Exxon Valdez Oil Spill
Restoration Project Final Report

Historical Analysis of Sockeye Salmon Growth Among Populations Affected by the *Exxon Valdez* Oil Spill and Large Spawning Escapements

Restoration Project 96048-BAA
Final Report

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December 1998

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Study History: The entire investigation, including data collected in 1997, was completed within Restoration Project 96048-BAA.

Abstract: Adult sockeye salmon scales, which provide an index of annual salmon growth in fresh and marine waters during 1965-1997, were measured to examine the effects on growth and adult returns of large spawning escapements influenced by the *Exxon Valdez* oil spill. Scale growth in freshwater was significantly reduced by the large 1989 spawning escapements in the Kenai River system, Red Lake, and Akalura Lake, but not in Chignik Lake. In the Kenai River system, juvenile sockeye growth recovered to historical levels during the second year of low escapement after the spill, but growth significantly declined following the moderately-high escapement in 1992. Growth of Akalura sockeye reached average levels four years after the oil spill; growth of yearling salmon co-inhabiting the lake with the 1989 fry also was reduced. Red Lake sockeye growth recovered to historical levels three years after the spill, then growth declined following a moderate escapement in 1992. These data suggest that sockeye growth in freshwater may be less stable following the large escapement. Furthermore, the observations of large escapement adversely affecting growth of adjacent brood years of salmon has important implications for stock-recruitment modeling. In Prince William Sound, Coghill Lake sockeye salmon that migrated through oil-contaminated waters did not exhibit noticeably reduced marine growth, but a model was developed that might explain low adult returns in recent years.

Key Words: Alaska, escapement, *Exxon Valdez*, growth, oil spill, *Oncorhynchus nerka*, scale, salmon, spawning, stock-recruitment.

Project Data: *Description of data:* Scale measurements of each life stage of individual sockeye salmon representing ten stocks in Alaska were compiled for adults returning during 1970-1997. Only the dominant age group of each stock was measured. *Format:* The dataset contains more than 18,000 records and is maintained in a comma delimited, text format. *Custodian:* Greg Ruggerone, Natural Resources Consultants, Inc., 4055 21st Avenue West, Suite 100, Seattle, WA 98199 (phone: 206-285-3480, fax: 206-283-8263, email: GRuggerone@aol.com or nrc@nrccorp.com).

Citation: Ruggerone, G.T. and D.E. Rogers. 1998. Historical analysis of sockeye salmon growth among populations affected by large escapement in 1989. *Exxon Valdez* Oil Spill Restoration Project Final Report (Restoration Project 96048-BAA), Natural Resources Consultants, Seattle, Washington.

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EXECUTIVE SUMMARY

Several sockeye salmon systems received exceptionally large spawning escapements as a result of the 1989 *Exxon Valdez* oil spill and management decisions to prohibit harvested of potentially contaminated salmon. Public concern was expressed regarding potentially adverse effects of the large escapements, including reduced growth of offspring, reduced survival, and lower production of adult salmon. River systems receiving large escapements include the Kenai River in Cook Inlet, Red Lake and Akalura Lake on Kodiak Island, and Chignik Lake on the Alaska Peninsula. Although comprehensive field studies were initiated as a result of the 1989 spill, relatively few data had been previously collected in most systems. Furthermore, scientists suggested that oil contamination in Prince William Sound may have exacerbated the decline of Coghill Lake sockeye salmon.

We measured growth patterns recorded on returning adult sockeye salmon scales, which are routinely collected by ADFG, to develop a historical index of sockeye growth during each life stage (freshwater and marine). These data were compared to spawning escapements during 1965-1992 (i.e., runs 1970-1997) in order to evaluate escapement effects on sockeye growth in nursery lakes. Previous research had shown high correlation between scale growth and sockeye growth in freshwater. Scale growth of Coghill Lake sockeye salmon, which migrated through Prince William Sound in 1989, was examined for indications of reduced growth during the first year at sea.

We measured scales from ten sockeye salmon stocks during each year of return, 1970 to 1997. For each stock and each year, we measured up to 100 scales from the dominant age group (age 1.3 for most stocks). In addition to the stocks listed above, we measured scales from Kasilof River, Black Lake, Bear Lake, and Nushagak Bay since these stocks were not affected by large escapements in 1989. Selected sockeye scales were measured on the Optical Pattern Recognition System (OPRS), which consists of a high resolution video camera mounted on a microscope and controlled by a computer program.

Kenai River, Upper Cook Inlet

The *Exxon Valdez* (1989) oil spill contributed to the large spawning escapement (1.38 million) that was approximately 2.5 times the management goal of 400,000 to 700,000 fish. This large escapement followed large escapements in 1988 (0.9 million) and 1987 (1.4 million), the year of the *Glacier Bay* oil spill in Upper Cook Inlet. These large escapements led to low freshwater scale growth of offspring compared to the historical average. Growth recovered to historical levels in brood year 1991, two years following the *Exxon Valdez* oil spill, but a moderately high escapement in 1992 lead to exceptionally low growth suggesting the Kenai River system may now be less stable. Multiple regression analysis indicated freshwater growth was influenced by the size of both parent spawning escapement and prior escapements. Adult sockeye return to the Kenai system was positively correlated with greater parent spawning escapement and to greater growth in freshwater, suggesting that continuously large spawning escapements that adversely affect growth of future sockeye fry may lead to somewhat smaller adult returns. The brood (1982) having the greatest growth in freshwater also produced the largest run (1987) to the Kenai River. Additional research is needed to examine the tradeoffs between spawning escapement, juvenile sockeye growth, adult return, and maximum sustained harvests in the Kenai system.

Red Lake, Kodiak Island

The oil spill contributed to an escapement of 768,000 sockeye salmon into Red Lake, approximately three times the escapement goal. This large spawning escapement led to reduced growth of juveniles during the first and second years in Red Lake. Growth of fry from the 1990 brood (second year following the spill), which co-inhabited the lake with yearlings from the 1989 brood, remained low compared to historical averages. Sockeye growth recovered during the third rearing season following the spill as both fry and yearling sockeye reached historical size levels. However, growth during the next two years (1991 and 1992 broods) was low compared to the historical average even though parent escapements were moderate, suggesting that Red Lake may be less stable following the large 1989 escapement. Regression analysis did not reveal a consistent relationship between spawning escapement and juvenile growth during the 28 year sampling period, although growth of fry and yearlings co-inhabiting the lake was highly correlated. Multiple regression analysis indicated adult sockeye return to Red Lake was positively correlated with parent escapement, growth during the first year in Red Lake, and growth during the first year at sea.

Akalura Lake, Kodiak Island

The 1989 escapement of 116,000 sockeye salmon into Akalura Lake was more than twice the escapement goal. Growth of fry from the 1989 brood and yearlings from the 1988 brood, which co-inhabited Akalura Lake in 1990, was the lowest of the 12 year observation period. Below average growth continued until it reached average levels during the fourth growing season (1993) after the spill. Multiple regression analysis indicated cumulative sockeye growth in the lake was negatively related to parent spawning escapement and escapement during the following year (i.e. adverse effect on yearlings), and positively related to average spring air temperature on Kodiak Island. Examination of adult runs since 1986 suggests the large escapement in 1989 and corresponding reduced juvenile growth may have influenced the relatively low run sizes during 1994-1996, i.e., years corresponding to escapements during 1989-1992. The 1997 run has yet to be estimated by ADFG.

Chignik Lake, Southern Alaska Peninsula

The moderately large spawning escapement in Chignik Lake during 1989 did not appear to affect growth of juveniles and the corresponding adult return was 40% above the recent 10 year average. Regression analysis did not reveal correlation between spawning escapement and growth in the lake, but spawning escapements have not varied much during the past 27 years. Field research indicated that the emigration of Black Lake sockeye to Chignik Lake adversely affects adult returns to Chignik Lake. Adult returns were not correlated with growth in freshwater, but adult runs to the Chignik system during 1952-1997 were positively correlated with growth during the first two years at sea, as discussed below.

Coghill Lake, Prince William Sound

We could not detect an effect of oil in Prince William Sound on annual marine growth of sockeye that migrated through the Sound in 1989. Analysis of growth in Coghill Lake did not reveal an adverse effect of the exceptionally large escapements during 1980-1982. However, freshwater growth declined steadily from brood years 1983 to 1988, encompassing a period of large escapements (1985 and 1987) and exceptionally low adult returns from the 1985-1990 brood years. During 1976-1992, growth in freshwater was negatively correlated with annual precipitation at Valdez. Multiple regression analysis indicated adult return to Coghill Lake was positively related to spawning escapement, negatively related to precipitation during the smolt migration period, and negatively related with average snow depth prior to the smolt migration period. These data suggest lake turbidity, which likely increases with runoff in this glacial lake, and food availability immediately prior to seaward migration might influence survival.

Marine Growth and Sockeye Run Size

Marine scale growth among the 10 sockeye stocks was examined to test whether growth at sea was correlated between stocks. The number of significant marine scale growth correlations (positive) among the stocks (up to 45 correlations) increased from 20% during the first year at sea, to 60% during the second year, to 100% during the third year (6 stocks). During the first year at sea, Bristol Bay sockeye stocks tended to be negatively correlated with stocks adjacent to the Gulf of Alaska, although most of these correlations were not statistically significant. These trends may reflect local differences in marine growing conditions in areas adjacent to natal freshwater systems and a tendency for the stocks to disperse and mix with other stocks in subsequent years.

Scale measurements of Chignik Lake sockeye were made from runs during 1952 to 1997, a time period encompassing both low and high salmon runs. Scale growth during the first two years in the ocean was positively correlated with both sockeye run size to the Chignik system and with sockeye run size to Central Alaska. Consistently higher growth at sea began in the mid-1970s, a time period corresponding to warmer sea-surface temperatures during winter and to greater salmon runs throughout Alaska.

Conclusions

This study demonstrated that large escapements related to the *Exxon Valdez* oil spill contributed to reduced growth of sockeye salmon rearing in the Kenai River system, Akalura Lake, and Red Lake, but not in Chignik Lake. Although sockeye scale growth reached average levels two to four years after the oil spill, growth of sockeye in the Kenai River system and in Red Lake appeared to be less stable in response to moderate escapement levels after the large 1989 escapement. This result suggests large escapements may continue to have an adverse effect on sockeye growth even after growth reaches average levels following average spawning escapements. Furthermore, the large escapements in each of these systems contributed to reduced growth of sockeye salmon originating from adjacent brood years. This finding of brood year interaction has important implications for stock-recruitment modeling, which is the primary tool for determining spawning escapements goals and establishing harvest rates.

Summary Table 1. Summary of results obtained in the study of sockeye salmon scales. NR = not relevant. Blank indicates topic was not evaluated.

Stock	Parent escapement effect on growth	Escapement effect on following brood(s)	Escapement effect on previous brood	Recovered from large escapement	Density-independent factors affect growth	Density-independent factors affect adult return	Adult return related to freshwater growth	Adult return related to escapement	Marine growth related to adult return	Oil in PWS affects marine growth
				Stocks influenced by the 1989 oil spill						
Kenai R.	Yes	Yes		yes?, BY 1991 growth now appears less resistent to large escapements	No	No	Yes (+)	Yes (+)	Yes (+), 3rd yr	
Red Lake	Not consistent	Yes	Yes	Yes?, 3rd yr after spill, growth now appears less resistent to moderate escapements	Yes, winter air temp.	No	Yes (+)	Yes (+)	Yes (+), 1st yr	
Akalura Lake	Yes	Yes	Yes	Yes, 4th yr after spill, but only one datum	Yes, spring air temp.	No	Yes (+)	?	?	
Chignik Lake	No	No	No	Yes	No	No	No	No, Black Lake interaction	Yes, 1st two yrs	
Coghill Lake	No, cyclic	Not consistent		NR	Yes, rain (-)	Yes, rain (-) snow (-)	Yes (+)	Yes (+)		Not detected
				Stocks not directly influenced by the 1989 oil spill						
Kasilof R	Yes?	Yes?		NR						
Black Lake	No	No		NR					Yes, 1st two yrs	
Bear Lake	No	No	No	NR						
Nushagak Bay	No	No		NR						

INTRODUCTION

The *Exxon Valdez* oil tanker ran aground in Prince William Sound on March 24, 1989, spilling approximately 258,000 barrels (10.8 million gallons) of crude oil. During the following month, approximately 20% of the oil evaporated, 20-25% dispersed into the water column of Prince William Sound, 40-45% deposited on beaches and subtidal substrate within Prince William Sound, and 25% of the oil exited Prince William Sound (Wolfe et al. 1993).

Alaskan salmon fisheries typically begin in late May and extend until fall, depending on the species and stock of salmon. Soon after the oil spill, the Alaska Department of Fish and Game (ADFG) developed a strategy to prohibit, if possible, harvest of oil contaminated salmon. Thus, the presence of oil in fishing areas greatly diminished fishing opportunity and salmon harvests in Prince William Sound, Cook Inlet, Kodiak and Chignik management areas, resulting in the escapement of large numbers of sockeye salmon (*Oncorhynchus nerka*) into some freshwater systems (Fig. 1). In the Kodiak Island area, about 768,000 sockeye salmon escaped into Red Lake (Ayakulik), approximately three times the management goal of 200,000 to 300,000 (Fig. 2). At Akalura Lake, Kodiak Island, the 1989 spawning escapement of 116,000 sockeye was about twice the management goal of 40,000 to 60,000 sockeye salmon. In Upper Cook Inlet, an estimated 1.38 million sockeye salmon escaped into the Kenai River system, approximately 2.5 times the management goal of 400,000 to 700,000 fish. The large escapement to the Kenai system in 1989 followed large escapements during 1987 (1.4 million) and 1988 (0.9 million). On the Alaska Peninsula, about 860 km from Bligh Reef in Prince William Sound, the presence of oil in and near Chignik Lagoon influenced an escapement of 557,000 sockeye salmon to Chignik Lake, more than twice the management goal of 250,000 sockeye salmon.

Some sockeye systems in vicinity of the oil spill did not receive exceptional spawning escapements, including Black Lake in the Chignik system (96% of 400,000 fish goal) and Coghill Lake in Prince William Sound (67% of 55,000 fish goal) (Fig. 3). However, juvenile sockeye salmon from Coghill Lake migrated through Prince William Sound during spring 1989 and Willette et al. (1996) suggested the presence of oil in the water column may have adversely affected these salmon. The Coghill Lake sockeye stock, which was the largest stock in Prince William Sound, had been declining in abundance since the last large return in 1987 and biologists were concerned that the oil spill may have exacerbated the decline.

Salmon returns typically increase with greater parent spawning escapement, but at exceptionally large escapements returns can decline. This effect is commonly described by the Ricker recruitment curve (Ricker 1954, Hilborn and Walters 1992) (Fig. 4). The adverse effect of exceptionally large escapements is generally believed to be caused by overcrowding on the spawning grounds or overcrowding in the rearing lake, although the mechanism is seldom documented because spawning escapements seldom are allowed to reach exceptional levels. In systems where spawning habitat is a primary factor limiting production, large escapements may lead to redd (nest) superimposition (e.g., Wood River Lake sockeye in 1980, personal observation). Numerous dead eggs in the gravel can be attacked by fungus or other diseases which may spread and cause additional mortality of previously undisturbed, healthy eggs. If the spawning grounds are not overcrowded and production of fry entering the lake rearing area is exceptionally great, then growth of the fry may be slowed and subsequent mortality factors, such as size-dependent predation or winter starvation, may cause increased mortality.

Following the large spawning escapements to several sockeye systems in 1989, Alaska Department of Fish and Game (ADFG) biologists expressed concern that the escapements would produce exceptional numbers of fry leading to overcrowded nursery lakes and low survival (Schmidt et al. 1995, 1996). Numerous sockeye fry can consume a significant portion of the zooplankton in a lake, leading to reduced growth of individual sockeye salmon. If sockeye growth and fat reserves are minimal at the end of the summer growing season, then significant mortality might occur during winter and early spring when little or no food are available (Schmidt et al. 1996, Ruggerone 1997).

In response to this concern, the *Exxon Valdez* Trustee Council funded a major, multi-year field investigation of the effects of the large sockeye salmon escapements into the Kenai River system, Akalura Lake and Red Lake (Schmidt et al. 1995a,b, Swanton et al. 1996). However, prior to the 1990 field season relatively little historical information on juvenile sockeye salmon growth and zooplankton abundance was available in these systems. Thus, a historical perspective of sockeye growth in relation to adult returns prior to the 1989 oil spill was not available for comparison to post-spill relationships.

We proposed that a historical index of sockeye growth during the freshwater phase of sockeye stocks could be developed from adult scales that have been routinely collected by ADFG. Length of juvenile sockeye salmon is correlated with total scale radius (e.g., Fig. 5; Clutter and Whitesel 1956, Bumgarner 1993, Fukuwaka and Kaeriyama 1997). Scales have been used to describe sockeye salmon growth in lakes (Henderson and Cass 1991, Zimmermann 1991, Bumgarner 1993, Ruggerone 1994) and the ocean (Rogers and Ruggerone 1993, McKinnell 1995).

The specific objectives of this investigation are as follows:

1. Measure annual and seasonal growth zones of sockeye salmon scales before, during, and after the oil spill from systems affected by the oil spill (Kenai River system, Akalura Lake, Red Lake, Coghill Lake, Chignik Lake).

2. Measure annual and seasonal growth zones of sockeye salmon scales from systems not influenced by large escapement in 1989 (Kasilof River, Black Lake, Bear Lake (early and late runs), Nushagak Bay), correlate freshwater growth of these control stocks with impacted stocks, and, if possible, compare observed scale growth of impacted stocks with that expected from the regression.

3. Describe the relationship between spawning escapement level and sockeye growth in freshwater, particularly in response to large escapements in 1989 and potential effects on juvenile growth during subsequent years.

4. Evaluate the possible effect of oil in Prince William Sound on sockeye growth of Coghill Lake sockeye salmon that migrated through the region in 1989.

These objectives were used to test the following hypotheses:

1. Large spawning escapements are associated with reduced growth of offspring in lakes.

2. Migration of juvenile sockeye salmon through oil contaminated waters of Prince William Sound was associated with reduced growth.

METHODS

Adult sockeye salmon scale impressions were obtained from ADFG for each stock described above. We attempted to measure scales from sockeye runs during 1970 to 1997, but scales were not available for some stocks during earlier years. Only scales from the dominant age group of each stock were selected for measurement. The age groups selected and years sampled to represent growth of each stock were as follows:

Impacted Stocks	Age	Years Sampled
Kenai	Age 1.3	1972-1997, excl. 1975
Akalura	Age 2.2	1986-1997
Red Lake	Age 2.2	1970-1997, excl. 1972
Chignik Lake	Age 2.3	1970-1997
Coghill Lake	Age 1.3	1974-1997, excl. 1975
Non-Impacted Stocks	Age	
Kasilof River	Age 1.3	1971-1997
Black Lake	Age 1.3	1970-1997
Nushagak Bay	Age 1.3	1970-1997
Bear Lake (early and late)	Age 2.2	1985-1997 & 1981

Age 1.3 refers to sockeye salmon that spent one winter in the lake and three winters in the ocean. These fish are in their fifth year at the time of return because they also spent one winter incubating in the spawning gravel. Thus, the parent spawning year (brood year) of age 1.3 sockeye salmon was five years prior to the year of return.

Nearly all scales were previously aged by ADFG personnel. Sex data collected by ADFG were recorded with the age information. Scales were selected for measurement only when 1) the scale technician agreed with the age determination made by ADFG, 2) the scale shape indicated the scale was removed from the "preferred area," and 3) circuli were clearly visible. Up to 100 scales per year, representing equal numbers of male and female salmon, were measured from each stock.

We attempted to obtain scales collected from adult sockeye salmon that recently entered freshwater in order to minimize potential mixing of other stocks. However, in the Chignik system, the early run Black Lake sockeye scales were collected in Chignik Lagoon during June, whereas the late run Chignik Lake sockeye scales were collected in the lagoon during August; this approach minimized interactions between the two stocks based on run timing patterns (Dahlberg 1968, Bumgarner 1993). Sockeye scales from Nushagak Bay (Bristol Bay) represented sockeye returning primarily to the Wood River Lake system and to a lesser extent Nushagak River and Igushik River (Zimmermann 1991). Some earlier scales from Black Lake, Chignik Lake and Nushagak Bay were measured previously by Bumgarner (1993) and Zimmermann (1991) and were used in this study.

Scale measurements followed procedures described by Davis et al. (1990), Zimmermann (1991) and Bumgarner (1993). Scales were measured with the Optical Pattern Recognition System (Model OPRS-512, BioSonics Inc., Seattle) at a magnification of 113x (freshwater growth) or 56x (marine growth). These magnifications allowed for minimum distances between adjacent measurements of 4.7 microns (μ) (< 1 mm juvenile fish length) for freshwater growth and 9.5 μ for marine growth. The measurement axis was determined by a perpendicular line drawn from each end of the first salt water annulus. Scales were measured from the scale focus to the outer edge of each freshwater annuli (FW1, FW2), spring plus growth (FWPL), each ocean annuli (SW1, SW2, SW3), and to the edge of the scale (SWPL) if resorption was not significant (Fig. 6). The outer portion of the scale (SWPL), which represented growth during the spring homing migration, were not analyzed because resorption was significant among some sockeye stocks. Measurement data and sex of the fish were recorded by the OPRS program then exported to a spreadsheet for subsequent analyses.

