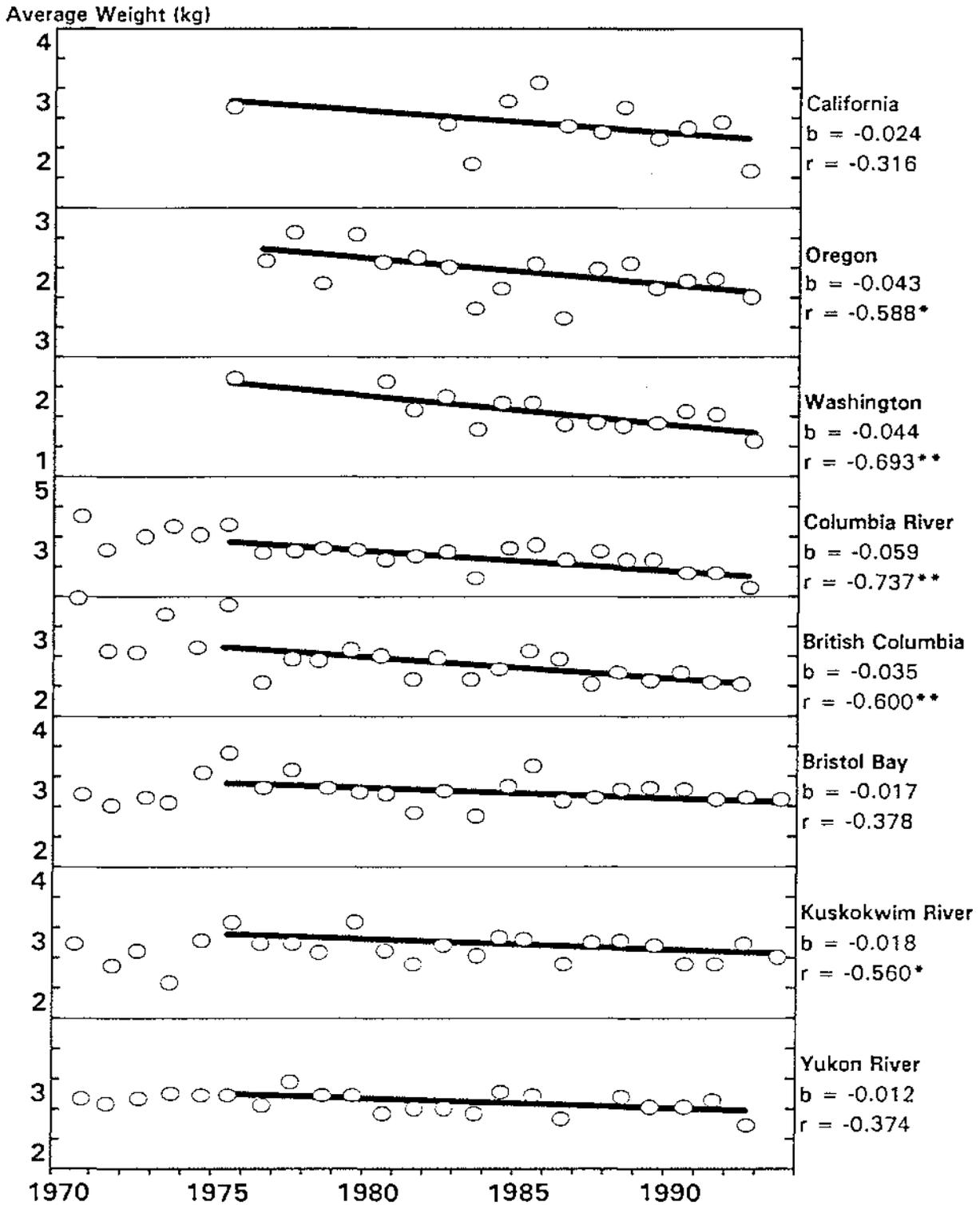


Figure 4. Mean weight, in kilograms, of coho salmon sampled from eight North American commercial fisheries. See text for data sources. (* = $P < 0.05$; ** = $P < 0.01$)