Sockeye scales were measured by three technicians, who trained together in order to maintain consistency when measuring scales. We also attempted to have one technician read all or most scales from one stock. To check for consistency between readers, scales were remeasured by another technician for comparisons. Paired t-tests of cumulative scale radii measurements at each growth zone were conducted. These tests indicated that the freshwater growth zones were consistently measured for the Kenai, Coghill, Chignik Lake, Akalura, and Red Lake ($p > 0.05$), but an adjustment was required to standardize the more recent Black Lake and Nushagak Bay scales with previously measured scales (Table 1). Most historical Black Lake and Nushagak scales were measured during a previous study and the technicians were not able to train with the earlier scale readers, although we maintained notes from the previous measurements and conversed with the earlier readers. Freshwater scale measurements for these two stocks were standardized using regression analysis, e.g. measurements of Black Lake scales during 1993-1997 were standardized to those prior to this period. Scale growth during the spring of seaward migration can be a difficult zone to consistently measure and we standardized measurements among three stocks. Scale growth representing the first year at sea was standardized for Kenai and Nushagak stocks and scale growth representing the third year at sea was standardized for Chignik Lake sockeye.

Scale measurements were compared with spawning and adult salmon return statistics (brood tables) maintained by ADFG (S. Moffitt, Cordova; D. Waltemyer, Cook Inlet; C. Swanton, Kodiak and Alaska Peninsula; D. Owen, Chignik), biological information collected from the lake systems (Schmidt et al. 1995 a, b; Swanton et al. 1996, Edmundson et al. 1994, 1997, D. Schmidt and G. Kyle, ADFG, pers. comm.) and seasonal air temperature and precipitation data recorded at Valdez, King Salmon and Cold Bay weather stations operated by the National Weather Service.

Data Analysis

Frequency distributions of cumulative and incremental scale measurements from each growth zone of each stock and year were plotted and analyzed for normality. Skewness of the frequency distributions may indicate size-biased mortality, which may be caused by predation on smaller individuals, starvation, or an increase in older smolts.

Mean annual scale measurements representing sockeye growth in freshwater among the ten sockeye stocks were tested for correlation to evaluate whether annual environmental conditions may have similarly influenced sockeye growth among stocks. For those impacted sockeye stocks showing positive correlation with non-impacted stocks, we used regression analysis to determine whether scale growth influenced by the large 1989 spawning escapement deviated significantly from the expected value based on growth of the non-impacted stock.

Regression analysis was used to test for significant relationships between freshwater scale growth and factors that might influence growth such as abundance of parent spawning escapement, abundance of spawning escapement during the previous year, and air temperature during spring and summer. Regression analysis was also used to test for factors influencing adult returns such as scale growth during each life stage, size of spawning escapement air temperature, and precipitation.

Partial residual analysis (Larsen and McCleary 1972) was used to examine relationships between dependent and independent variables observed in multiple regression analysis. Regression corrected plots show partial residuals and the effect of each independent variable on the dependent variable while incorporating information contributed by other independent variables in the multiple regression. This type of analysis was used to search for nonlinear relationships and to visually describe the partial effect of each independent variable within the multiple regression. The mean partial residual value is equal to the observed mean value of the dependent variable. In some cases, a partial residual value might be above or below the range of observed values, a situation that indicates the relatively strong effect of the independent variable. Partial residuals shown in regression corrected plots are labeled as adjusted dependent variables.

RESULTS

Frequency Distributions

Frequency distributions of cumulative and incremental scale growth measurements of each life stage of sockeye salmon were graphed and inspected for each sockeye stock. More than 2,000 plots were examined. The graphs show that frequency distributions of scale measurements were typically normally distributed, suggesting significant size-dependent mortality, in which most fish below a threshold size died, was not common. An example of typical frequency distributions is shown for sockeye returning to the Kenai River in 1987, the first year of an exceptionally large run (Fig. 7). Less frequently there was some positive skewness, such as that shown in the 1994 Kenai run that was produced by the large 1989 escapement, which might reflect mortality of small fish or small fry that became age-2 smolt (Fig. 8). There were no signs of bimodal distributions that might suggest differential growth differences of sockeye stocks within a system.

The normal distributions also indicated transformations were not necessary prior to statistical analyses. However, spring plus growth during seaward migration of smolts often displayed positive skewness where most values were small and a few were large.

Comparison of Average Freshwater Scale Growth and Smolt Length

Estimated mean smolt size and fry size in the lake were compared with freshwater scale measurements when fish size data were available. Typically, few fish data were available for each system, thereby limiting the range in observed values and the ability to detect correlations. Correlations may also be hampered by elongation of sockeye smolt length during the smoltification process (Rankis 1987), differential proportions of sockeye fry holding over in lakes for a second year (Burgner 1991), biased sampling of fry or smolt (e.g., larger smolts migrate during day versus night (Ruggerone and Rogers 1984)), and size-biased mortality of salmon after leaving freshwater.

Freshwater scale growth of Kenai sockeye salmon was highly correlated with average fall fry length in Kenai and Skilak lakes (weighted by estimated abundance) during brood years 1985 and 1988-1992 (r = 0.83, n = 6).

Kasilof River fry and smolt size data have been collected since the 1979 brood year. Sockeye fry weight during fall was correlated with freshwater scale growth (r = 0.61, n = 14), but smolt length was less correlated with freshwater scale growth (r = 0.43, n = 11).

Akalura smolt length (age-2) was highly correlated with cumulative freshwater scale growth (r = 0.84), but only six years of data were available (brood years 1987-1992).

Red Lake smolt length was marginally correlated with freshwater scale growth, but only six years of data were available (r = 0.47).

Coghill smolt weight was highly correlated with freshwater scale growth, but only four years of data were available (r = 0.98, n = 4).

Comparison of Mean Scale Growth Between Stocks

Mean sockeye scale growth was compared at the end of the first growing season in freshwater, the end of freshwater residence of both age-1 and age-2 juveniles, and at the end of the spring plus growth period.

Scale growth at the end of the first growing season was typically greater among sockeye that spent only one year in freshwater (e.g., Kenai, Kasilof, Nushagak, and Black Lake stocks) compared to those that spent two years in freshwater (Bear Lake, Chignik Lake and Red Lake stocks) (Fig. 9). Among those stocks typically spending only one year in freshwater, scale growth was relatively great among Kenai, Kasilof and Nushagak sockeye compared to Black Lake and Coghill Lake sockeye. Mean scale growth of Coghill sockeye was exceptionally low and was similar to growth of stocks typically spending two years in freshwater.

At the end of freshwater residence, but prior to spring plus growth, cumulative scale growth of sockeye spending two years in freshwater exceeded growth of stocks spending one year in the lakes (Fig. 9). Scale growth of late run Bear Lake sockeye, which was approximately 50% of early run sockeye after the first year in the lake, was much greater during the second year and cumulative growth of late run fish nearly equaled that of early run fish from Bear Lake.

Exceptional spring plus growth occurred among Black Lake, Chignik Lake, and Nushagak sockeye salmon (Fig. 9). Spring plus growth of Black and Chignik lake sockeye occurs in Chignik Lagoon where smaller sockeye salmon spend greater time prior to migrating to sea (Phinney 1968).

Cumulative scale growth prior to entering the ocean was exceptionally low for Coghill Lake sockeye and moderately low for Kenai, Kasilof and Akalura sockeye salmon compared to other stocks. Cumulative scale growth was relatively large for Red Lake, Bear Lake, Nushagak, Chignik Lake and Black Lake sockeye salmon.

Growth Correlations Between Stocks

Freshwater

Mean annual scale measurements representing sockeye growth in freshwater were compared among the ten sockeye stocks to evaluate whether annual environmental conditions may have similarly influenced sockeye growth among stocks. If a positive correlation was observed between two nearby stocks, then this relationship could be used to test whether large spawning escapement in 1989 adversely influenced scale growth relative to the correlated stock that did not receive a large escapement. Brood years during and after 1989, which may have been affected by the large escapement, were excluded from the analysis.

Few of the examined stocks exhibited freshwater scale patterns that were correlated with those of nearby stocks prior to the *Exxon Valdez* oil spill, indicating that factors within the lake tend to control annual variation in growth rates. Chignik and Black Lake scales were highly correlated at the end of the first year in the lake ($r = 0.53$, $n = 24$), but sockeye scale growth in Chignik Lake during the second year was not correlated with growth during the same season of age-0 Black Lake sockeye or age-1 sockeye from nearby Akalura Lake, Bear Lake or Red Lake ($p > 0.05$). Kenai River, Akalura Lake, and Red Lake sockeye scales were not correlated with scale growth of nearby stocks such as Kasilof River, Coghill and Black Lake. Kenai scales were correlated with Nushagak Bay scales ($r = 0.44$, $n = 19$, excluding brood years after 1986), but the common influence of this correlation is questionable given the geographic distance of these systems. Not surprisingly, early and late run sockeye scales from Bear Lake were highly correlated (e.g., FW2: $r = 0.95$, $n = 9$), although early run juveniles were larger, as previously described.

In summary, only scales from Black Lake could be used to determine whether Chignik Lake sockeye growth of the 1989 brood deviated significantly from expectation as a result of the large escapement.

Marine

Marine scale growth among the 10 sockeye stocks was examined to test whether growth at sea was correlated between stocks. All available years were used in this analysis.

Incremental growth during the first year at sea was significantly correlated among 20% of the 45 possible combinations. Significant ($p < 0.05$) positive correlations tended to occur among nearby stocks, e.g, Bear Lake and Nushagak Bay, Chignik and Black Lakes, Kenai and Kasilof systems. Negative correlations in first year marine growth frequently occurred (71%) between the Bristol Bay stocks (early and late Bear Lake and Nushagak Bay) and stocks that directly enter the Gulf of Alaska, but most of these correlations were not statistically significant. Nevertheless, these negative trends provide evidence that growing conditions in Bristol Bay may not be positively correlated with those in the Gulf of Alaska. Incremental growth during the first year at sea was positively correlated with time in eight of 10 stocks. The exceptions were early and late Bear Lake stocks for which data were available only in recent years.

Incremental growth during the second year at sea was significantly correlated (positive) among 60% of the 45 possible combinations. Insignificant correlations occurred when Akalura, early Bear Lake or, to a lesser extent, late Bear Lake stocks were involved. Only the 13 most recent years were available for these three stocks, therefore correlations involving these stocks did not encompass the mid-1970s when a major shift occurred in the North Pacific Ocean (Rogers 1984, Francis and Hare 1994). All but one correlation between stocks (including statistically insignificant relationships) was positive (98%). Second year growth at sea was positively correlated with year of return for all 10 sockeye stocks, although most correlations were not statistically significant.

Incremental growth during the third year at sea was significantly correlated among 100% of the 15 possible combinations (6 stocks). All correlations were positive. Five of six stocks were negatively correlated with year of return, although none was statistically significant.

In summary, the number of significant marine scale growth correlations among the 10 sockeye stocks increased with each year at sea. This trend may reflect local differences in marine growing conditions in areas adjacent to natal freshwater systems and a tendency for the stocks to disperse and mix with other stocks in subsequent years. After the first year at sea, most sockeye stocks tended to display similar responses to oceanic conditions.

Freshwater Scale Growth and Spawning Escapement

Kenai River, Cook Inlet

Freshwater scale growth measurements of Kenai sockeye salmon were available for brood years 1967-1992, corresponding to adult returns in 1972-1997. Scales were not available for the 1970 brood year.

Freshwater scale growth of Kenai sockeye was relatively high during brood years 1968-1986 (avg. 392 µ) when spawning escapement was relatively low (avg. 373,000 fish), then growth declined approximately 21%, on average, during 1987-1992 following the exceptionally large escapements beginning in 1987 (avg. 905,000 fish) (Fig. 10). During the two years prior to the first large escapement in 1987, spawning escapements were relatively small (410,000) and scale growth was great (378 µ). Sockeye scale growth resulting from the 1987 spawning escapement (1.4 million fish) declined abruptly to 324 µ, the lowest recorded growth up to that year. In 1988, escapement declined from the 1987 level but it was still high relative to most years (898,000 fish) and sockeye scale growth increased slightly to 332 µ, a value that was still exceptionally low. In 1989, the year of the *Exxon Valdez* oil spill and another exceptional spawning escapement (1.38 million fish), scale growth declined to its lowest recorded level (308 µ) up to that year. In 1990, spawning escapement decreased significantly (515,000 fish), but scale growth continued to decline (297 μ). In 1991, spawning escapement was small again (430,000 fish) and scale growth increase markedly to a level (353 μ) that approached the pre-1987 average (378 μ). However, in 1992, spawning escapement increased again to 806,000 sockeye salmon and the corresponding scale growth declined to the lowest level (240 μ) of the 21 year period. Spring and summer air temperatures (Kodiak and Cordova) corresponding to the 1992 brood year were above average, thus low temperature does not explain the low growth.

A key factor leading to the first exceptionally large escapement in 1987, in addition to the obvious effect of oil in the harvest areas, was the record large run to the Kenai system. The total Kenai run in 1987 was 8.9 million sockeye, approximately 3.8 times greater than the previous five year average. Scale growth of the age-1.3 sockeye salmon (481.5 μ) that produced 84% of this large run was significantly greater than all other years, 1972-1997 (Bonferronni/Dunn multiple contrast test, $p<0.001$). Furthermore, scale growth during the third year at sea was the greatest of the 21 year sample period (772 μ vs. avg. 623 μ) (Fig. 11), approximately 24% greater than average.

A single factor ANOVA indicated that mean Kenai sockeye scale growth in freshwater during years following the large oil spill-related escapement in 1987 (309 μ) was significantly smaller than scale growth during the 15 years prior to the large escapement (392 μ) ($df = 2472$, $p < 0.001$). A Bonferroni/Dunn multiple comparison test shows that average freshwater scale growth in a given year is typically different from all other means except those of the closest four years (Table 2).

Regression analysis was used to further describe the relationship between scale growth during freshwater residence and spawning escapement. Sockeye scale growth significantly decreased when greater numbers of parent sockeye escaped to the spawning grounds (Fig. 12; $n = 21$, $p = 0.033$, $r^2 = 0.22$). However, the effect on scale growth was best explained by average spawning escapement of the parents and the three previous brood years (Fig. 12; $n = 21$, $p < 0.001$, $r^2 = 0.48$). Potential factors, such as spring and summer air temperatures or percentage of the parent escapement spawning in the mainstem of the Kenai River, did not contribute significant new information to the regression. These results suggest that exceptionally large spawning escapements in the Kenai system may have a lingering effect on sockeye fry growth in subsequent brood years.

Slow growth of sockeye salmon during the first year in freshwater can lead to a greater percentage of the fry population delaying seaward migration and migrating after two years in freshwater rather than one year (Burgner 1991). However, the percentage of the total brood return represented by sockeye salmon spending two years in freshwater (age 2.x) was not correlated with freshwater scale growth, abundance of parent spawners, nor spawners during previous years ($n = 20$, $p > 0.05$), suggesting slow growth did not influence more Kenai fish to remain in the lakes for a second year.[1]

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[1] Multiple regression analysis indicated adult return per spawner (LN R/S) was negatively related to the percentage of 2.x sockeye in the brood return (partial $p = 0.002$), negatively related to

Freshwater scale growth of Kenai sockeye salmon, which represent the entire Kenai system, was compared to sockeye fry and zooplankton data collected in the Kenai and Skilak lakes (i.e., the two large mainstem lakes) by ADFG during years corresponding to the 1985-1992 broods. Multiple regression analysis indicated freshwater scale growth was negatively correlated with abundance of sockeye fry in Skilak and Kenai lakes (partial $p = 0.011$) and negatively correlated with average spawning escapement of the previous three broods ($p = 0.11$; $r^2 = 0.81$, $n = 8$, overall $p = 0.016$), indicating that Kenai scale growth was correlated with fry abundance in the two primary nursery lakes and growth was influenced by prior spawning escapements (Fig. 13).

The previous analyses indicated that sockeye growth was reduced by both exceptionally high fry densities and larger spawning escapements during previous years, but an important question is whether numerous small sockeye leads to reduced salmon returns. In other words, what is the tradeoff between fry abundance in a lake, growth of the fry and subsequent survival? Total sockeye return was positively correlated with both parent spawning escapement (partial $p = 0.003$) and freshwater scale growth at the end of the spring migration period (partial $p = 0.072$, overall $p = 0.01$, $n = 20$, $r^2 = 0.42$) (Fig. 14). Given the range of observations shown in this investigation, Fig. 14 indicates total sockeye return to the Kenai River is larger when both escapement and fry growth are relatively large. For example, the adult return from the large 1987 escapement was considerably greater than the return from the large 1989 escapement (*Exxon Valdez* oil spill) and sockeye growth at seaward migration was larger for fish from brood year 1987 compared to those from brood year 1989.

Further multiple regression analyses indicated total sockeye return to the Kenai River was positively correlated with parent spawning escapement (partial $p < 0.001$) and scale growth during the third year at sea (partial $p = 0.010$) and negatively correlated with spawning escapement during the previous year (Fig. 15, partial $p = 0.028$, $n = 20$, overall $p = 0.002$, $r^2 = 0.59$). This relationship provides further evidence that continuously large escapements can reduce total sockeye return to the Kenai system.

In summary, freshwater scale growth of Kenai sockeye salmon was reduced by numerous fry produced by large parent spawning escapements beginning in 1987 and continuing through the 1989 (*Exxon Valdez* oil spill). Growth recovered to historical levels in 1991 brood year, two years following the *Exxon Valdez* oil spill, but a moderately high escapement in 1992 lead to exceptionally low growth. Regression analysis indicated freshwater growth was influenced by both parent spawning escapement and prior escapements. Adult sockeye return to the Kenai system was positively correlated with greater parent spawning escapement and greater freshwater growth, suggesting that continuously large spawning escapements that adversely affect growth of future sockeye fry may lead to smaller adult returns. Additional research is needed to examine the tradeoffs between

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the percentage of parents spawning in the Kenai mainstem (partial $p = 0.012$) and positively related to freshwater scale growth (partial $p = 0.019$) ($n = 20$, $r^2 = 0.52$, overall $p = 0.002$).

spawning escapement, juvenile sockeye growth, adult return, and maximum sustained harvests in the Kenai system.

Red Lake, Kodiak Island

The *Exxon Valdez* oil spill influenced the spawning escapement of 768,000 sockeye salmon into Red Lake in 1989, approximately three times the escapement goal (Fig. 2). An exceptionally large escapement (774,328 sockeye) also occurred in 1980 as a result of an unexpectedly large run.

On average, approximately 68% of sockeye salmon returning to Red Lake spend two years in the lake. Scale growth of the 1989 year class during the first year in the lake (236 μ) was third lowest of the time series, averaging 81% of the previous 23 year mean (Fig. 16). Growth of the 1989 year class was markedly lower compared to the consistently high growth during the previous six years (avg. 324 μ), even though Kodiak air temperature during spring and summer were above average. Incremental growth during the second year in the lake was 76% of the long-term average (Fig. 17). Cumulative growth at the end of the second year (420 μ) was 80% of average and it was also markedly lower than growth during the previous six years (avg. 572 μ).

Although spawning escapement declined in years after 1989, scale growth of first and second year sockeye inhabiting Red Lake remained low during the 1991 rearing year (i.e., brood years 1989 and 1990) (Figs. 16 and 17). However, growth of both age groups increased markedly during the 1992 rearing year, two years following lake entry of the 1989 year class, then declined again during the 1993 rearing year, a period when spring and summer air temperatures were above average. In contrast to the apparent effects of the large spawning escapement in 1989, growth of sockeye in freshwater was not noticeably reduced by the large spawning escapement in 1980. The effects of the large 1980 escapement may have been compensated, in part, by the exceptionally warm spring air temperature.

Scale growth during the first year in the lake was positively correlated with incremental scale growth of yearling sockeye that co-inhabited the lake (Fig. 18, $r^2 = 0.62$, $n = 25$, $p < 0.001$). For example, growth of sockeye from the 1988 brood year, which inhabited the lake as yearlings when the 1989 fry emerged, was below average (Fig. 16). This relationship indicated that factors influencing growth in the lake, such as food availability and temperature, acted on both year classes that co-inhabited the lake. The relationship also supports the premise that sockeye scale growth represents fish growth in the lakes since scale measurements of these fish were derived from a series of adjacent runs.

Incremental scale growth during each year in the lake was regressed on parent escapement, previous escapement, subsequent escapement and spring, summer and winter air temperature at Kodiak. Incremental scale growth during the first and second years were not correlated with these variables ($p > 0.05$), even though sockeye growth seemed to be adversely influenced by the large 1989 escapement, as previously described.

Slow growth in freshwater can influence a greater proportion of a sockeye population to inhabit the lake for an additional year (Burgner 1991). In Red Lake, the large 1989 spawning escapement resulted in the greatest percentage of returning sockeye salmon spending three years in the lake (14.1%) compared to other brood years (avg. 1.6%). The 1988 brood year, which co-inhabited the lake with the 1989 brood year during its second year, also produced an exceptionally large percentage of sockeye spending three years in the lake (5.8% of adult return).

Multiple regression analysis indicated that the percentage of adult sockeye return spending two or more years in Red Lake was negatively correlated with scale growth during the first year in the lake (partial $p < 0.001$) and negatively correlated with winter air temperature (Kodiak, November to March[2]) prior to the second year in the lake (partial $p = 0.019$, overall $p < 0.001$, $n = 24$, $r^2 = 0.50$), indicating more Red Lake sockeye delay seaward migration when growth during the first year is slow and when conditions potentially influencing growth during their second spring, such as temperature, are less conducive to growth.

Total sockeye return to Red Lake during brood years 1966-1992 was positively correlated with both parent escapement (partial $p < 0.001$) and growth during the first year in freshwater (Fig. 19, partial $p = 0.006$, overall $p < 0.001$, $r^2 = 0.52$, $n = 25$), suggesting that more sockeye returned when numerous, relatively large juveniles inhabited the lake. The multiple regression model was further improved by the addition of incremental scale growth during the first year at sea (partial $p = 0.03$, overall $p < 0.001$, $r^2 = 0.61$)[3].

The natural log of sockeye return per spawner was positively correlated with scale growth during the first year in the lake ($r^2 = 0.34$, $n = 25$, $p = 0.002$) and with cumulative growth through the first year at sea ($r^2 = 0.29$, $n = 25$, $p = 0.005$). Red Lake sockeye return per spawner (log) was not correlated with other variables such as escapement and air temperature.

In summary, the large 1989 spawning escapement led to reduced growth of 1989 offspring during the first and second years in Red Lake. Growth of fry from the 1990 brood (second year following the spill), which co-inhabited the lake with yearlings from the 1989 brood, remained low compared to historical levels. Sockeye growth recovered during the third rearing season following the spill as both fry and yearling sockeye reached historical size levels. However, growth during the next two years (1991 and 1992 broods) was relatively low. Regression analysis did not reveal a consistent relationship between spawning escapement and juvenile growth during the 28 year period, although growth of fry and yearlings co-inhabiting the lake was highly correlated. Multiple regression

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[2] Spring air temperature was also negatively correlated with the percentage of hold-overs but winter temperature provided a higher correlation.

[3] We evaluated the Ricker recruitment curve as a means to enhance the relationship between return and escapement but the relationship was not statistically significant. However, one could visually fit a Ricker curve through the data, including the moderate returns from the two large escapements.

analysis indicated adult sockeye return to Red Lake was positively correlated with parent escapement, growth during the first year in Red Lake, and growth during the first year at sea.

Akalura Lake, Kodiak Island

The *Exxon Valdez* oil spill contributed to the escapement of 116,000 sockeye salmon into Akalura Lake, more than twice the escapement goal of 60,000 sockeye salmon (Fig. 2). Periodic spawning escapement counts have been made since 1923 and escapements exceeding 100,000 spawners were observed during 1926, 1934, 1936, 1937, and 1945 (Edmundson et al. 1994). However, age composition of the runs was not estimated prior to 1986 and harvest estimates are subject to error associated with the mixed-stock fishery.

Most sockeye emigrate from Akalura Lake after two years in freshwater; approximately 71% of the brood returns during 1988-1990 spent two years in the lake. Thus, scale measurements were made from age 2.2 sockeye returning to the lake during 1986-1997 (brood years 1981-1992).

Growth of offspring produced by the 1989 brood was exceptionally small during the first year in the lake, averaging only 76% of the previous eight year mean (Figs. 20 and 21). Growth during the second year was nearly average, but total growth at the end of the second year was only 80% of the previous mean.

Second year growth of sockeye from the previous brood year (1988), which inhabited the lake when the 1989 fry emerged, was exceptionally low, averaging only 71% of the previous mean (Fig. 21). Scale growth during the second year in the lake was highly correlated with scale growth of first year sockeye that co-inhabited the lake ($r^2 = 0.83$, $n = 11$, $p < 0.001$).

Cumulative freshwater growth of Akalura sockeye was exceptionally low during the 1988 and 1989 brood years, which were directly influenced by the large 1989 escapement (Fig. 20). Cumulative growth increased steadily for the 1990 and 1991 brood years, but it remained below historical growth prior to the *Exxon Valdez* oil spill, even though Kodiak air temperature during spring and summer was above average. However, cumulative growth of the 1992 brood year increased substantially (411 μ) and was similar to growth prior to the oil spill (avg. 418 μ), suggesting that sockeye growth returned to average levels four years after the oil spill. Kodiak air temperature during 1993 was above average.

Scale measurements were compared to spawning escapement counts during 1986-1992 because escapement estimates were not available during 1981-1985. Multiple regression analysis indicated scale growth during the first year in the lake was negatively correlated with parent spawning escapement (partial $p = 0.013$) and positively correlated with Kodiak air temperature during April to May (partial $p = 0.055$) ($r^2 = 0.51$, $n = 7$, overall $p = 0.030$).

A similar effect of escapement and air temperature was observed for scale growth during the second year in the lake. Multiple regression analysis indicated scale growth during the second year in the lake was negatively correlated with subsequent spawning escapement that produced fry co-inhabiting the lake (partial $p = 0.006$) and positively correlated with Kodiak air temperature during April to May (partial $p = 0.030$) ($r^2 = 0.82$, $n = 8$, overall $p = 0.015$).

Further analysis indicated escapement and air temperature significantly influenced cumulative scale growth in Akalura Lake. Multiple regression analysis indicated cumulative scale growth through the second year in the lake was negatively correlated with the spawning escapement that produced fry co-inhabiting the lake (partial $p = 0.001$), negatively correlated with parent spawning escapement (partial $p = 0.003$), and positively correlated with average Kodiak air temperature during April to May when the fish inhabited the lake as fry and yearlings (Fig. 22, partial $p = 0.009$) ($r^2 = 0.98$, $n = 7$, overall $p = 0.003$).

These analyses indicate growth of Akalura sockeye that inhabit the lake for two years are influenced by parent spawning escapement, escapement that produces fry that co-inhabit the lake, and spring air temperature.

Too few data (three years) were available to statistically test the effects of scale growth on abundance of adult sockeye salmon returning to Akalura Lake. However, it is worthwhile to note that average run size corresponding to parent years 1989 and thereafter (i.e., 1994-1996: avg. 25,000 sockeye salmon) was only 22% of corresponding runs eight years prior to the large escapement (1986-1993: avg. 110,000 sockeye salmon), suggesting that large escapement and reduced growth may have contributed to the small returns.

In summary, growth of fry from the 1989 brood and yearlings from the 1988 brood, which co-inhabited Akalura Lake in 1990, was the lowest of the 12 year observation period. Below average growth continued until the fourth growing season (1993) after the spill. Regression analysis indicated cumulative growth in Akalura Lake was negatively related to parent spawning escapement and escapement during the following year, and positively related to average spring air temperature on Kodiak Island. Examination of adult runs since 1986 suggests the large escapement in 1989 and corresponding reduced juvenile growth may have influenced the relatively low run sizes during 1994-1996.

Chignik Lake, Southern Alaska Peninsula

The *Exxon Valdez* oil spill influenced the escapement of 557,000 sockeye salmon into Chignik Lake, more than twice the escapement goal of 250,000 (Fig. 2). Spawning escapements to Chignik Lake (and Black Lake) have been monitored by a weir since 1922 and escapements have exceeded 500,000 during 16 years. However, since the spawning escapement goal was established in 1965, the largest escapement (other than in 1989) was 426,000 in 1990.

Among sockeye salmon systems receiving large sockeye escapements as a result of the *Exxon Valdez* oil spill, Chignik was the only system that did not receive funds to conduct field studies to investigate the effects of the large escapement.

During August 1989, when it became apparent that the restricted commercial fishery could not adequately harvest the large Chignik Lake run, we recommended aerial surveys of the spawning grounds to document the distribution and relative density of fish on the spawning grounds. However, ADFG funds were not available for the additional task and surveys were not conducted.

On average, approximately 73% of sockeye salmon returning to Chignik Lake spend two years in the lake and 79% spend three years at sea. First year freshwater scale growth of sockeye produced by the 1989 brood (232 μ) was slightly above average (208μ) (Fig. 23). Scale growth during the second year in the lake (139 μ) was slightly below average (146 μ) (Fig. 24). Cumulative growth in freshwater (371 μ)) was slightly above average (354 μ). Thus, we could not detect an adverse effect of the large 1989 spawning escapement on Chignik sockeye growth. The adult return produced by the 1989 escapement (1.8 million fish) was markedly larger than average during the past 20 years (1.27 million fish).

Chignik scale growth during the first year in the lake was not correlated with second year scale growth of yearling sockeye that co-inhabited the lake ($p = 0.24$, $n = 28$), suggesting that growth of Chignik fry and yearling may be influenced by different factors in the lake.

First year scale growth of Chignik Lake sockeye was positively correlated with growth of Black Lake sockeye ($r^2 = 0.40$, $p < 0.001$, $n = 27$). Incremental and cumulative growth of yearling sockeye in Chignik Lake were also correlated with growth of Black Lake fry ($r^2 = 0.25$, $p = 0.007$, $n = 27$). These regressions were used to test whether freshwater growth of the 1989 brood year was reduced compared to that expected from the relationship with Black Lake sockeye salmon. The observed scale growth of Chignik Lake fry was 232 μ compared to the predicted growth of 207 μ, indicating growth during the first year in the lake was greater than expected. The observed incremental scale growth of Chignik Lake yearlings was 139 μ compared to the predicted growth of 148 μ, indicating growth during the second year in the lake was slightly lower than expected but well within the range of past estimates. Cumulative scale growth of Chignik Lake yearlings was 371 μ compared to the predicted growth of 355 μ, indicating cumulative freshwater growth was slightly greater than expected. Thus, this approach indicated that sockeye growth in Chignik Lake was not reduced by the large spawning escapement induced by the *Exxon Valdez* oil spill in 1989.

Adult sockeye return to Chignik Lake was not correlated with scale growth in freshwater ($p > 0.05$). However, previous research indicated the total Chignik sockeye run is correlated with incremental scale growth during the first and second years at sea (Bumgarner 1993). An update of this analysis is shown in Fig. 25 ($r^2 = 0.56$, $p <0.001$, $n = 46$). Sockeye run size to Central Alaska systems is also correlated with marine scale growth, as shown in the figure ($r^2 = 0.46$, $p <0.001$, $n = 46$). This relationship between run size and scale growth at sea is related to consistently greater growth at sea and greater run sizes that began in the mid-1970s, a time period when winter ocean temperatures increased (Rogers 1984).

In summary, the moderately large spawning escapement in Chignik Lake during 1989 did not appear to affect growth of juveniles and the corresponding adult return was 40% above the recent 10 year average. Regression analysis did not reveal correlation between spawning escapement and growth in the lake, but spawning escapements have not varied considerably during the past 27 years. Scale growth during the first two years in the ocean were positively correlated with both sockeye run size to the Chignik system and with sockeye run size to Central Alaska, 1952-1997. Consistently great growth at sea began in the mid-1970s, a time period corresponding to warmer sea-surface temperatures during winter and to greater salmon runs throughout Alaska.

Coghill Lake, Prince William Sound

Coghill Lake received exceptional spawning escapements during the mid-1980s, but not during 1989, the year of the *Exxon Valdez* oil spill (Fig. 2). During peak escapement years (1980-1982, 1985 and 1987), sockeye escapement averaged 166,000 fish which is nearly three times the 30-year mean escapement. Coghill Lake has been the subject of enhancement activities following a sharp decline in returning adults in 1990 (1985 brood year) (Edmundson et al. 1997). The decline in sockeye production, which remained low through the 1994 run (1990 brood year) was believed to be related to excessive spawning escapements leading to overgrazing of zooplankton by numerous sockeye in the lake (Edmundson et al. 1997). During 1991-1994, up to 889,000 sockeye smolts from a hatchery were released near Coghill River. Approximately 330,200 fry were released into the lake in 1994 and in 1995 approximately 900,000 pre-smolts were released into the lake.

Willette (1993) suggested that pink salmon experienced reduced growth when emigrating through oil-contaminated waters in western Prince William Sound. Furthermore, Willette et al. (1996) suggested that the oil spill may have exacerbated the decline in Coghill sockeye production.

We examined Coghill sockeye growth during the first year at sea to evaluate whether sockeye growth was reduced by the presence of oil in Prince William Sound in 1989. We note that reduced sockeye growth in PWS would need to be significant if we were to detect it from annual growth at sea, since sockeye presumably spend a small portion of the first year in PWS.

Examination of incremental scale growth during the first year at sea indicated the 1987 brood year (1182 μ), which migrated through oiled waters in 1989, was typical of scale growth occurring during the previous 17 years of scale growth data (avg. 1122 μ) (Figs. 26 and 27). Growth of Coghill sockeye during the first year at sea was relatively high during years following the 1989 oil spill (1226 μ). We conclude that we could not detect an influence of the oil spill on growth of sockeye salmon that migrated through PWS in 1989. However, detection of an adverse effect would require a major impact on sockeye growth in PWS because the methodology employed here examined growth during the entire year.

Scale growth of Coghill sockeye in freshwater appears to be cyclical with peaks in brood years 1971, 1978, 1983, and 1991, and valleys in 1973, 1980, and 1987 (Fig. 26). Escapements during 1967-1979 were less than 85,000 fish, but from 1980-1982 escapements were exceptionally large (142,000 to 180,000 sockeye salmon). Surprisingly, freshwater scale growth increased steadily during this period of large escapements, exceeding all previous scale growth measurements. This finding is opposite that suggested by Edmundson et al., who hypothesized the high escapements during 1980-1982 may have caused overgrazing of the zooplankton forage base. Adult returns from these three years of large escapements and above average freshwater growth were exceptional (474,000 to 612,000 fish). In 1983, escapement declined to 39,000 fish and freshwater growth increased to its maximum value during the 30 year study period, suggesting superior growing conditions continued after the exceptional 1980-1983 brood years. However, the adult return from the 1983 brood produced only 106,000 sockeye salmon.

Escapement and freshwater growth were inversely related during 1983-1985 and the 1985 brood year produced exceptionally few adults from the relatively large escapement. Very low returns continued from the 1985-1990 brood years, a period when freshwater growth was average to below average. Return per spawner during 1985 to 1989 was ≤0.70. In 1991, the escapement was low, scale growth increased and the return per spawner increased markedly (16:1). In 1992, escapement increased to 29,000 sockeye salmon, freshwater scale growth was moderate and the adult return per spawner was modest (approx. 3.8:1).

Freshwater scale measurements suggest that the exceptionally large spawning escapements during 1980-1982 did not result in overgrazed zooplankton population and reduced fry growth. Apparently the lake was able to sustain numerous sockeye fry produced by the 1980-1982 broods, which survived to produce large adult returns. Freshwater scale growth from the modest escapement in 1983 was exceptional, which further suggests that the large escapements during 1980-1982 did not have a lasting effect on sockeye growth. However, sockeye growth declined steadily from 1983 to 1988 encompassing the period of exceptionally low adult returns that began with the 1985 brood year. Large escapements during 1985 and 1987 (163,000 and 187,000 fish) may have contributed to reduced growth of sockeye in the lake, but it appears that some other factor may have influenced the exceptionally low returns from the 1985-1990 brood years (1990-1995 runs).

Regression analysis was used to evaluate factors correlated with freshwater scale growth of Coghill sockeye salmon. The time period of analysis was limited to brood years 1976 to 1992 because some key environmental data were available beginning in 1976. During this period, freshwater scale growth was negatively correlated with annual precipitation (Valdez station, November to October), i.e. winter prior to fry emergence through first growing season ($r^2 = 0.27$, $n = 17$, $p = 0.03$). However, an outlier was observed corresponding to the 1977 brood year which produced an exceptional adult return. Precipitation corresponding to the 1977 brood year was the lowest on record, suggesting freshwater growth should have been high, based on the above regression model. Actual scale growth of the 1977 brood (225 μ) was slightly below average. We suspect that numerous sockeye inhabited Coghill Lake in 1978, resulting in reduced freshwater growth and an exceptional adult return.

If we remove the 1977 brood from the analysis because of likely density-dependent effects, then the correlation between precipitation and freshwater scale growth improves considerably ($r^2 = 0.47$, $n = 16$, $p = 0.003$). This analysis suggests that high precipitation prior to and during the lake residence period adversely effects sockeye growth, presumably because of greater turbidity in this glacial lake.

Regression analysis was used to evaluate factors correlated with Coghill sockeye returns. The time period of analysis was limited to brood years 1976 to 1992 because some key environmental data were available beginning in 1976. Factors examined included scale growth in the lake and ocean, escapement, air temperature, precipitation, and snow depth. Of these factors, only precipitation (Valdez station) during May and June of the smolt migration year was significantly correlated (negative) with the adult return ($r^2 = 0.25$, $n = 17$, $p = 0.04$). However, if the 1977 brood year, which produced 40 adult sockeye per spawner (32,000 spawners), is removed from the analysis, then several factors become correlated with return. Coghill sockeye return was positively related to escapement (partial $p < 0.001$), negatively correlated with precipitation during the smolt period (partial $p < 0.001$), and negatively correlated with snow depth (partial $p = 0.018$) prior to the smolt migration period (avg. November to May) (Fig. 28, $r^2 = 0.85$, $n = 16$, overall $p < 0.001$).

The negative relationship between precipitation and adult return or juvenile growth was hypothesized prior to the statistical analyses. Greater precipitation and greater run-off is likely correlated with higher turbidity in this glacial system, which likely influences food availability for sockeye salmon (M. Willette, ADFG, pers. comm.). High inflow from rain and snow melt might also cause some loss of zooplankton to downstream transport since freshwater is limited to the upper 30 m of this small lake due to the presence of a permanent anoxic layer of saline water extending to the bottom. Sockeye return was not significantly correlated with scale growth during lake residence (summer or spring migration), but total freshwater growth was negatively correlated with precipitation during the smolt period ($r = -0.39$). These relationships are consistent with the hypothesis that adult return and juvenile growth are influenced by precipitation, but a significant effect of growth on return could not be detected in the dataset. Future research should continue to evaluate this hypothesis.

In summary, we could not detect an effect of oil in PWS on marine growth of sockeye that migrated through PWS in 1989. Analysis of sockeye growth in Coghill Lake did not reveal an adverse effect of the exceptionally large escapements during 1980-1982. However, freshwater growth declined steadily from brood years 1983 to 1988, encompassing the period of large escapements (1985 and 1987) and the exceptionally low adult returns from the 1985-1990 brood years. During 1969-1992, growth in freshwater was negatively correlated with annual precipitation at Valdez. Multiple regression analysis indicated adult return to Coghill Lake during brood years 1979 to 1992 was positively related to spawning escapement, negatively related to precipitation during the smolt migration period, and negatively related with average snow depth prior to the smolt migration period. These data suggest lake turbidity, which likely increases with runoff in this glacial lake, might influence survival.

Stocks Not Receiving Exceptional Escapements

Correlations between freshwater scale growth and spawning escapement of sockeye stocks not influenced by the large escapements in 1989 were examined (Figs. 29-38). Freshwater scale growth was not correlated with spawning escapement in Bear Lake, Black Lake, and Nushagak Bay ($p > 0.05$). Of these three stocks, only Nushagak Bay received an exceptionally large escapement (1980), a result of the large run and a fishing strike. The exceptional escapement caused substantial redd superimposition and mortality of eggs on the spawning grounds. Fry density in the Wood River lakes was not exceptional (Rogers, unpublished data) and thus little effect of parent escapement on freshwater growth was expected.

Freshwater scale growth in the Kasilof River system was negatively correlated with parent escapement ($r = -0.44$ $n = 20$, $p = 0.05$) and escapement prior to the parent year ($r = -0.52$ $n = 20$, $p = 0.018$). The relationship was influenced, in part, by the exceptional escapement in 1985.

DISCUSSION

Adult Scales as an Index of Growth in Freshwater

Relationships between spawning escapement, growth of juvenile sockeye salmon in freshwater and adult return were examined using scale measurements from sockeye salmon that survived smoltification and two to three years at sea. Previous research indicated larger juvenile sockeye salmon may have greater marine survival (Henderson and Cass 1991, Koenings et al. 1993), suggesting scale measurements of surviving salmon might overestimate the size of smolts during years when freshwater growth is low. Since we did not attempt to back-calculate smolt size from adult scales, the key concern is whether the degree of size-dependent mortality significantly varied from year to year, thereby masking a relationship between mean juvenile length and mean scale radius of returning adults. If size-dependent mortality is a dominant factor within a system but varies from year-to-year, then it might prohibit detection of a relationship between scale growth and spawning escapement or adult return. However, if the underlying relationship between juvenile growth and escapement is strong and size-dependent mortality is relatively weak, then the effect of escapement on growth will likely be detected from adult salmon scales. The brief review of published studies shown below supports this conclusion.