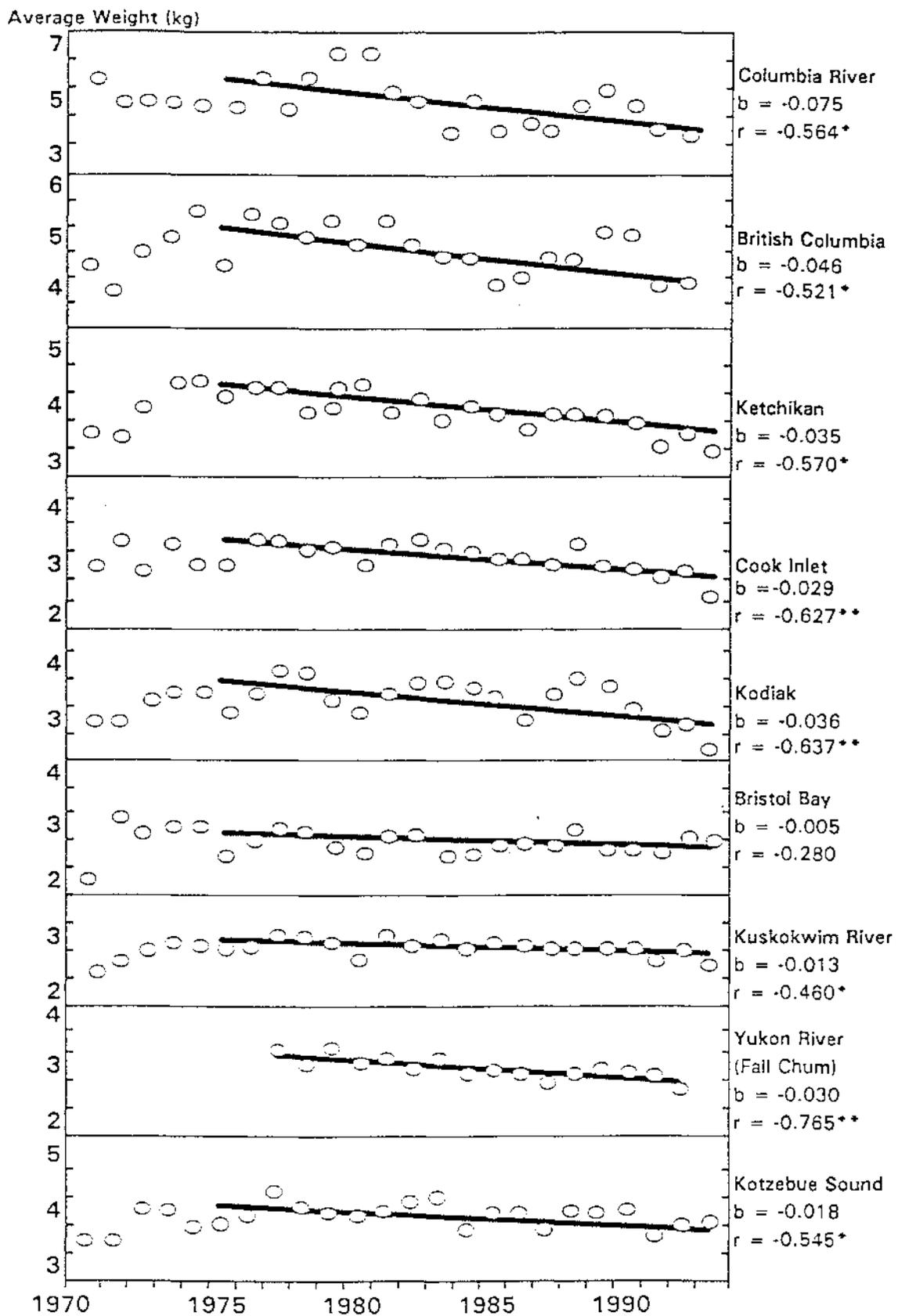


Figure 5. Mean weight, in kilograms, of chum, salmon sampled from seven North American commercial fisheries. See text for data sources. (* = $P < 0.05$; ** = $P < 0.01$)

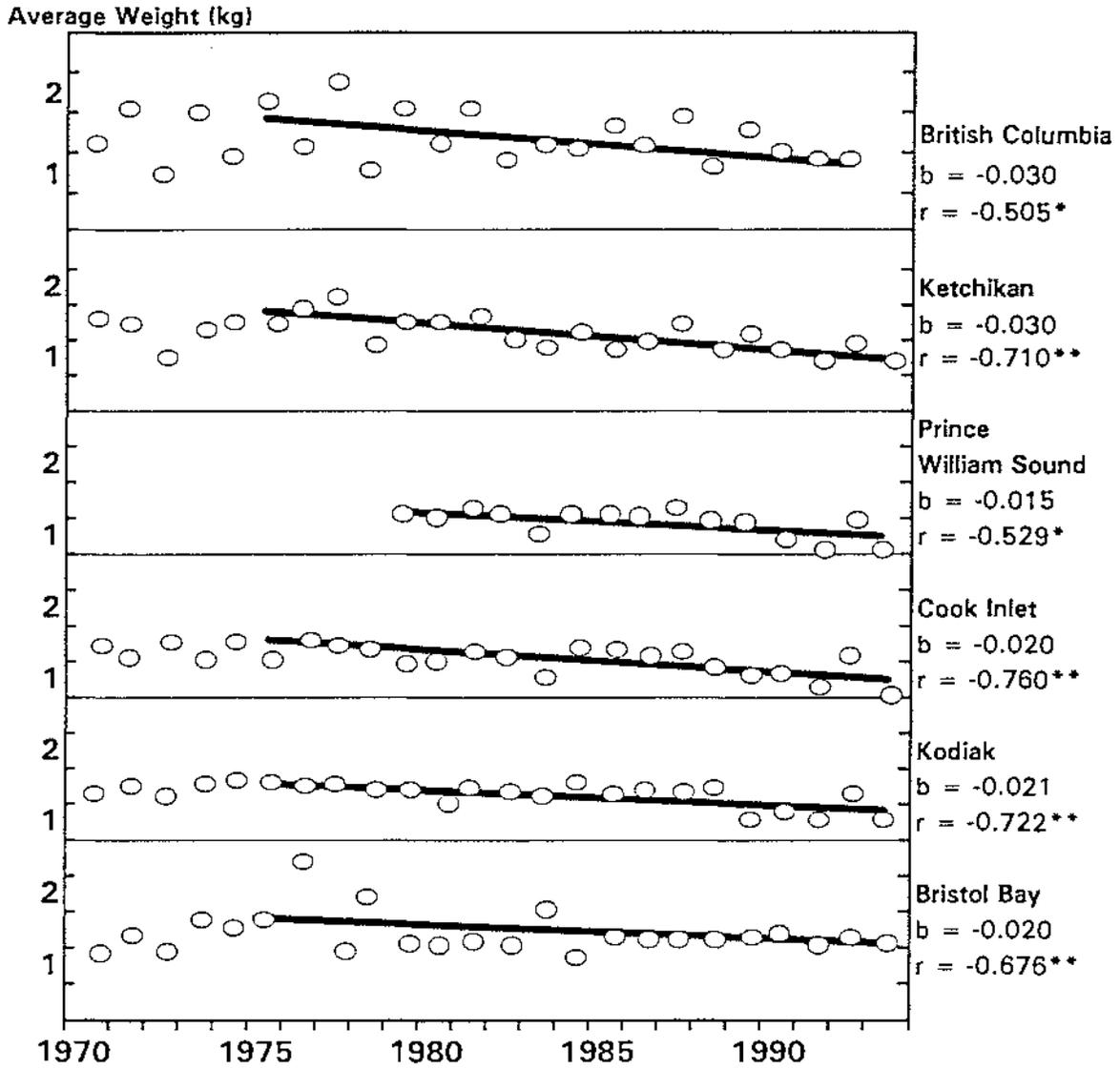


Figure 6. Mean weight, in kilograms, of pink salmon sampled from five North American commercial fisheries. See text for data sources. (* = $P < 0.05$; ** = $P < 0.01$)