Comparison of Chilko Lake sockeye smolt length with length back-calculated from adult sockeye scales by Henderson and Cass (1991) indicated size-dependent mortality in two of three years examined. However, the average difference between estimated smolt size calculated from adult scales and observed smolts was <1 mm. Henderson and Cass could not detect a significant relationship between smolt-to-adult survival and mean annual smolt length during a 34 year investigation period and suggested that the lack of a relationship was probably caused by limited variation in mean annual smolt length and the significant effect of other factors, independent of smolt size, that affect survival. This study suggests error associated with adult scales as an index of juvenile growth would be small.

The relationship between mean sockeye smolt size and smolt-to-adult survival (SAS) reviewed by Koenings et al. (1993) was based on a variety of sockeye salmon stocks, which varied considerably in mean size from stock to stock. Comparisons within stocks showed inconsistent relationships: Cultus Lake sockeye smolt length (age 1) was positively correlated with SAS, Kvichak smolt length was not correlated with survival, and Karluk Lake sockeye smolt lengths, which were exceptionally large on average, exhibited a negative relationship with survival. The comprehensive review by Koenings et al. does not provide evidence that adult scales would significantly mis-represent juvenile sockeye growth.

We suggest that the range in mean size of juvenile sockeye salmon produced within a lake system will likely overshadow year-to-year variation in size-dependent mortality at sea and the resulting index of size measured from adult salmon scales. When a significant relationship between scale growth and escapement was detected in this study, it likely reflects the underlying effect between juvenile growth and escapement. When no relationship was found, we believe that factors such as constant escapement level or environmental conditions were likely significant, although size-dependent mortality may have contributed some error to the underlying relationship.

Spawning Escapement, Growth in Lakes, and Adult Returns

This study supports field studies indicating large spawning escapements into the Kenai River system, Red Lake and Akalura Lake adversely affected sockeye growth and that reduced growth of juveniles may lead to fewer adult returns. However, the impact magnitude of reduced juvenile growth on adult returns was much lower than implied by field studies, especially those in the Kenai River. The historical scale study provided the first evidence that growth and adult return of sockeye from Chignik Lake were not adversely affected by the large escapement in 1989.

One advantage of the sockeye scale study is the long time series of growth measurements (up to 28 years) that could be compared. Analysis of scales indicated sockeye growth in the lakes recovered to historical levels two or four years after the large escapement in 1989, although low scale growth returned in the Kenai and Red Lake systems. In the Kenai River system, low scale growth followed the moderately-high escapement in 1992, whereas Red Lake received moderate escapements during 1990 to 1993. Spring and summer air temperatures at Kodiak and Cordova were above average, thus low growth cannot be explained by low temperature. The decline in scale growth of Kenai and Red Lake sockeye salmon followed moderate escapement levels, suggesting these systems may be less stable following the large escapement in 1989. Recovery of Akalura Lake is based on only one year of data, therefore the stability of this system in response to moderate escapement levels was unknown.

Recent field studies in the Kenai River system demonstrated that large numbers of sockeye fry, which were produced by large escapements, could lead not only to reduced growth of the progeny but also to reduced growth of the subsequent year class of sockeye salmon (Schmidt et al. 1995a, b, 1996). The link between the year classes was *Cyclops*, an important prey that overwinter and provide food for newly emerged fry during spring. Examination of historical sockeye scale growth in the Kenai system provides supporting evidence that large spawning escapements can influence growth of fry one or more years in the future.

Schmidt et al. (1996) estimated a steep decline in Kenai smolt production between the 1987 and 1990 brood years and suggested the collapse of smolt production was caused by low food availability and severe overwinter mortality, especially in the mainstem lakes (Kenai and Skilak). Estimated smolt production per brood year declined from 30.2 million in 1987 to 3.0-5.7 million in 1988-1989 to only 286,000 in 1990, but Schmidt et al. cautiously noted that smolt estimates should be verified with adult return data. Estimated adult returns from these smolt estimates declined from 10 million (1987 brood year) to 2.0-3.6 million (1988 and 1989 brood years) to 1.1 million (1990). Clearly, the 1989 and 1990 smolt production estimates were in error and the anticipated effect of reduced growth and overwinter mortality was much less than indicated by the smolt data. Furthermore, about 82-87% of the total escapement produced by these smolts spawned in mainstem areas (1992-1994, 1995 not available), indicating Kenai and Skilak Lakes still produced the majority of the adult return.

Analysis of adult return, spawning escapement, and juvenile scale growth of Kenai sockeye salmon suggests adult return is relatively great when both parent spawning escapement and juvenile growth are great. This relationship reflects the adverse effect of successive large spawning escapements on juvenile sockeye growth in the Kenai River system. Successively large escapements should be avoided in the Kenai River system, but further analyses of adult return per spawner and interactions between brood years, such as that by Ruggerone (1996), should be conducted to identify adequate escapement levels. This analysis might incorporate juvenile growth estimates developed in this study.

Measurements of sockeye scales from Red Lake demonstrated growth of fry and yearling sockeye co-inhabiting the lake were highly correlated, indicating environmental conditions similarly influenced the two year classes inhabiting the lake. Although the large escapement in 1989 appeared to cause reduced growth of offspring, we could not demonstrate a consistent effect of escapement on juvenile growth in Red Lake during the 28 year period. Apparently key environmental factors overshadowed the effect of escapement on growth in some years, e.g., the large escapement in 1980 lead to above average growth, whereas below average escapement in 1978 led to below average growth of juveniles. Nevertheless, adult sockeye returns to Red Lake during 1970-1997 were positively correlated in a multiple regression with parent escapement, scale growth during the first year in the lake, and growth at sea.

During field investigations of Akalura sockeye salmon, Swanton et al. (1996) noted that relatively small runs during 1994-1996 were produced by relatively small smolt populations and a shift toward older smolts (age-3) that began with the large escapement in 1989. Older smolts and lower smolt abundances were associated with smaller juveniles, as indicated by scale measurements. The 1997 run to Akalura has yet to estimated by ADFG, but growth of juveniles associated with this run was similar to growth prior to 1989.

Growth of sockeye in Akalura Lake was affected by the large escapement, as indicated by Swanton et al. (1996) and this study. Multiple regression analysis indicated that scale growth of Akalura sockeye salmon was negatively correlated with parent spawning escapement and escapement during the following year, and positively related to average spring air temperature. This relationship indicated the adverse effect of large escapement on growth of yearlings from the preceding year.

Edmundson et al. (1994) tabulated historical escapement and run size estimates for Akalura Lake, which were available periodically since 1923. During this period, escapements exceeded 100,000 fish on at least six occasions. All runs produced by these large escapements equaled or fell short of the parent spawning escapement, assuming the majority of the adults returned five years after the parent spawning year. Too few data are available to adequately test the relationship between escapement and adult return in Akalura Lake, but this trend suggests large escapements produce little harvestable surplus.

For Chignik Lake sockeye, we could not demonstrate a relationship between escapement, scale growth or adult return. Scale growth resulting from the large escapement in 1989 was average and the resulting adult return was above average.

The lack of a significant relationship for Chignik Lake may not be surprising given the complex interactions between stocks and the environment. Ruggerone (1994, 1997) documented an inverse relationship between Chignik and Black Lake sockeye runs, which appears to be caused by significant emigration of sockeye fry from Black Lake to Chignik Lake in order to avoid potentially adverse winter conditions in this shallow lake (<1.1 m). Early emigration from Black Lake appears to have increased since the mid-1960s because the lake has become increasingly shallow. The emigration of robust Black Lake juveniles appears to affect yearling rather than fry in Chignik Lake through competition for food during late fall and early spring. This effect was not observed on scales, apparently because it occurs during a brief time period.

Willette (1993) reported that juvenile pink salmon emigrating through moderately oiled areas of Prince William Sound in 1989 appeared to be affected by oil contamination. We examined Coghill sockeye scales from adults that migrated through Prince William Sound in 1989 but could not detect an adverse effect on scale growth during the first year at sea. This result does not mean that an impact on growth did not occur, only that we could not detect an effect using this approach.

Coghill scale growth in freshwater was negatively correlated with annual precipitation, apparently because precipitation increases turbidity in the glacial lake and reduces food availability. Growing conditions appeared to be favorable during 1980-1983 brood years and the large escapements during 1980-1982 did not appear to affect growth, a finding that is opposite that suggested by Edmundson et al. (1997). However, subsequent large escapements during 1985 and 1987 may have affected growth. Regression analysis indicated high precipitation during the smolt emigration period reduced adult returns. These results provide a hypothesis that may be further tested by additional field monitoring of Coghill Lake.

The findings of this investigation of scale growth have important implications for stock recruitment modeling. The study provides evidence that large spawning escapements can influenced both the freshwater growth of their offspring and the growth of progeny produced by adjacent brood years. This effect was demonstrated for the Kenai River system, Red Lake and Akalura Lake. For such systems, it follows that recruitment resulting from any spawning stock size cannot be used to forecast recruitment without considering the sizes of escapements preceding and immediately following the year in question.

Analysis of Marine Growth

The primary purpose of this investigation was to examine trends in the freshwater growth of sockeye salmon. However, we also presented a few results from our analysis of sockeye growth at sea.

Marine scale growth of Chignik sockeye salmon during 1952-1997 was correlated with Chignik run size. Furthermore, marine growth of Central Alaska stocks since 1970 or later tended to be correlated with Chignik Lake sockeye. Sockeye run size to Central Alaska, 1952-1997, was correlated with marine growth of Chignik Lake sockeye salmon. Marine growth was consistently high beginning in the mid-1970s, suggesting that significant changes in the marine environment in the mid-1970s (Rogers 1984, Beamish and Bouillon 1993, Francis and Hare 1994) led to enhanced sockeye salmon growth during the first two years at sea and to greater salmon production in Alaska.

ACKNOWLEDGMENTS

We wish to acknowledge the support of the Alaska Department of Fish and Game for contributing sockeye scales and associated data for use in this project. A number of ADFG biologists provided assistance, including Steve Moffitt, John Wilcock and Mark Willette (Cordova), Charlie Swanton, Patty Nelson, Chris Hicks and Lew Coggins Jr. (Kodiak), Dave Owen (Chignik), Bev Cross, Jim Menard and Dan Grey (Bristol Bay), and Ken Tarbox, David Waltemyer, Dana Schmidt, Gary Kyle and Terri Tobias (Cook Inlet). Kate Myers and Jeff Condiotty provided assistance with the OPRS system. Brenda Rogers, Kristina Ramstad, Megan Ferguson and Alyssa Reichauer spent numerous hours aging, selecting and measuring the sockeye scales and their effort is appreciated. We appreciate the constructive comments of an anonymous reviewer.

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Table 1. Comparison of sockeye scale measurements by different individuals. Results based on paired t-tests. Years requiring standardization between readers are shown.

Growth Zone	Kenai R.	Coghill	Red Lake	Akalura	Chignik Lake	Black Lake	Nushagak
	df = 60	df = 38	df = 38	df = 66	df = 26	df = 29	
FW1	NS P = 0.35	NS P = 0.07	NS P = 0.14	NS P = 0.27	NS P = 0.31	S P < 0.01 d = 46 μ 1993-97	S P < 0.01 d = 70 μ 1995-97
FW2	NR	NR	NS P = 0.05	NS P = 0.50	NS P = 0.07	NR	NR
FWPL	NS P = 0.33	S P = 0.004 d = 15 μ	NS P = 0.99	NS P = 0.17	S P < 0.01 d = 103 μ 1989, 1991-97	S P < 0.01 d = 109 μ 1993-97	S P < 0.01 d = 35 μ 1995-97
SW1	S P = 0.003 d = 32.5 μ 1972-80, 82, 84, 86	NS P = 0.16	NS P = 0.91		NS P = 0.08	NS P = 0.32	S P = 0.02 d = 35 μ 1995-97
SW2	NS P = 0.14	NS P = 0.71	NS P = 0.10		NS P = 0.06	NS P = 0.06	NS P = 0.93
SW3	NS P = 0.37	NS P = 0.50	NR		S P < 0.01 d = 51 μ 1989, 1991-97	NS P = 0.10	NS P = 0.17

Table 2. Results of a Bonferronni/Dunn multiple comparison test to examine annual differences of freshwater scale growth of Kenai sockeye salmon, brood years 1967-1992. The vertical bars indicate mean values that were not statistically different at α = 0.05. Note that this test required p <0.0002 in order to be statistically significant at this level.

Return Yr	Brood Yr	Scale Growth (μ)	Significance										
97	92	240											
95	90	297	|										
94	89	308	|	|									
92	87	324	|	|	|								
73	68	329	|	|	|								
93	88	332	|	|	|	|							
89	84	336		|	|	|	|						
84	79	348			|	|	|	|					
96	91	353			|	|	|	|					
81	76	359			|	|	|	|	|				
72	67	367				|	|	|	|	|			
83	78	368				|	|	|	|	|			
88	83	372					|	|	|	|	|		
80	75	374						|	|	|	|		
90	85	376						|	|	|	|		
91	86	380						|	|	|	|		
74	69	393							|	|	|	|	
78	73	394							|	|	|	|	
82	77	398								|	|	|	|
76	71	399								|	|	|	|
77	72	410									|	|	|
85	80	419									|	|	|
86	81	426										|	|
79	74	435											|
87	82	482											

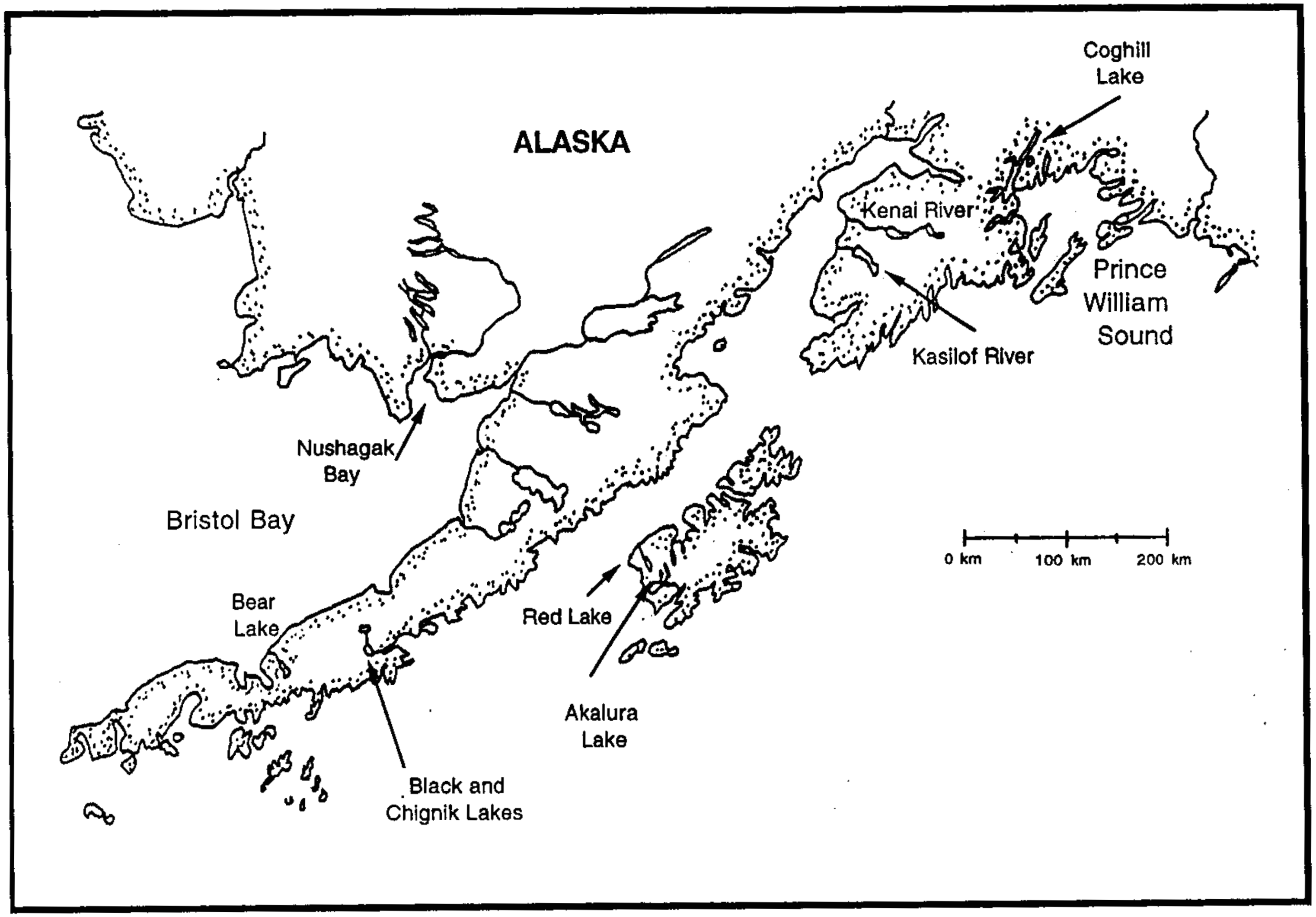

Fig. 1. Location of study area. Oil from the *Exxon Valdez* extended from Prince William Sound to near Ivanoff Bay, approximately 75 miles southwest of Chignik Bay on the Alaska Peninsula.

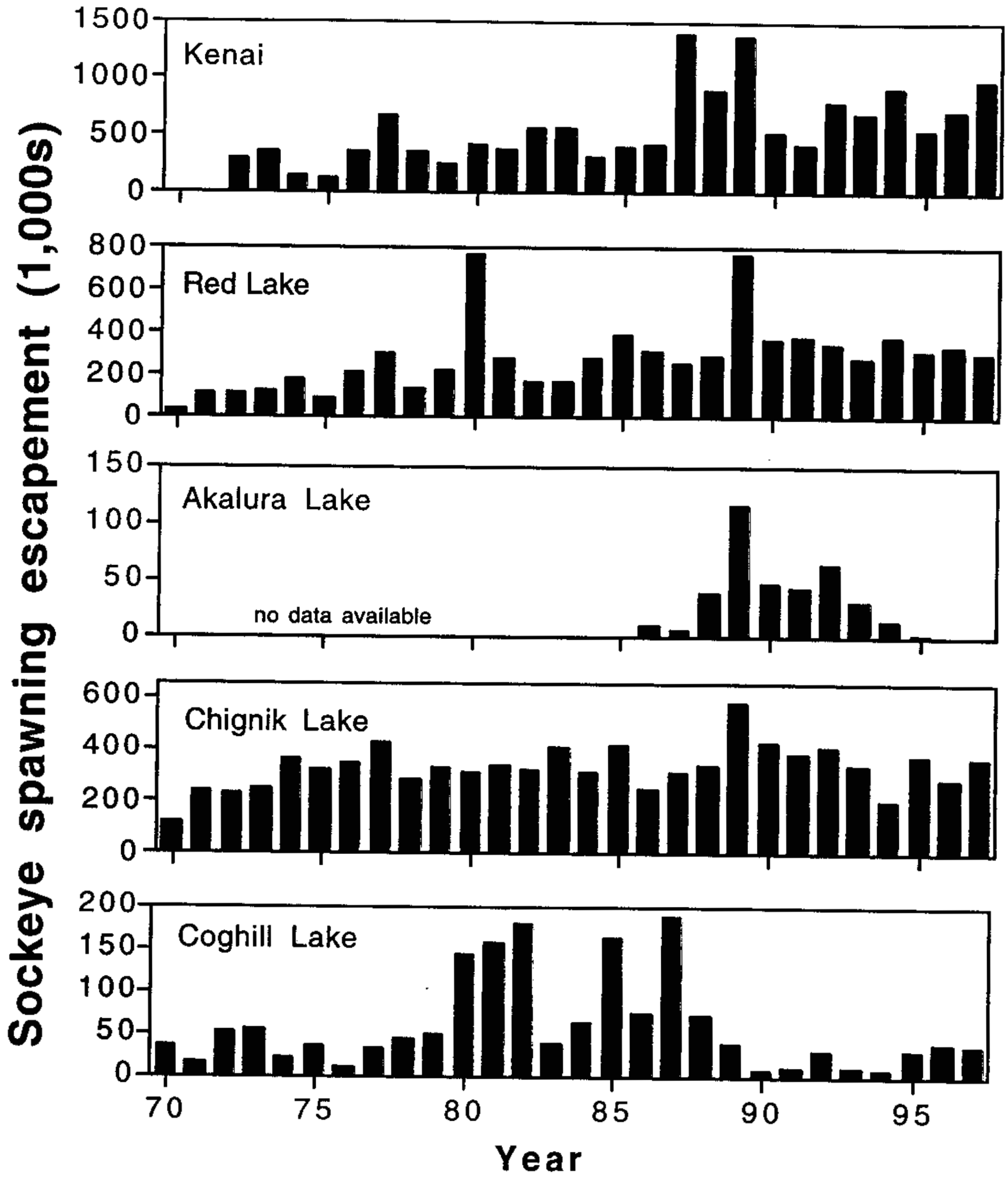

Fig. 2. Spawning escapement of sockeye salmon in systems potentially affected by the *Exxon Valdez* oil spill in 1989. Escapement data not available for all years.