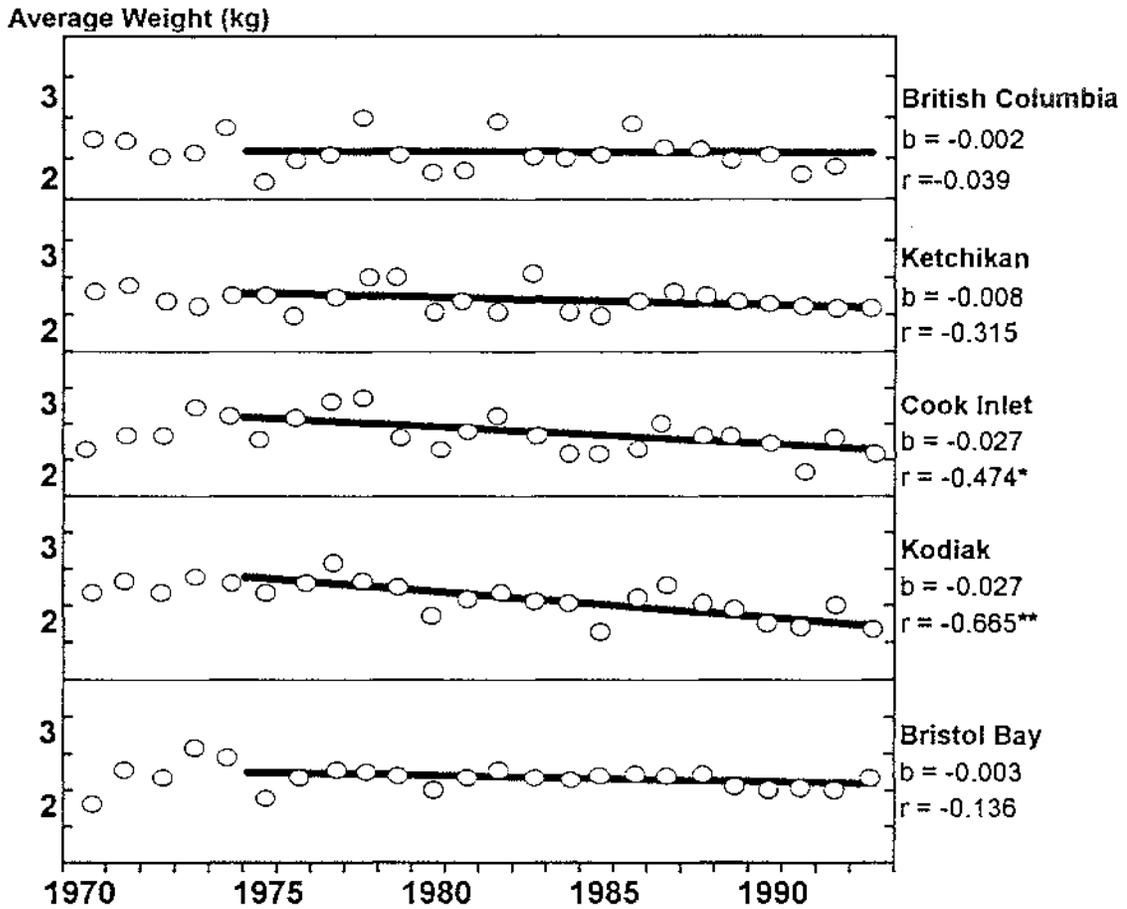


Figure 7. Mean weight, in kilograms, of sockeye salmon sampled from five North American commercial fisheries. See text for data sources. (* = $P < 0.05$; ** = $P < 0.01$)

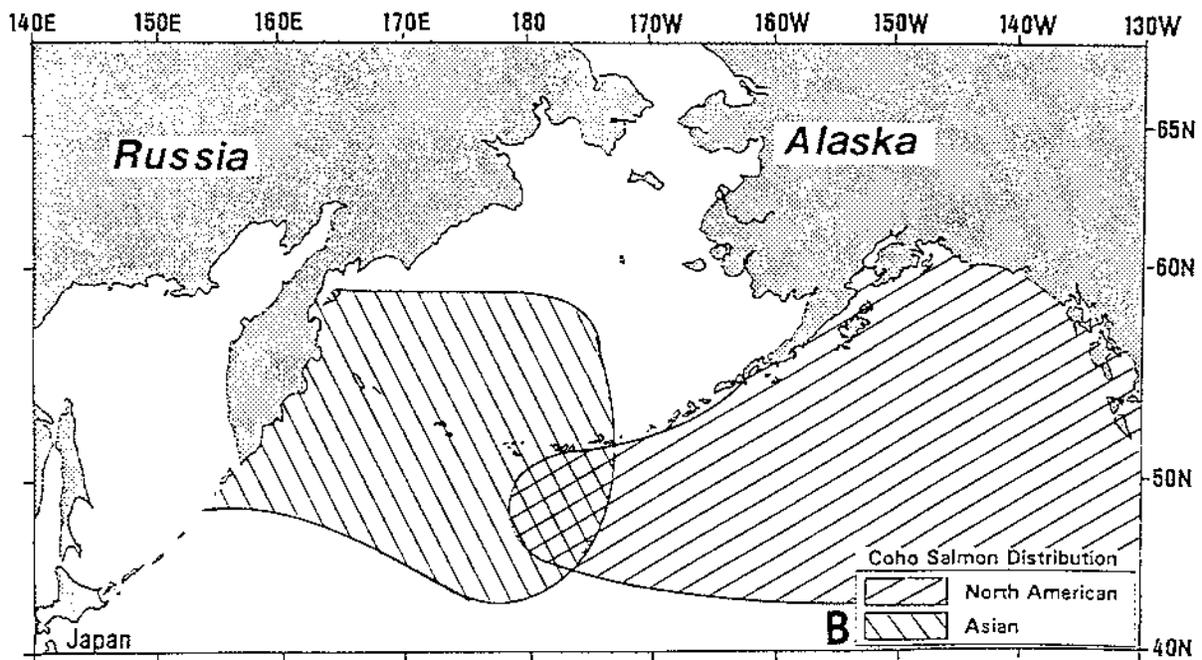
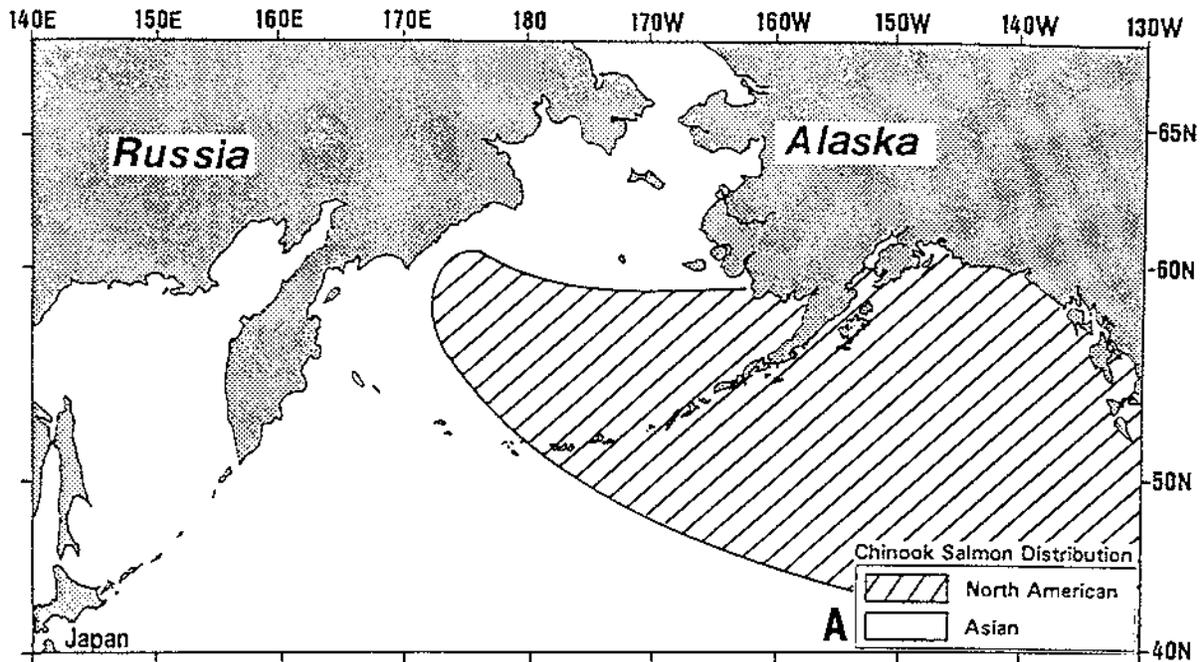


Figure 8. Oceanic distribution of chinook (A), coho (B), chum (C), pink (D) and sockeye (E) salmon, according to Myers et. al. (1990). Migration routes between spawning rivers and rearing areas is omitted for clarity. Special Note: Insufficient data to conclude the distribution of Asian chinook.

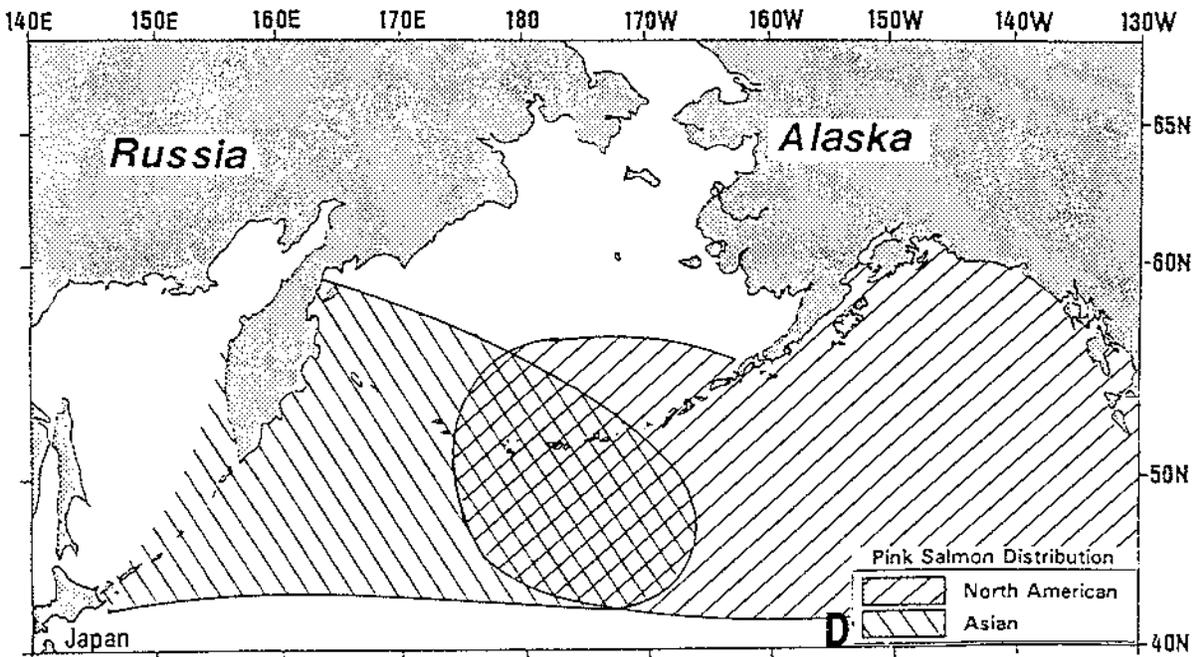
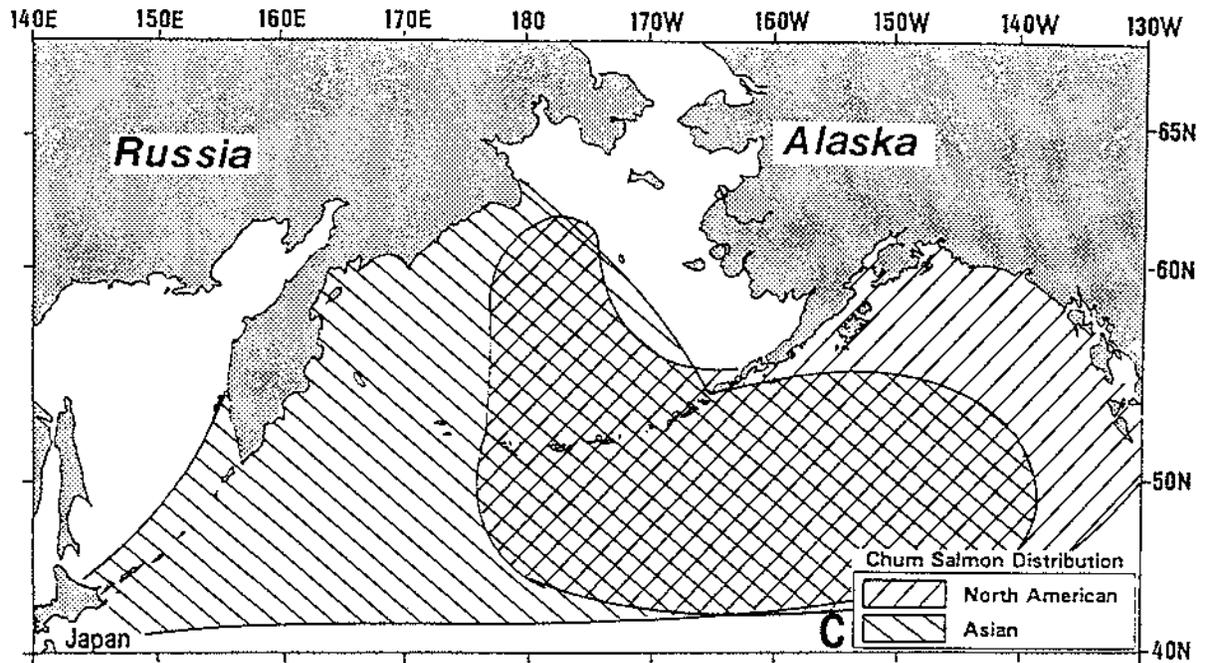