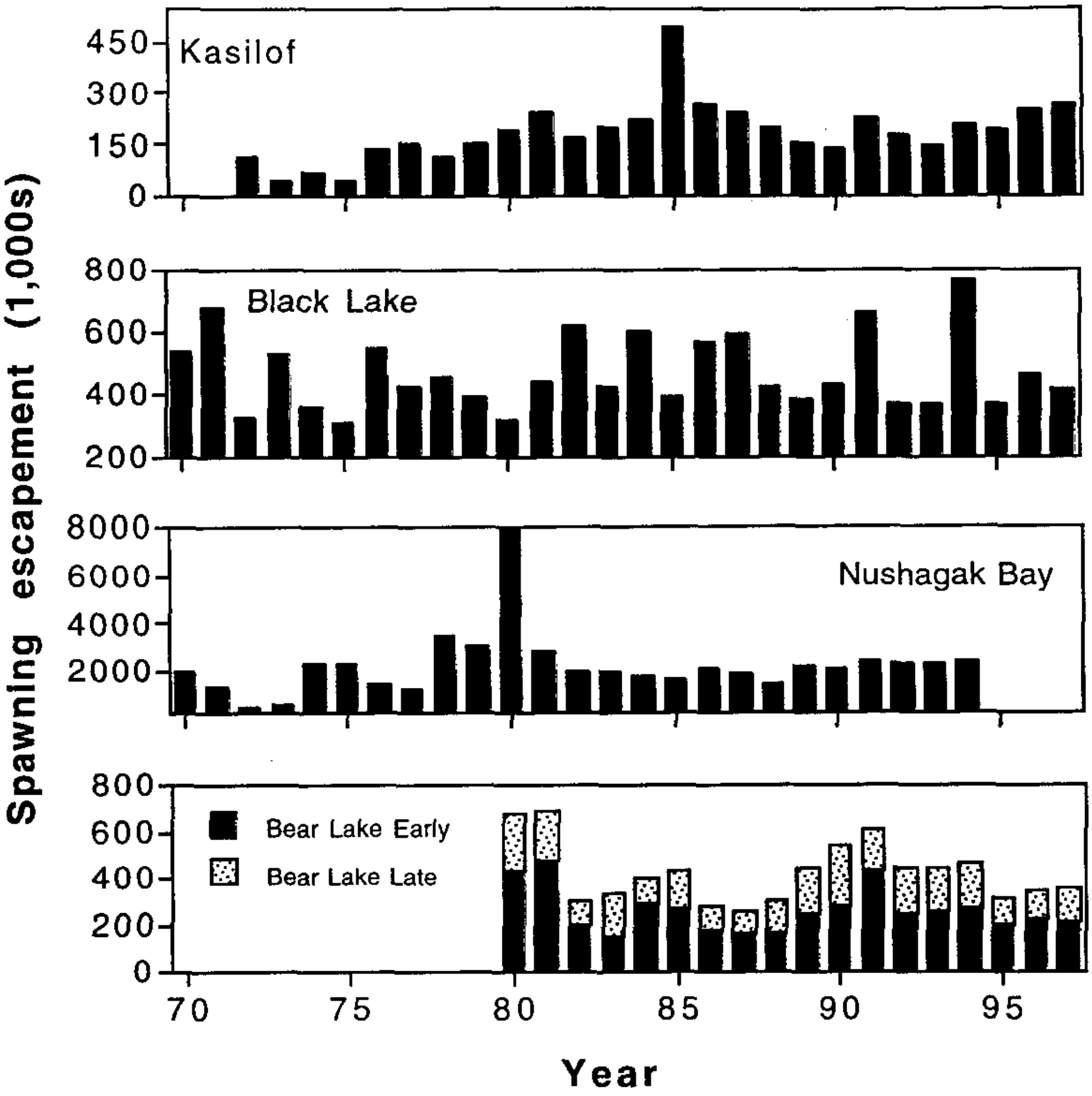

Fig. 3. Spawning escapement of sockeye salmon in systems not influenced by the *Exxon Valdez* oil spill in 1989. Escapement data not available for all years.

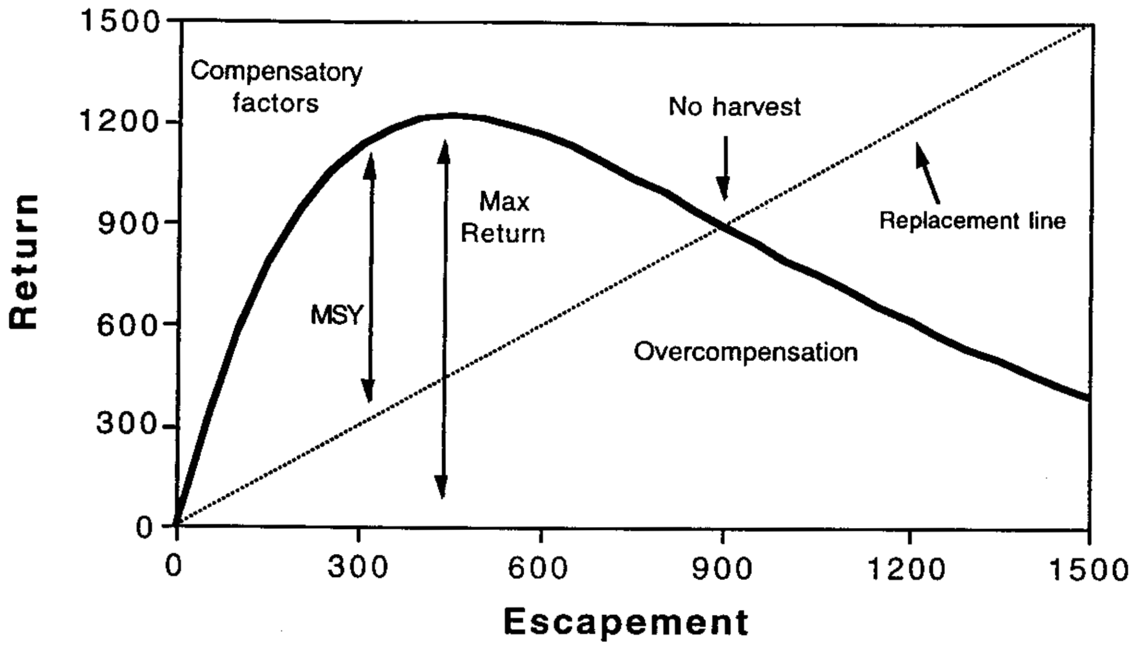

Fig. 4. Example of a Ricker recruitment curve showing the generalized relationship between parent spawning escapement and the corresponding adult return.

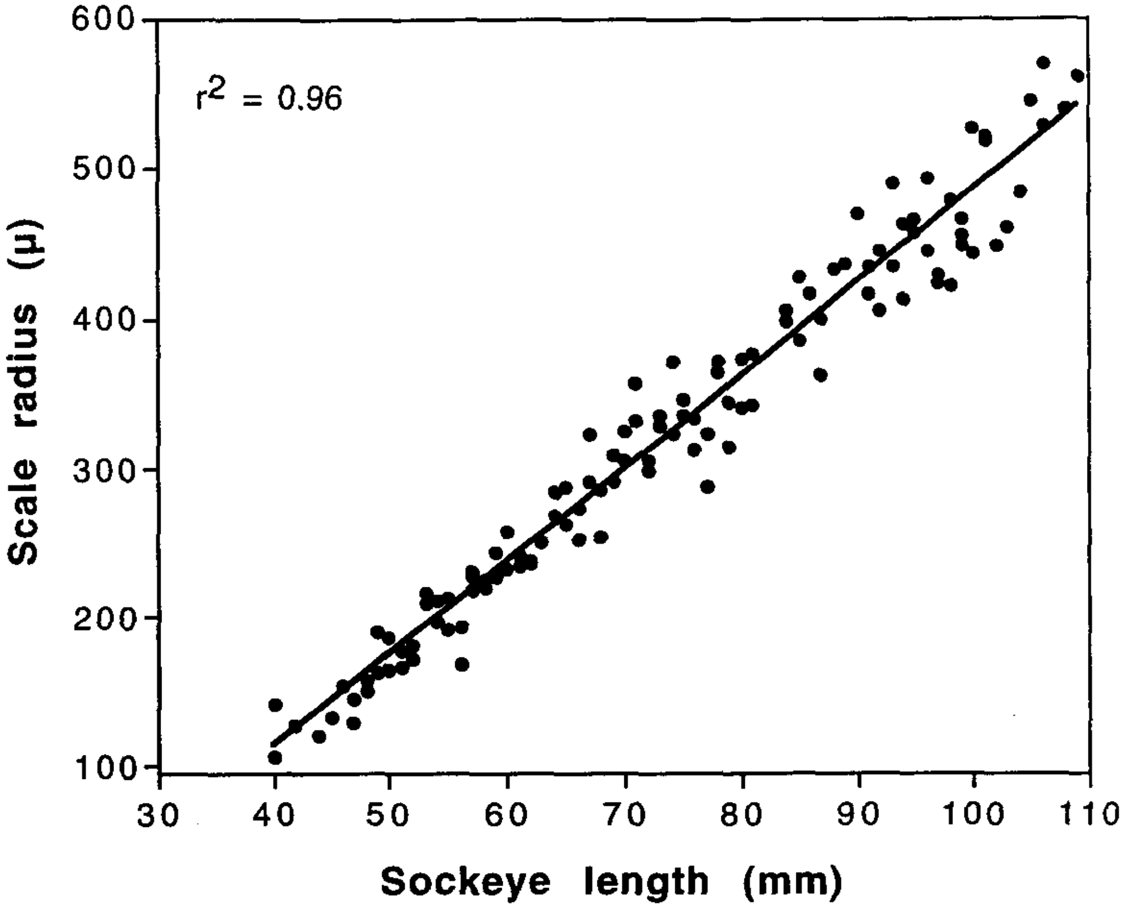

Fig. 5. Relationship between scale radius and length of sockeye salmon fry and smolt collected from the Chignik lake system.

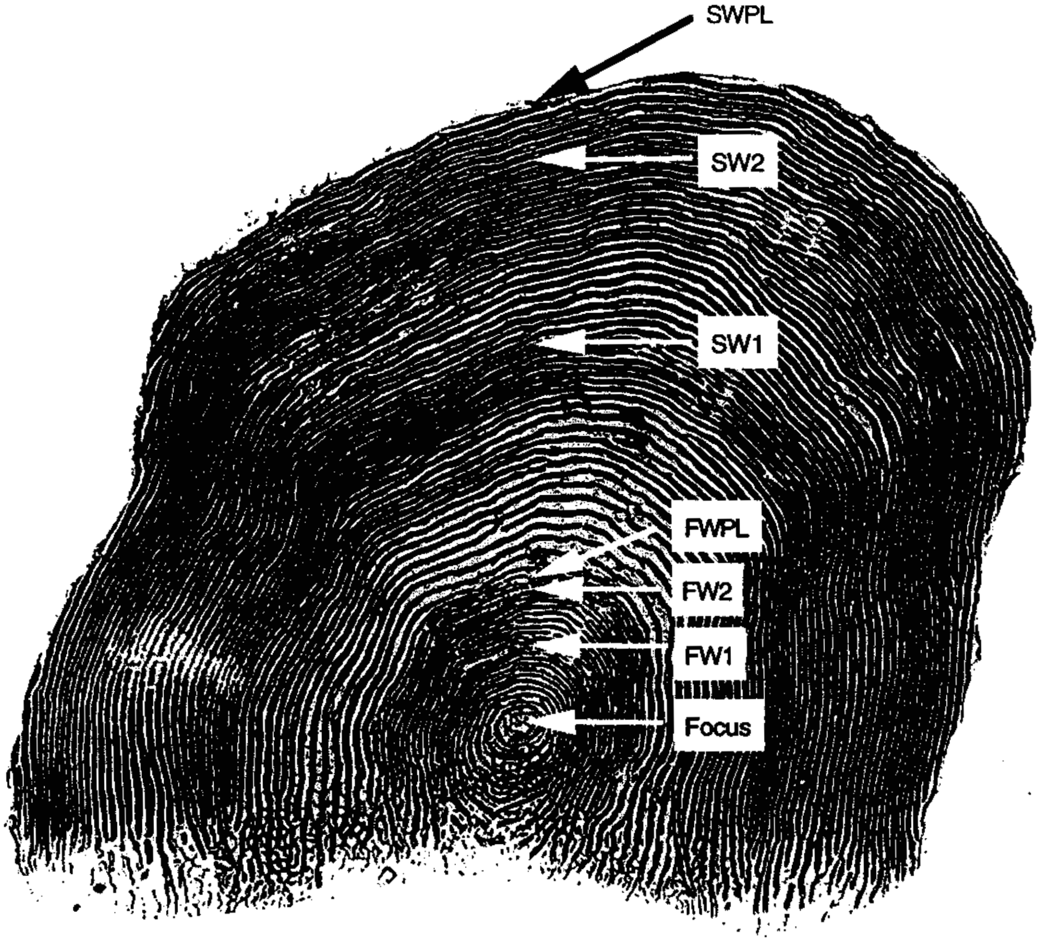

Fig. 6. Sockeye salmon scale (age 2.2) showing the scale focus and measurement locations at each annulus and at the end of spring growth. Note scale resorption along sides of the scale.

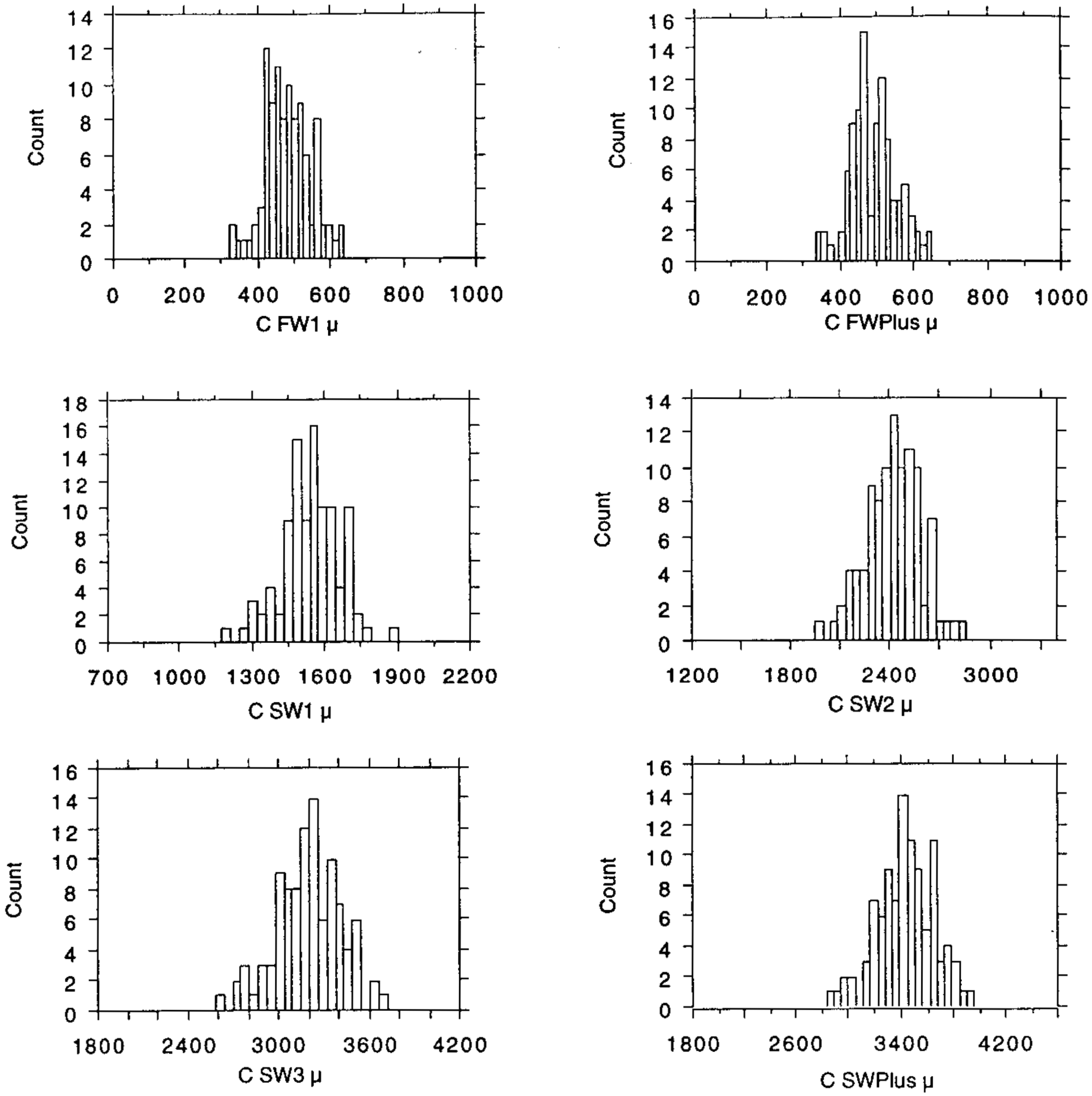

Fig. 7. Frequency distribution of Kenai sockeye salmon scales collected during 1987 (1982 brood year), the first exceptionally large return.

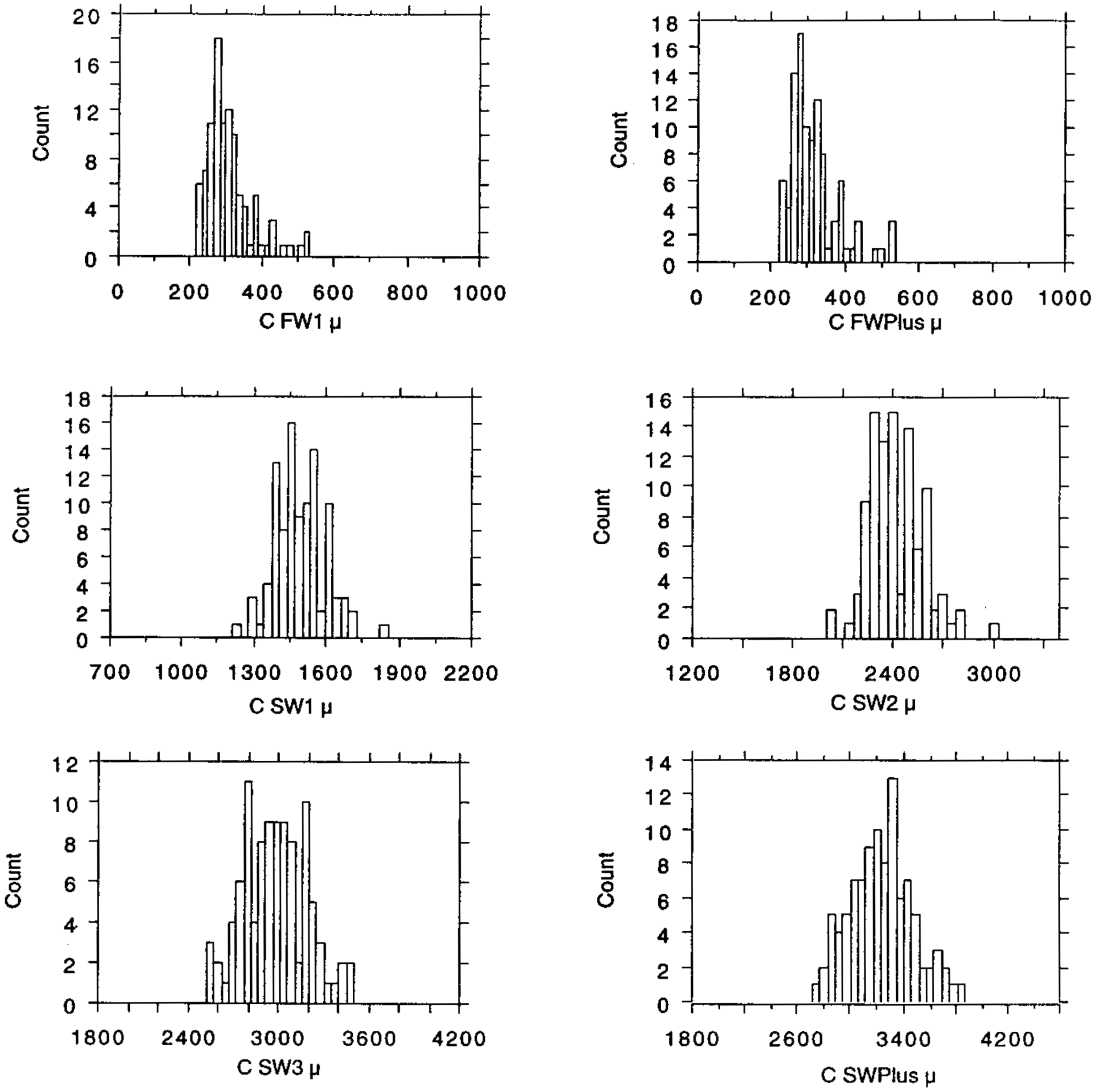

Fig. 8. Frequency distribution of Kenai sockeye salmon scales collected during 1994 (1989 brood year). These scale represent sockeye returning from 1989 spawners.