Figure 8. Oceanic distribution of chinook (A), coho (B), chum (C), pink (D) and sockeye (E) salmon, according to Myers et. al. (1990). Migration routes between spawning rivers and rearing areas is omitted for clarity. (Continued)

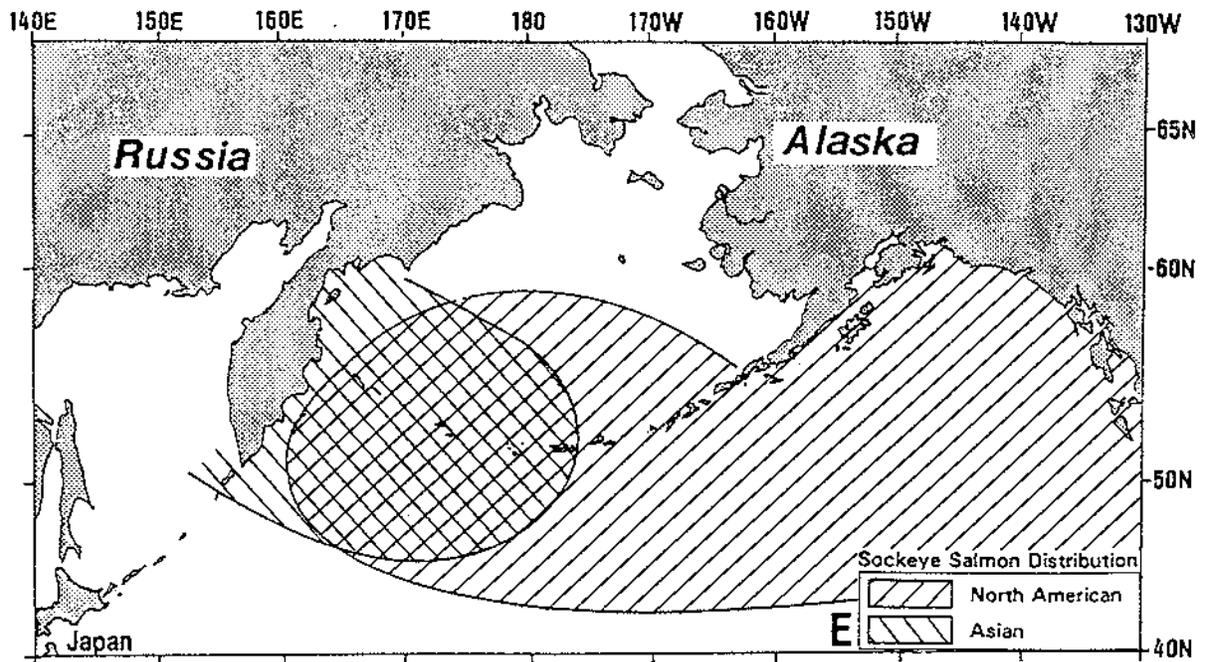


Figure 8. Oceanic distribution of chinook (A), coho (B), chum (C), pink (D) and sockeye (E) salmon, according to Myers et. al. (1990). Migration routes between spawning rivers and rearing areas is omitted for clarity. (Continued)

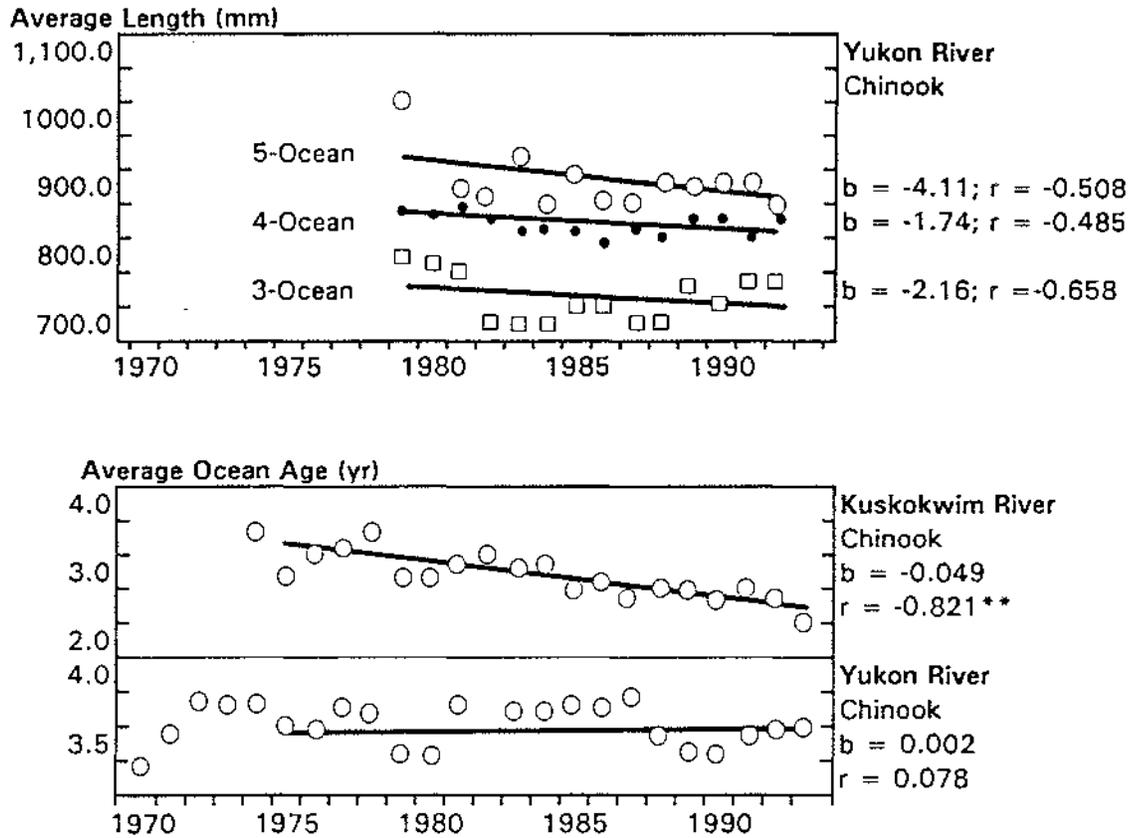


Figure 9. Change in average length (mm) and age (yr) among Kuskokwim and Yukon River chinook salmon. Data from ADFG computer archives (P.O. Box 25526, Juneau). The value "b" is the calculated average annual change in each variable. (** = $P < 0.01$)

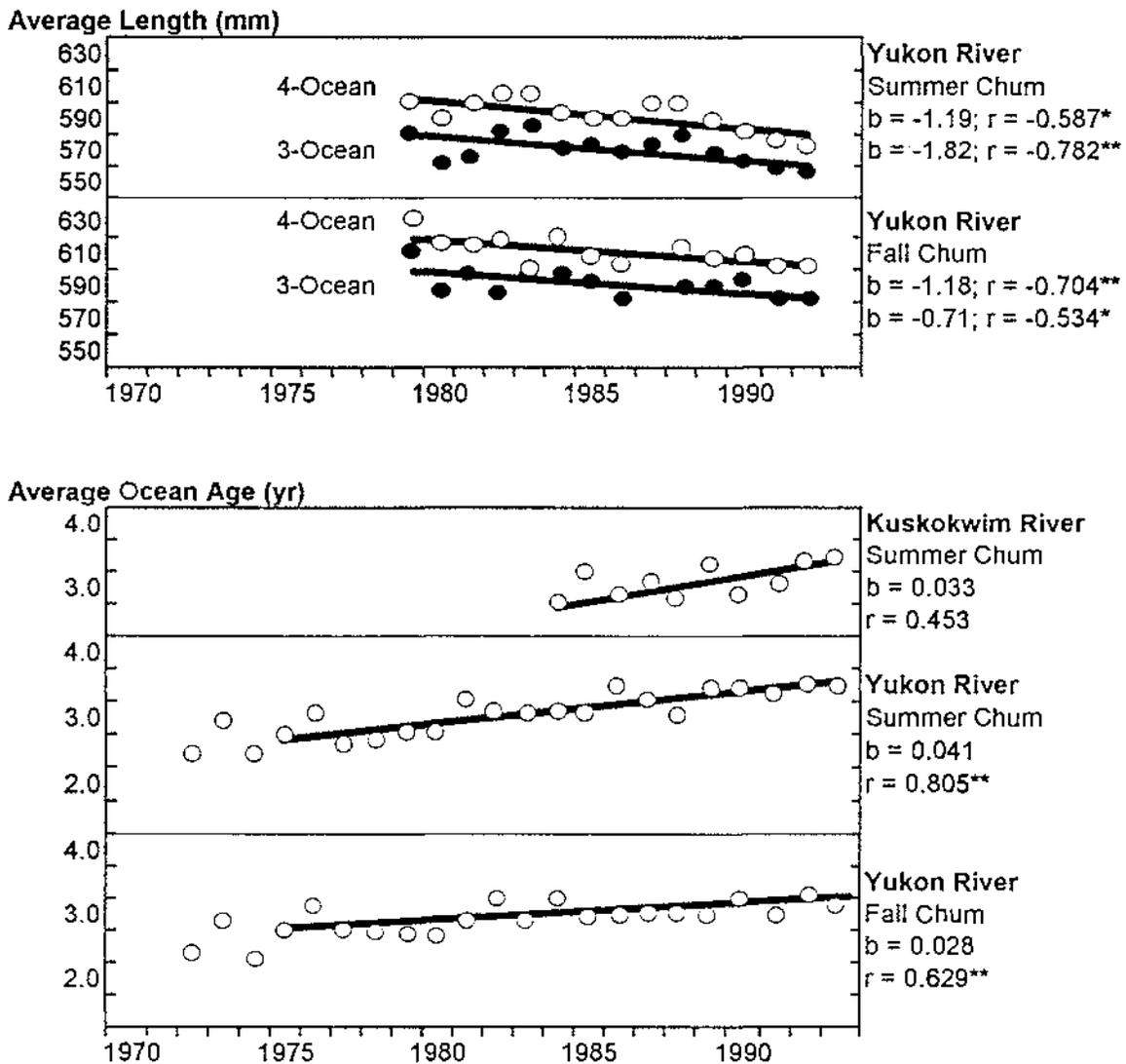


Figure 10. Change in average length (mm) and age (yr) among Kuskokwim and Yukon River chum salmon. Data from ADFG computer archives (P.O. Box 25526, Juneau, Alaska). The value "b" is the calculated average annual change in each variable. (* = $P < 0.05$; ** = $P < 0.01$)