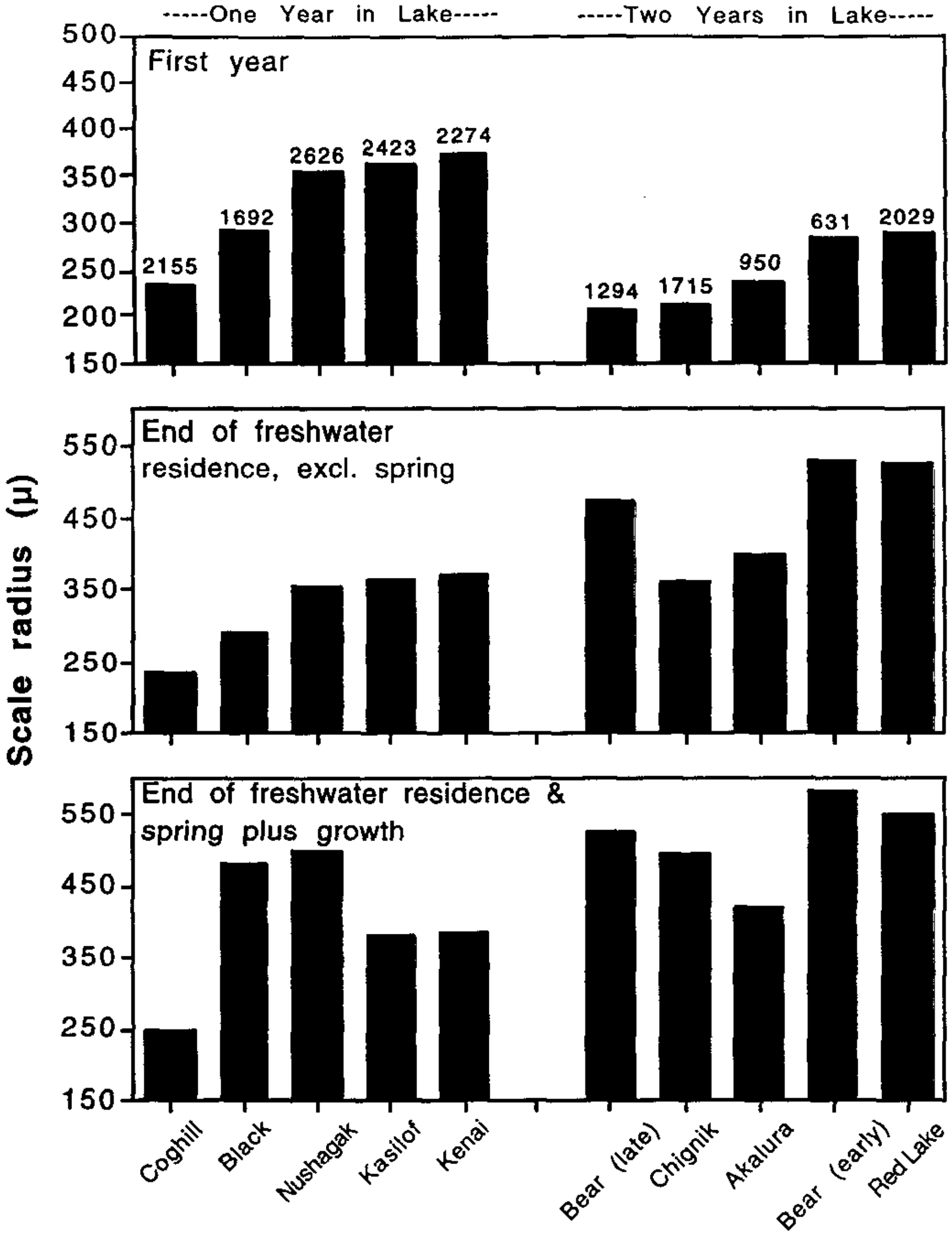

Fig. 9. Comparison of mean freshwater scale growth of the 10 sockeye salmon populations during the study period. Analysis excludes data from those populations and years influenced by oil spills. Stocks grouped on left are spent one year in freshwater, whereas those on left spent two years in freshwater. The upper 95% confidence intervals were small (<2% of mean values) and not shown. Sample size is shown.

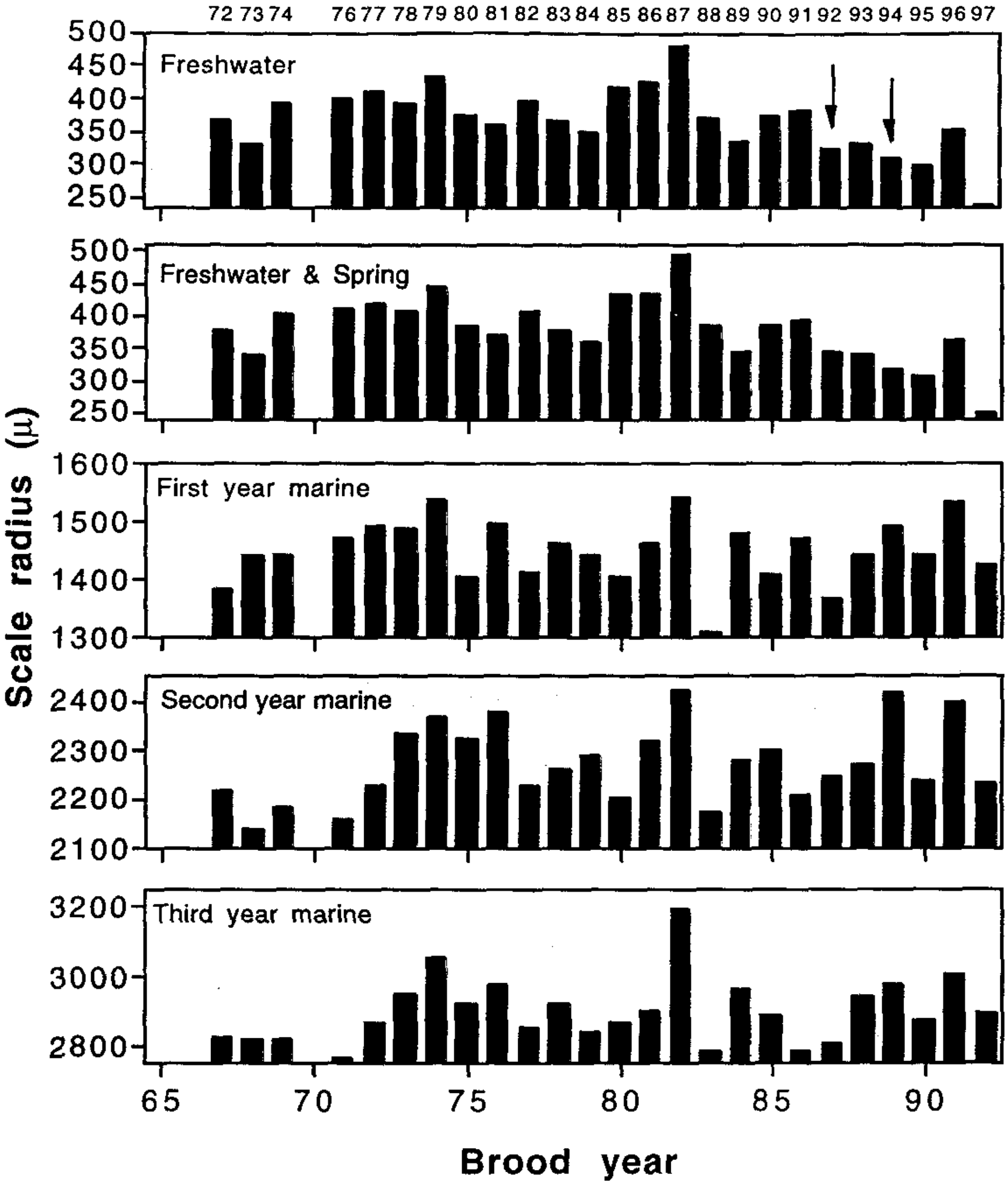

Fig. 10. Mean cumulative scale radii measurements of Kenai River sockeye salmon, brood years 1967-1992. The arrow associated with the 1989 brood year identifies the *Exxon Valdez* oil spill. The previous arrow in 1987 identifies the year when large escapements and runs began. Standard errors were too small to display. No scales were available in 1970.

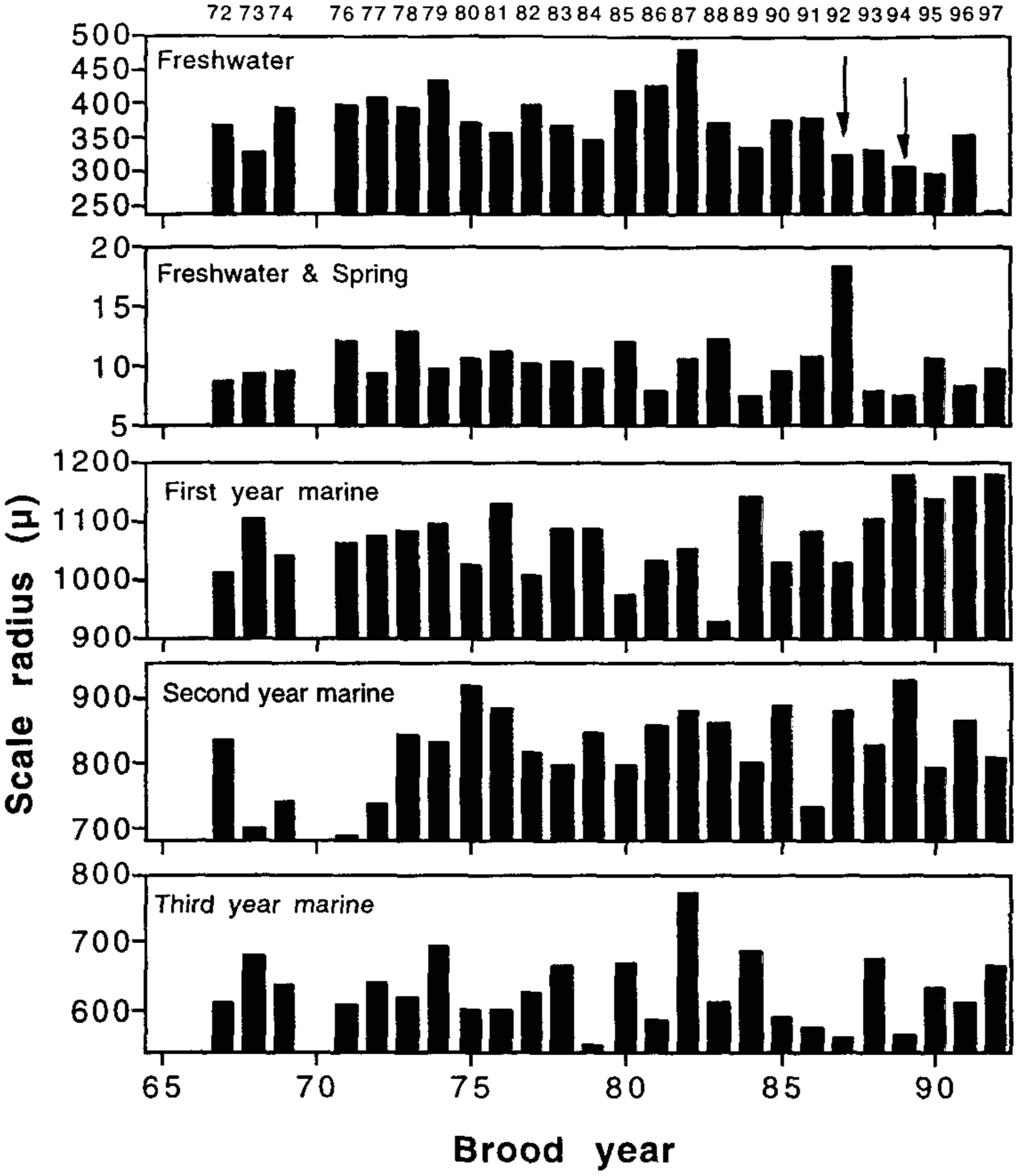

Fig. 11. Mean incremental scale radii measurements of Kenai River sockeye salmon, brood years 1967-1992. The arrow associated with the 1989 brood year identifies the *Exxon Valdez* oil spill. The previous arrow in 1987 identifies the year when large escapements and runs began. Year of adult return is shown above the top figure. Standard errors were too small to display. No scales were available in 1970.

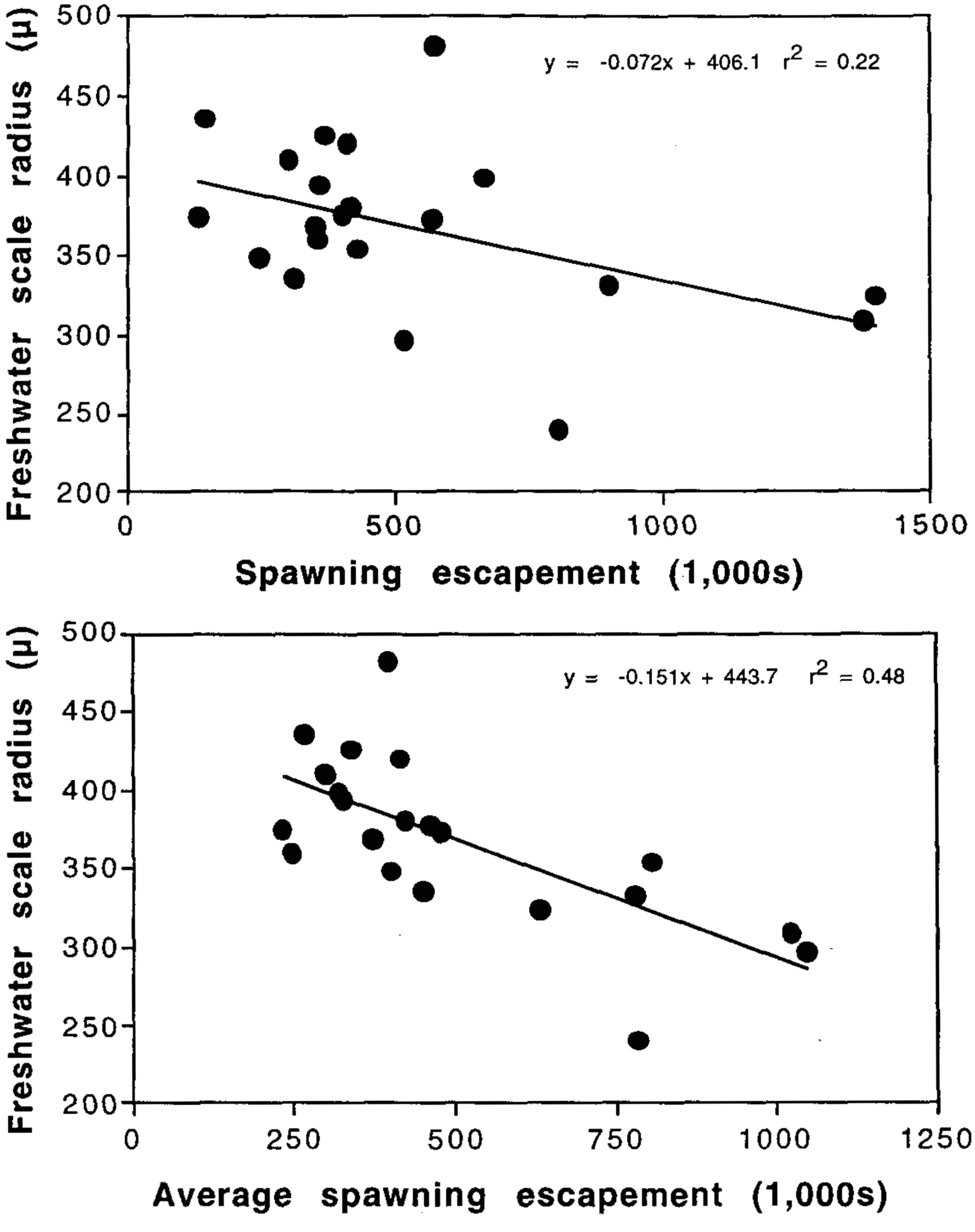

Fig. 12. Relationship between freshwater scale growth of Kenai sockeye salmon and parent spawning escapement (upper graph) and the average spawning escapement of the parents and the three previous escapements.

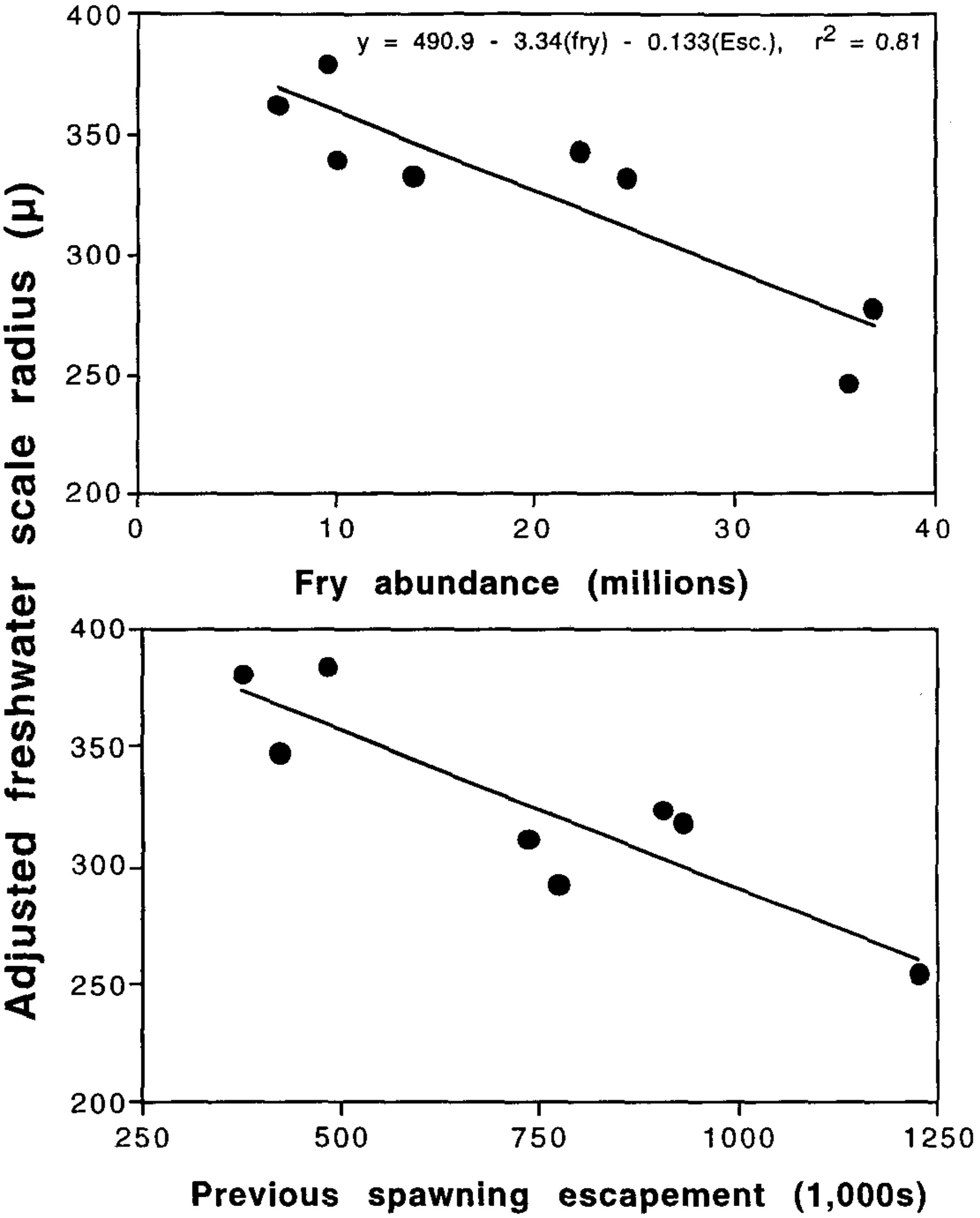

Fig. 13. Multiple regression corrected plots showing the partial effect on sockeye scale growth of fry abundance (upper graph) and average spawning escapement during the three previous years (lower graph). Data represent brood years 1985-1992.