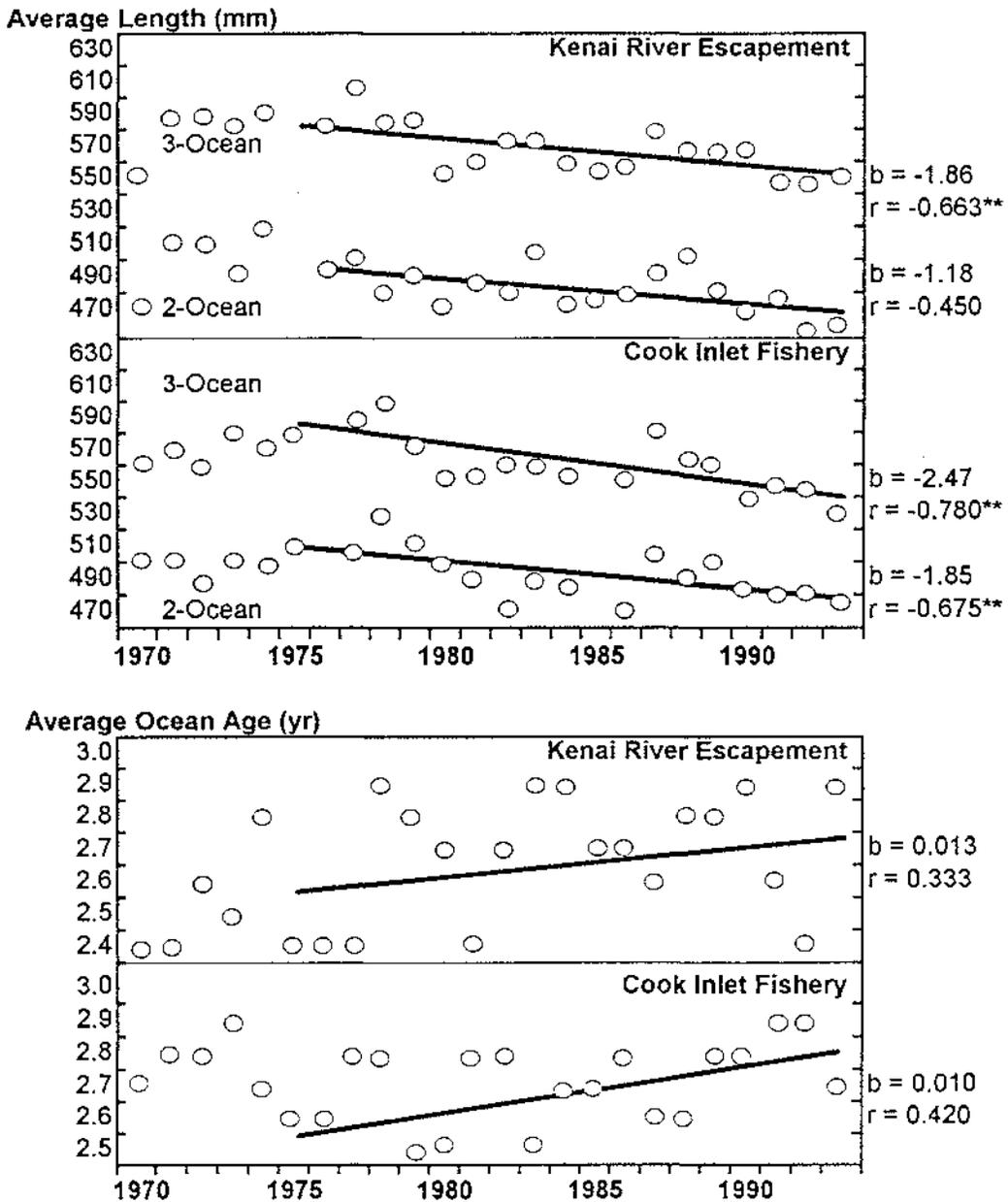


Figure 11. Change in average length (mm) and age (yr) among Kenai River escapement and Cook Inlet commercial sockeye salmon harvest, 1970-1993. Data from ADFG regional reports (K. Tarbox, 34828 K-Beach Road, Soldotna, Alaska 99669-8367). The value "b" is the calculated average annual change in each variable. (* = P<0.05; ** = P<0.05)

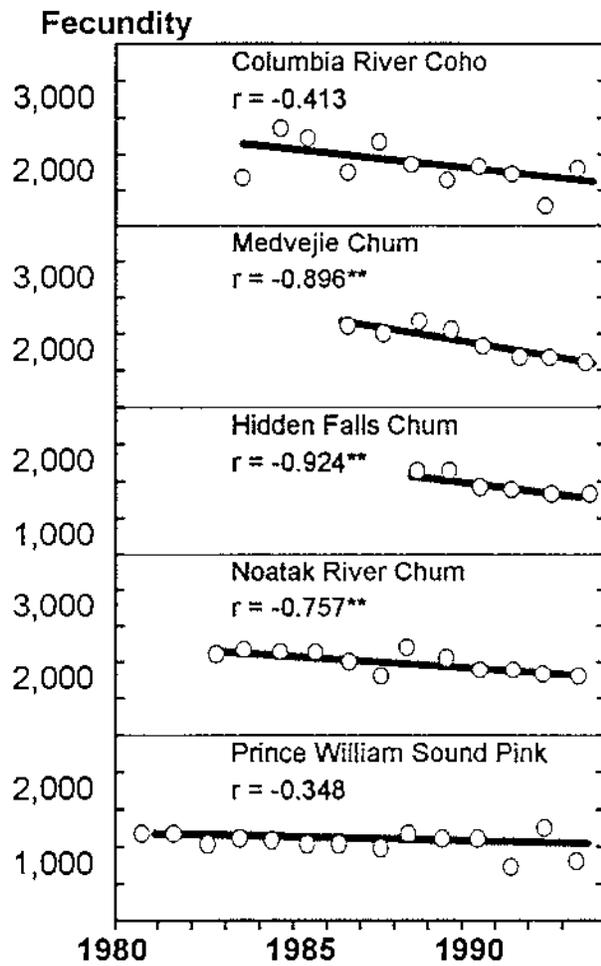


Figure 12. Mean fecundity of hatchery coho, chum and pink salmon, 1982-1993. (**P>0.01) See text for data sources.

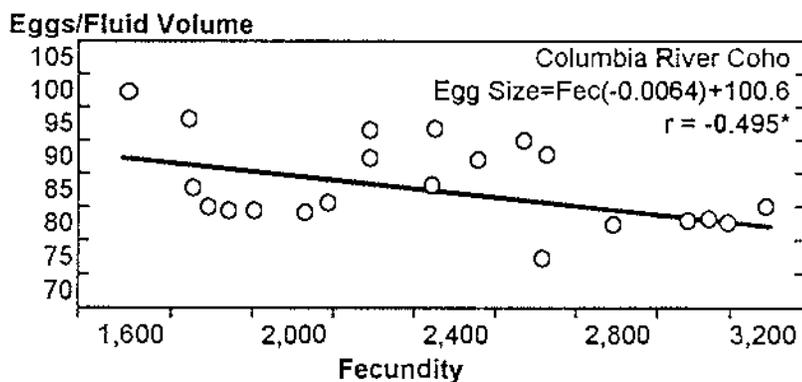
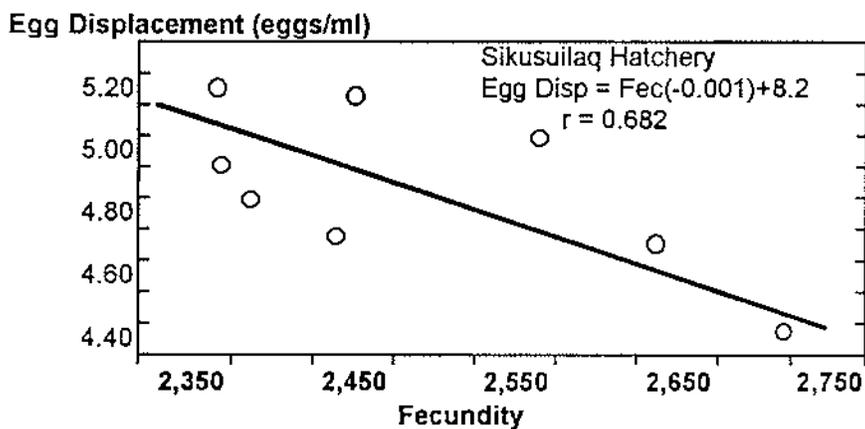
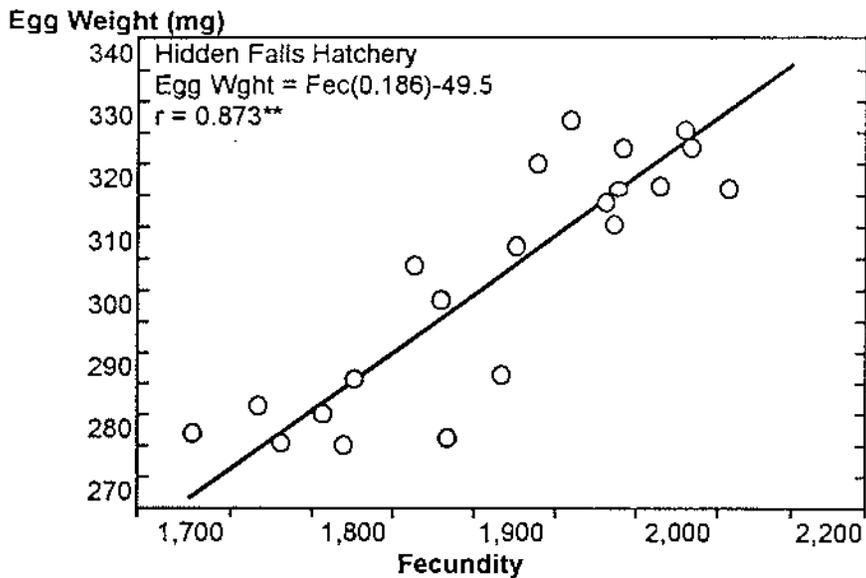
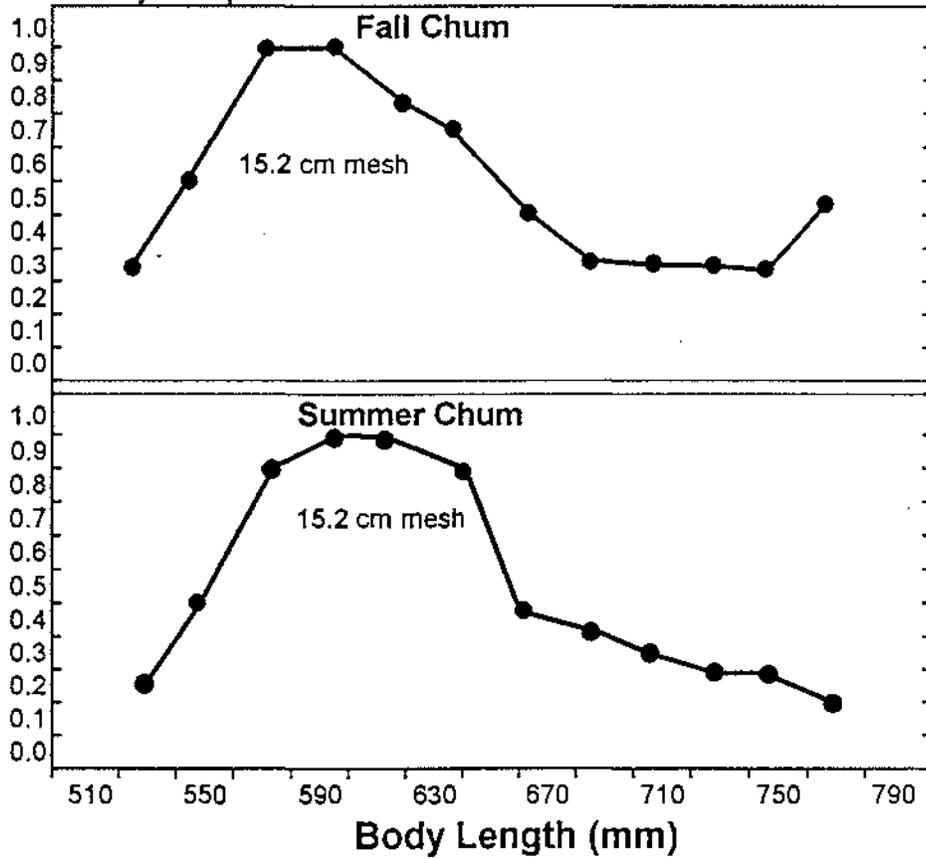


Figure 13. Measurement of decreasing egg size with decreasing fecundity in summer chum (top), fall chum (middle) and coho (bottom) salmon, based on studies conducted at hatcheries in Alaska and Washington State.
 (* = $P < 0.05$; ** = $P < 0.01$)

Relative Efficiency of Capture



Relative Efficiency of Capture

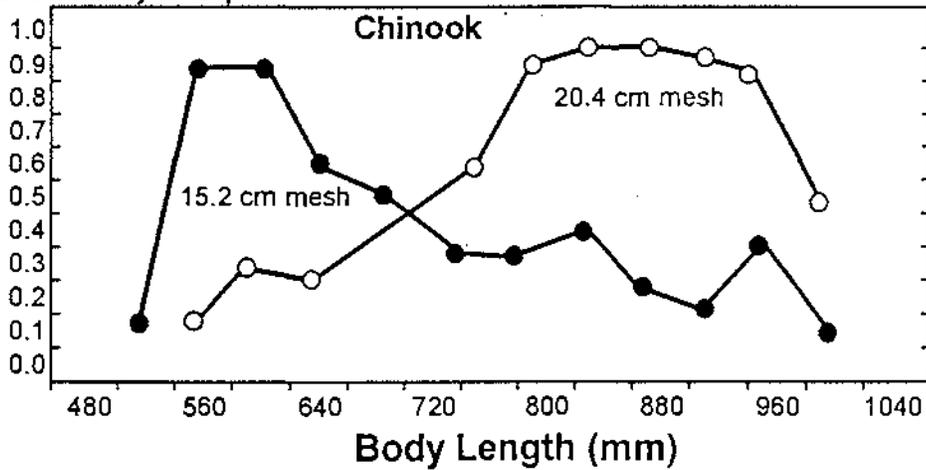


Figure 14. Net selectivity curves for 15.2 cm (6 in.) and 20.4 cm (8 in.) stretched mesh gill nets. Based on curves developed by Fleischman (333 Raspberry Road, Anchorage, Alaska 99518-1599).