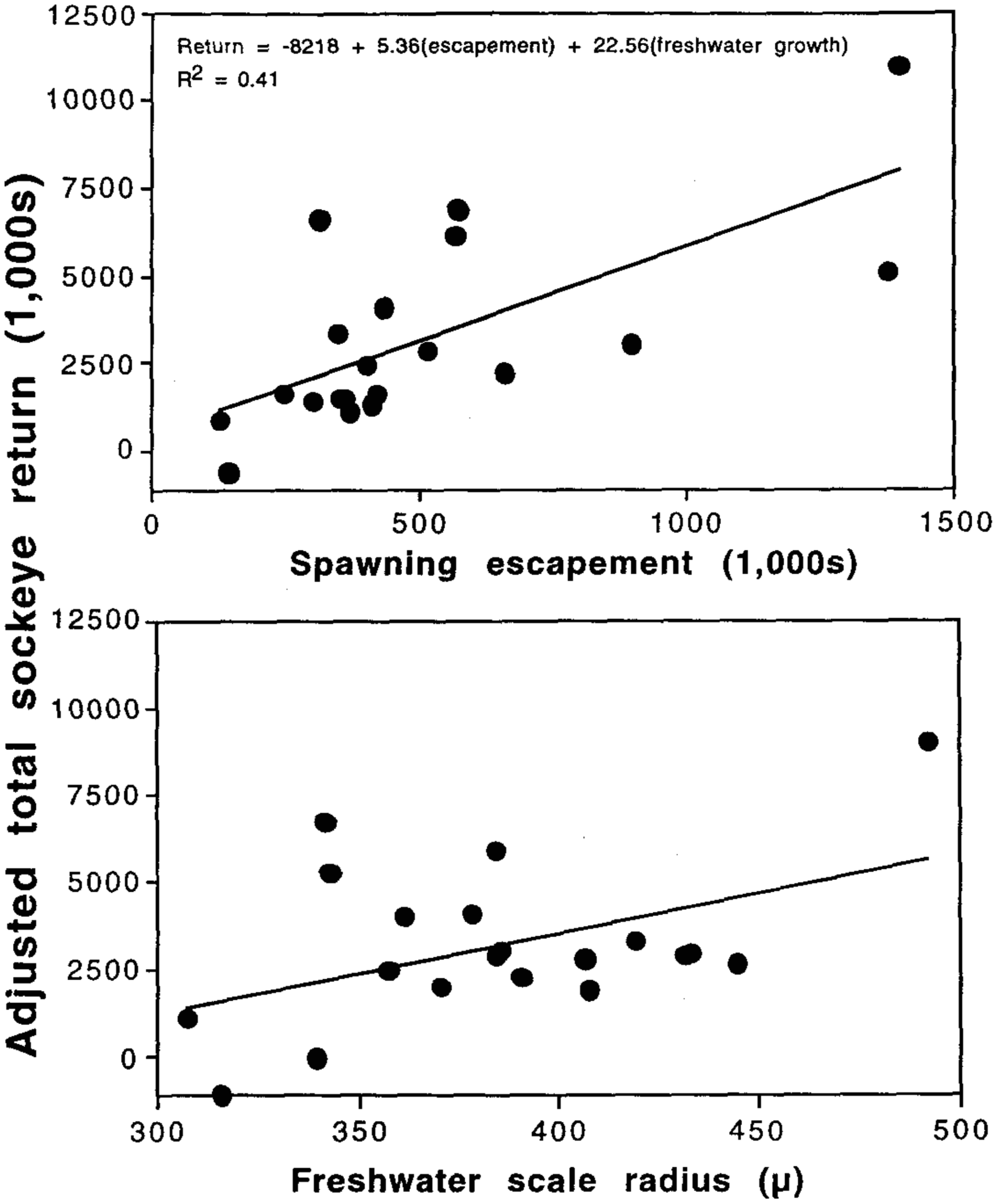

Fig. 14. Multiple regression corrected plots showing the partial effect of parent spawning escapement (upper graph) and freshwater scale growth at the time of seaward migration (lower graph) on total return of Kenai sockeye salmon. Data represent brood years 1972-1991.

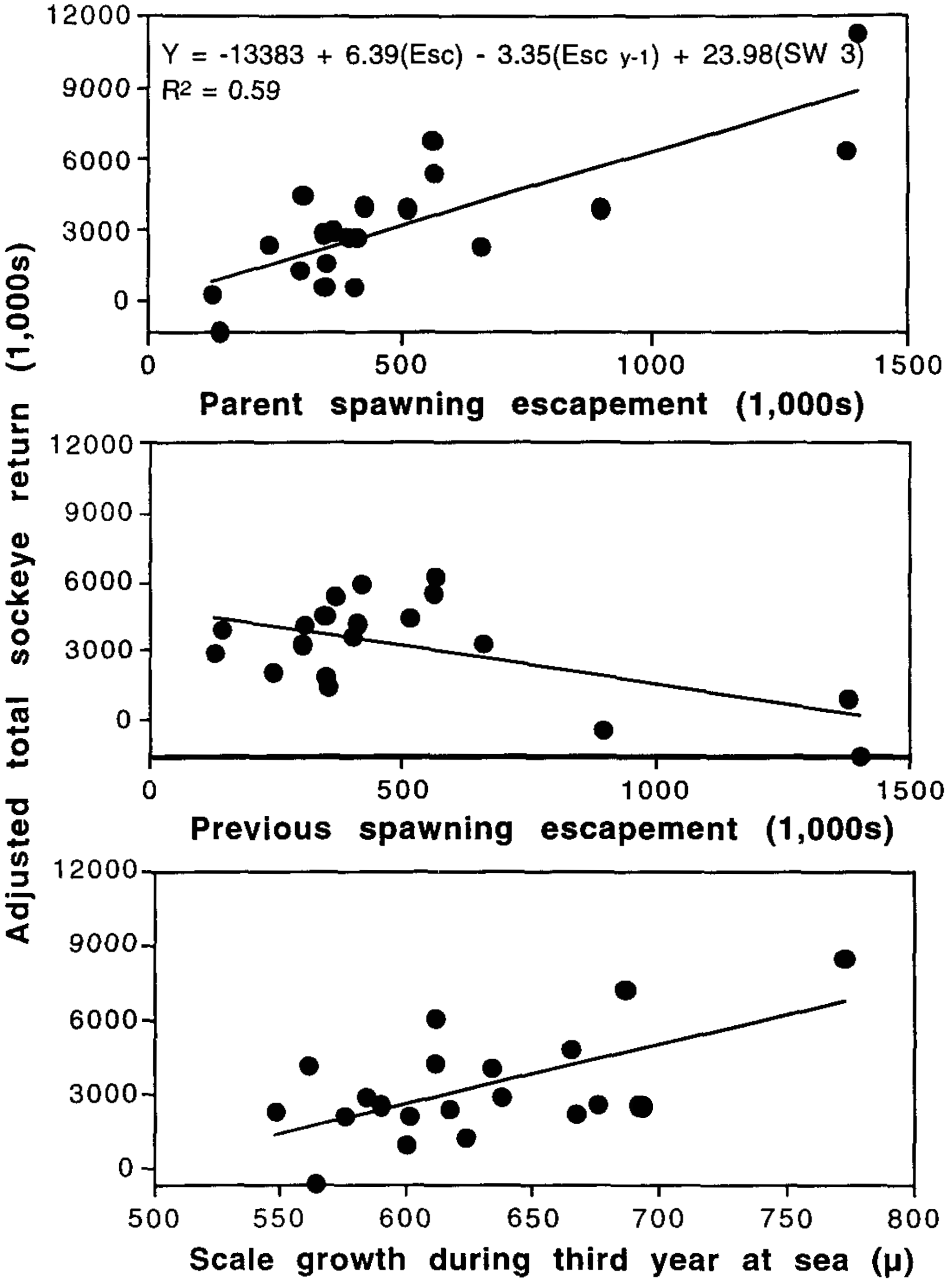

Fig. 15. Multiple regression corrected plots showing the relationship between total sockeye return to the Kenai River and parent spawning escapement, escapement during the previous year and scale growth during the third year at sea, brood years 1972-1991.

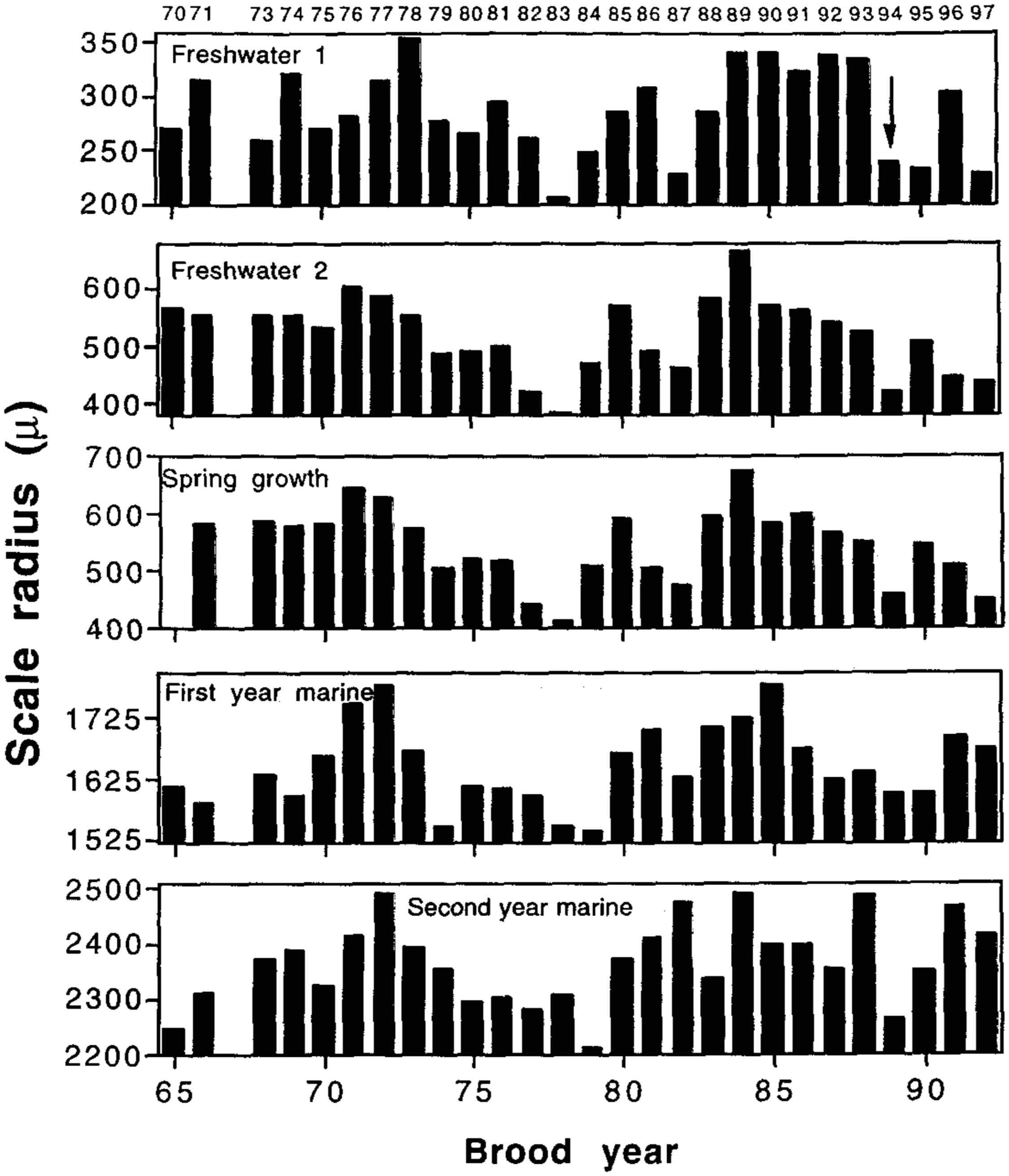

Fig. 16. Mean cumulative scale radii measurements of Red Lake sockeye salmon, brood years 1965-1992. Standard errors were too small to display. No scales were available in 1967.

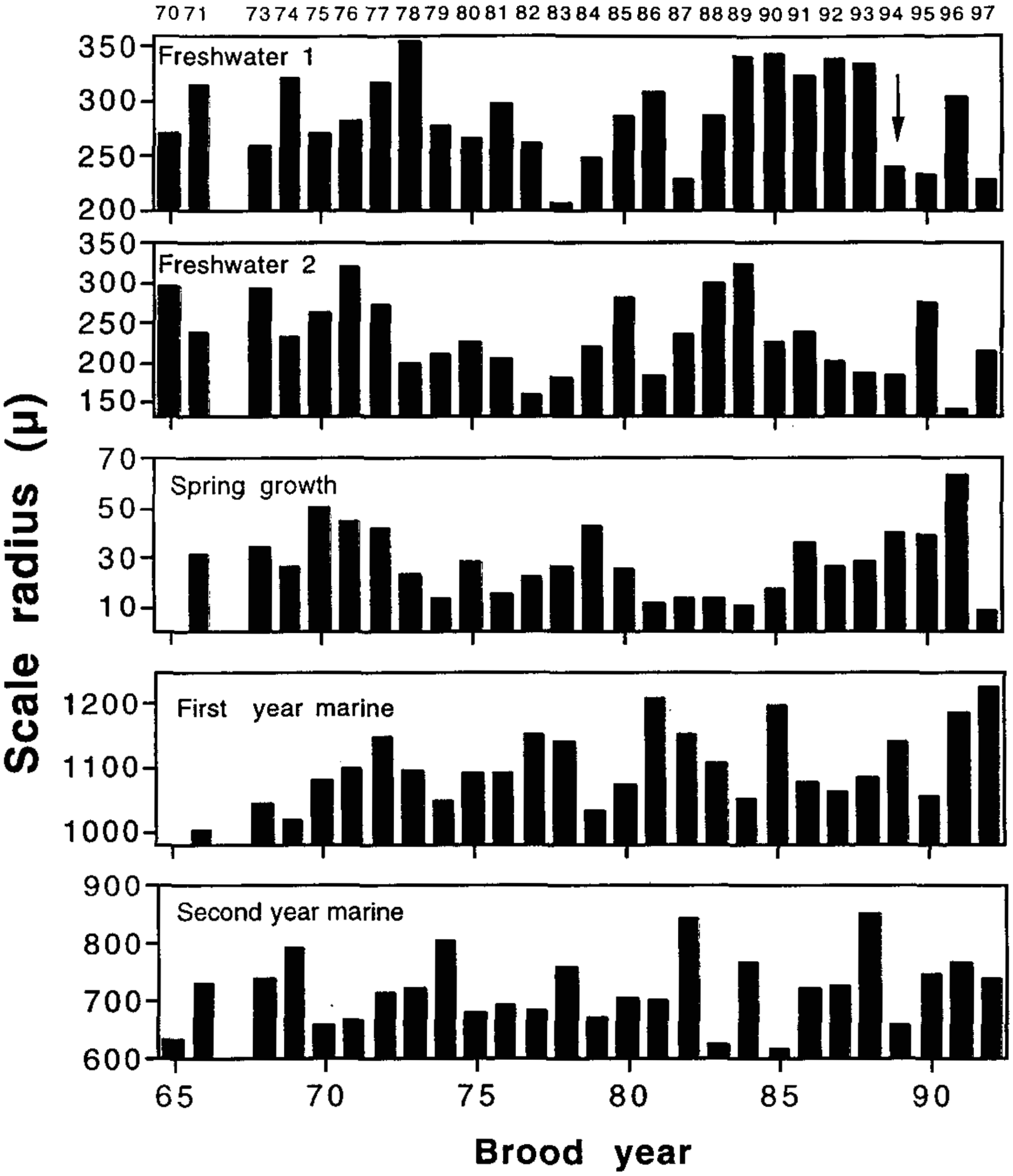

Fig. 17. Mean incremental scale radii measurements of Red Lake sockeye salmon, brood years 1965-1992. Standard errors were too small to display. No scales were available in 1967.

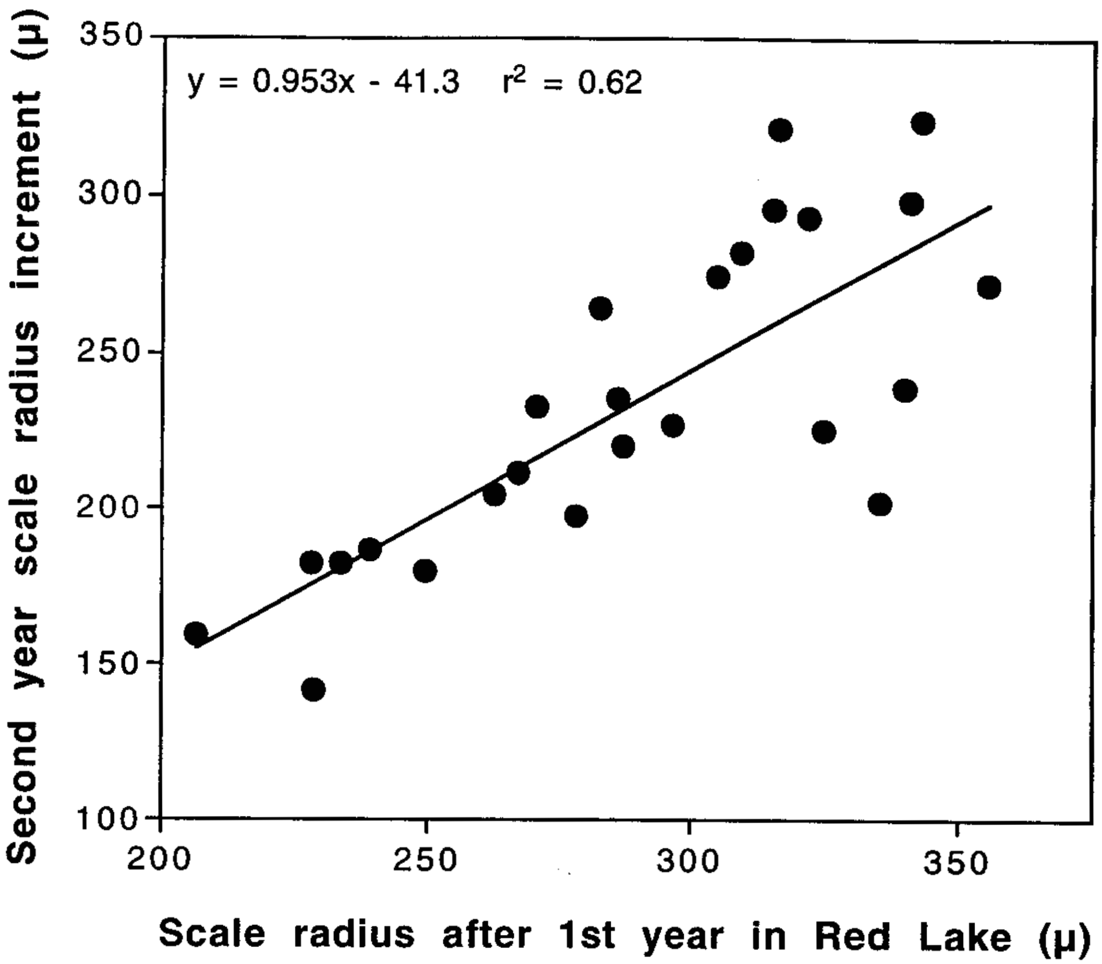

Fig. 18. Relationship between freshwater scale growth of age-1 and age-2 sockeye salmon co-inhabiting Red Lake during rearing years 1967-1993.

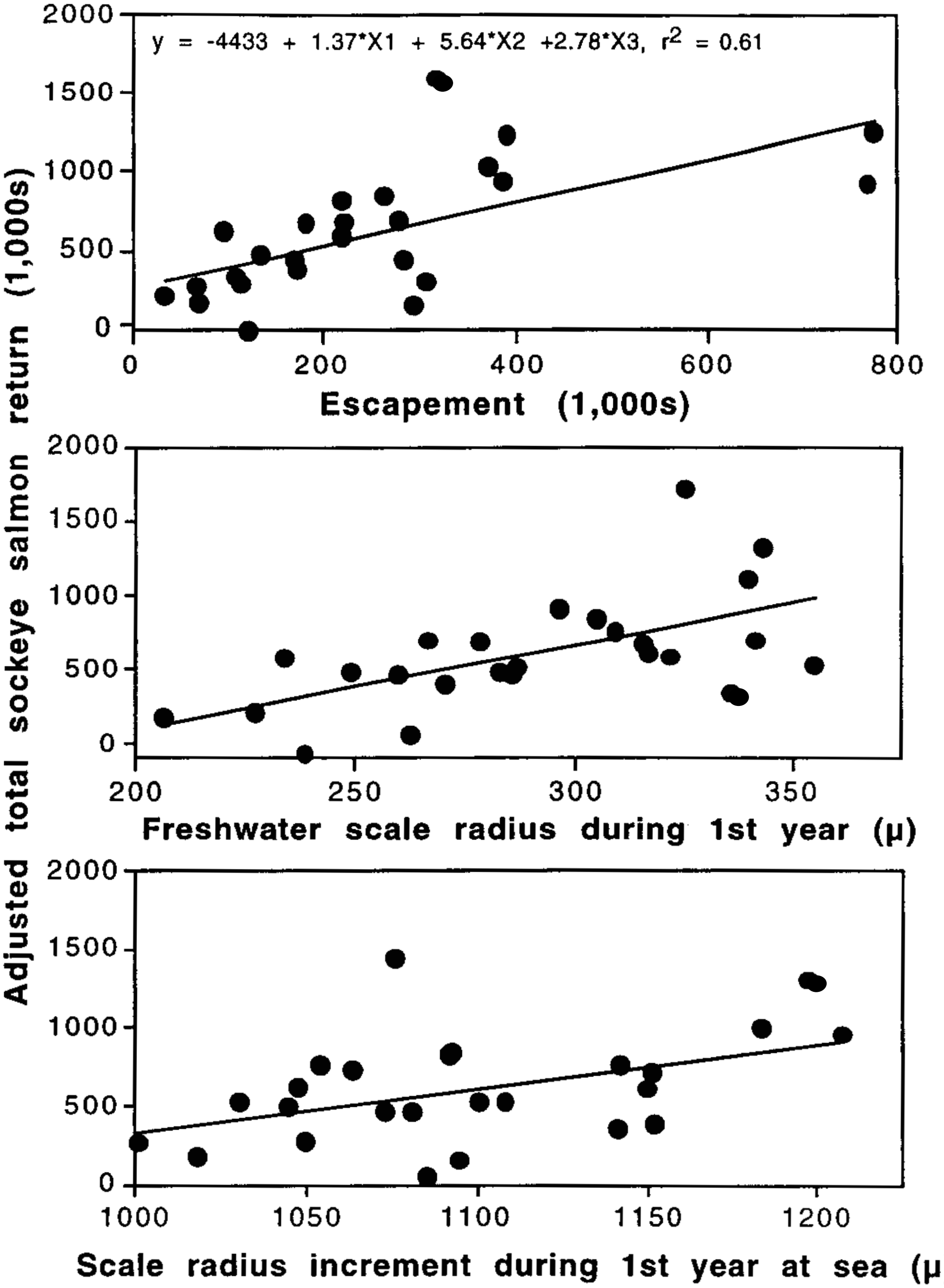

Fig. 19. Regression corrected plots showing the effect on sockeye return to Red Lake of parent spawning escapement (upper graph), growth during the first year in the lake (middle graph), and incremental growth during the first year at sea (lower graph). Multiple regression equation describing sockeye return to Red Lake is shown in top graph.

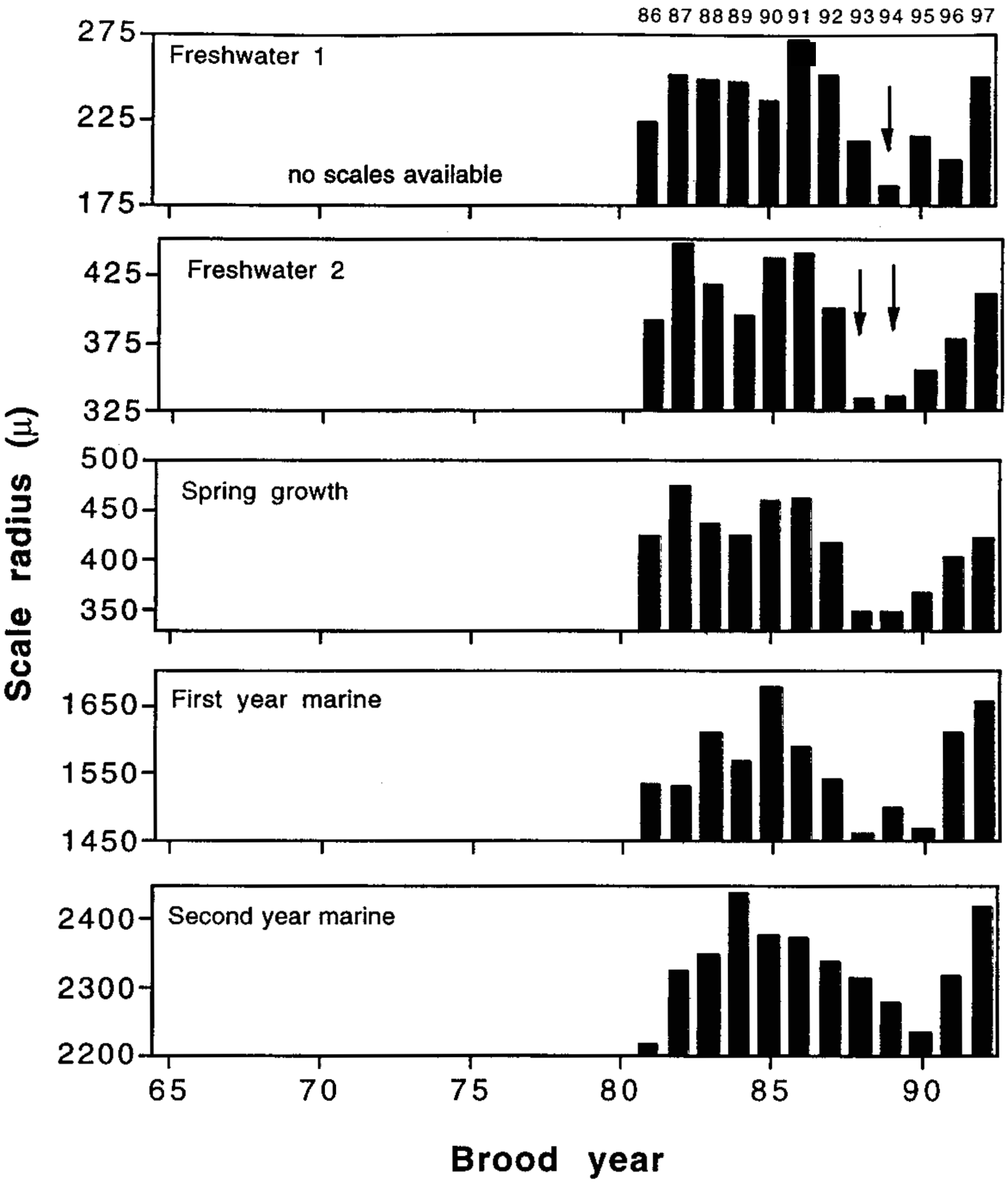

Fig. 20. Mean cumulative scale radii measurements of Akalura Lake sockeye salmon, brood years 1981-1992. Arrows indicate years influenced by large escapement in 1989. Standard errors were too small to display. No scales were available prior to 1981.

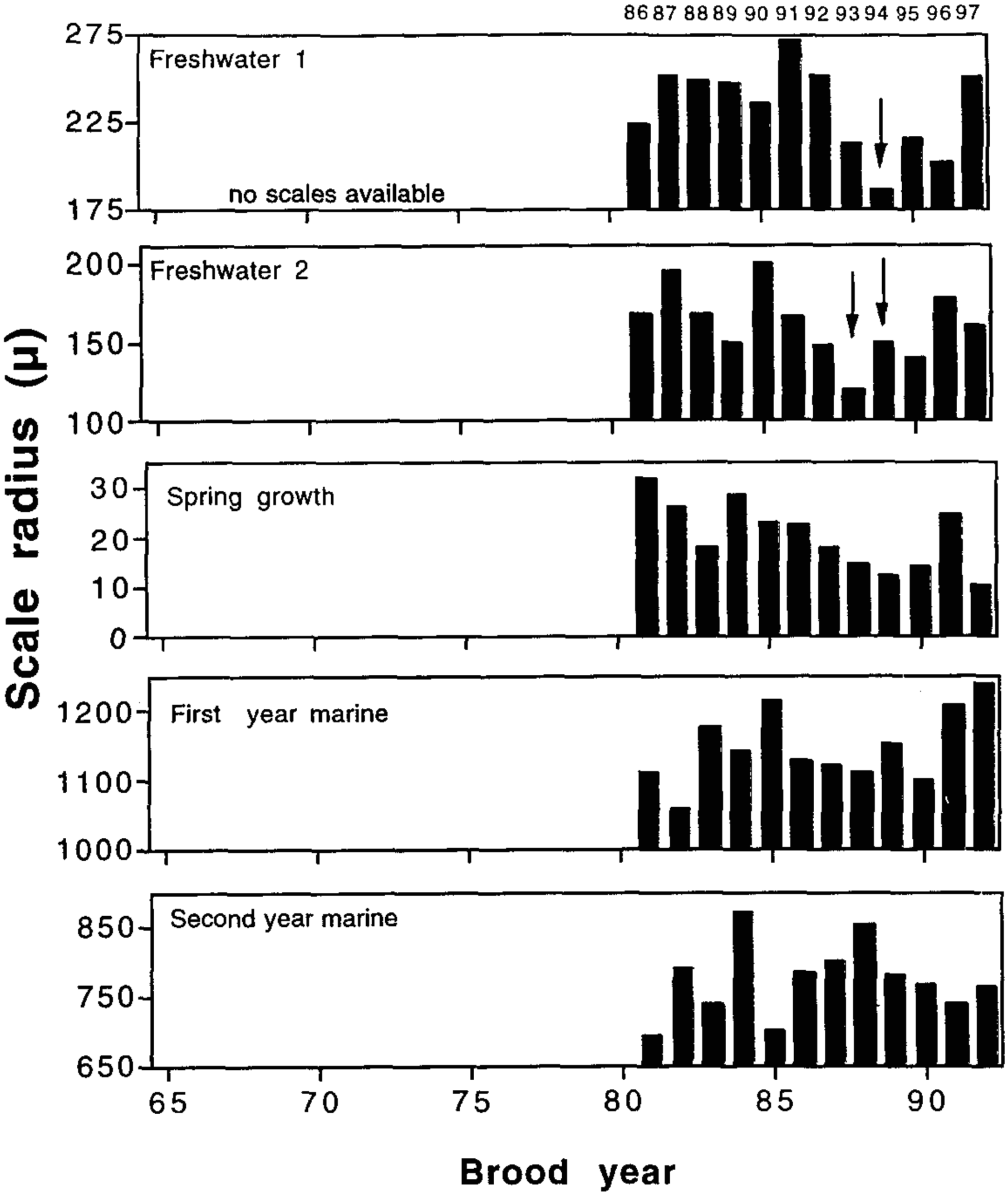

Fig. 21. Mean incremental scale radii measurements of Akalura Lake sockeye salmon, brood years 1981-1992. Arrows indicate years influenced by large escapement in 1989. Year of adult return is shown above the top figure. Standard errors were too small to display. No scales were available prior to 1981.

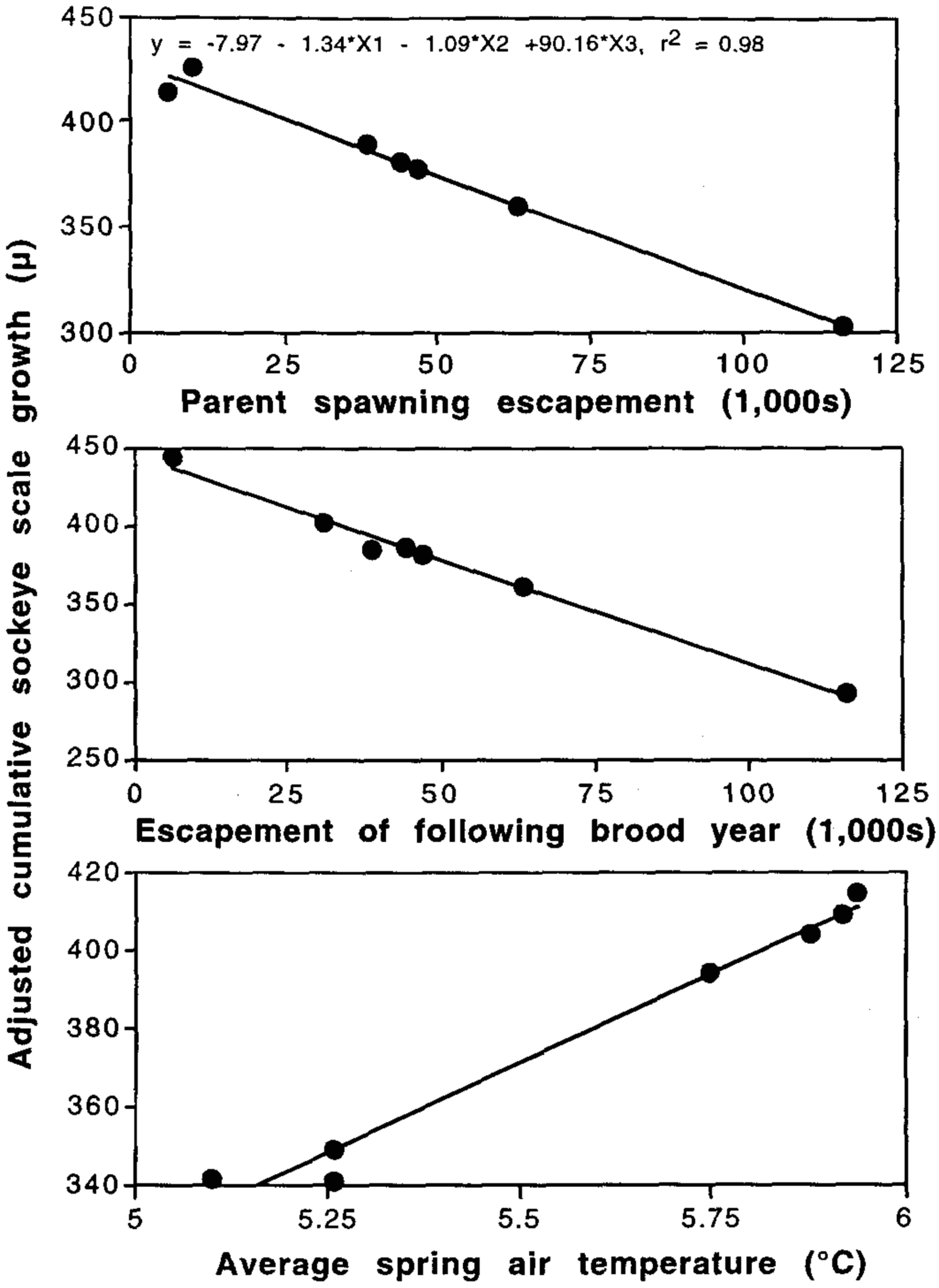

Fig. 22. Regression corrected plots showing the effect on Akalura sockeye scale growth at the end of the second growing season of parent spawning escapement, escapement of the following brood year that produced fry that co-inhabited the lake, and average Kodiak air temperature during April to May corresponding to the first and second years in the lake. Multiple regression equation is show at top.

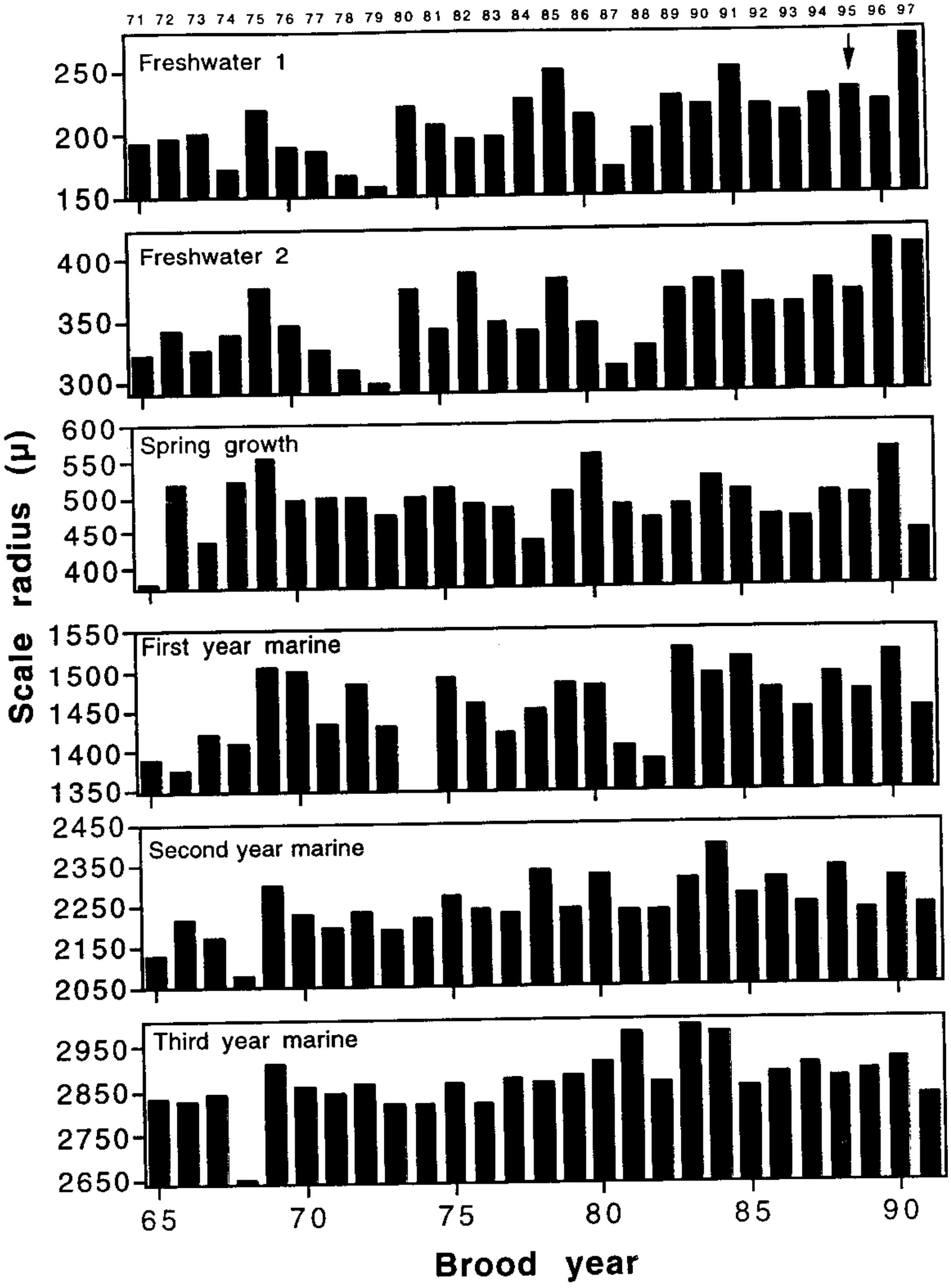

Fig. 23. Mean cumulative scale radii measurements of Chignik Lake sockeye salmon, brood years 1965-1991. Year of adult return is shown above the top figure. Standard errors were too small to display.

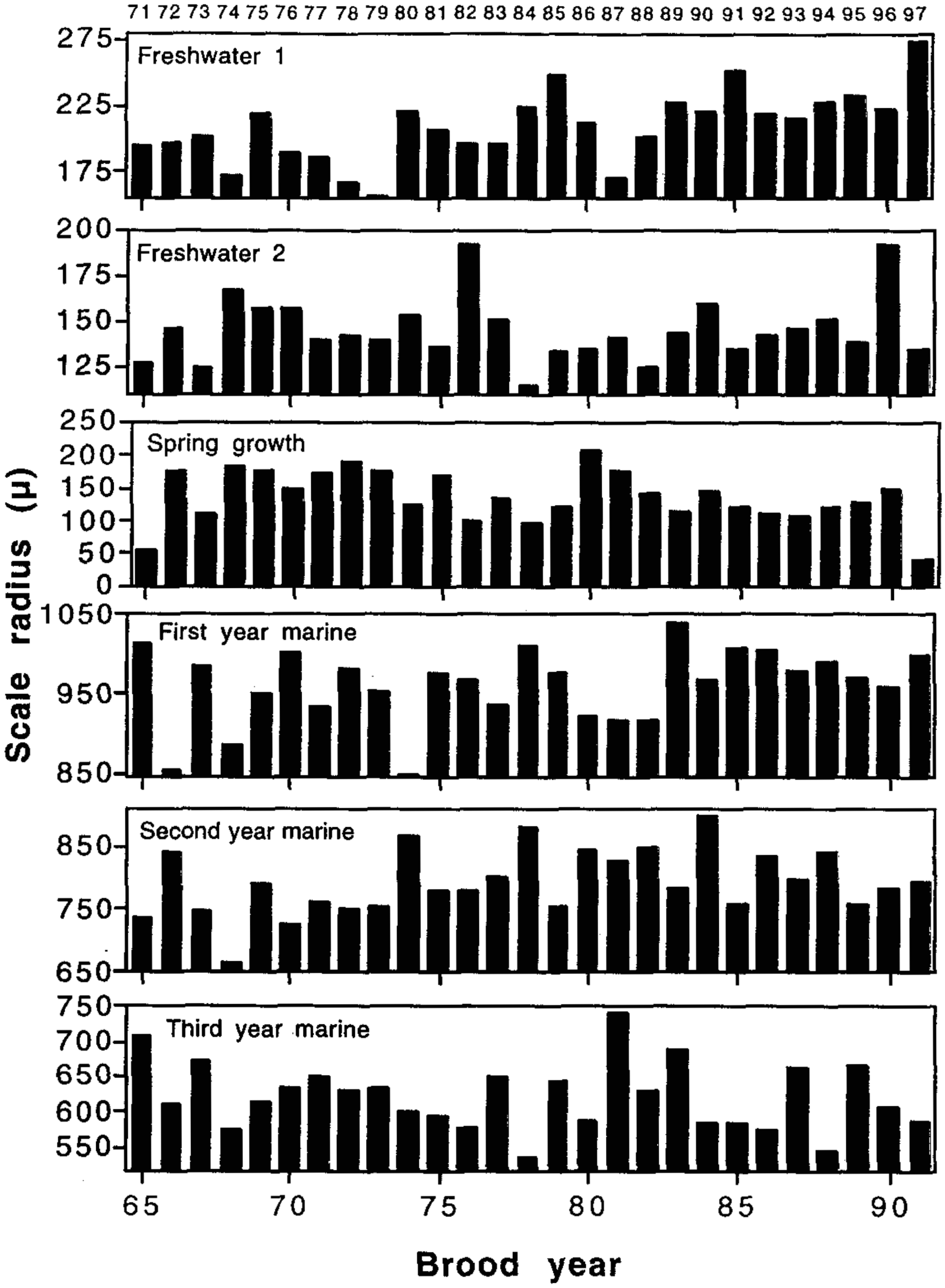

Fig. 24. Mean incremental scale radii measurements of Chignik Lake sockeye salmon, brood years 1965-1991. Year of adult return is shown above the top figure. Standard errors were too small to display.

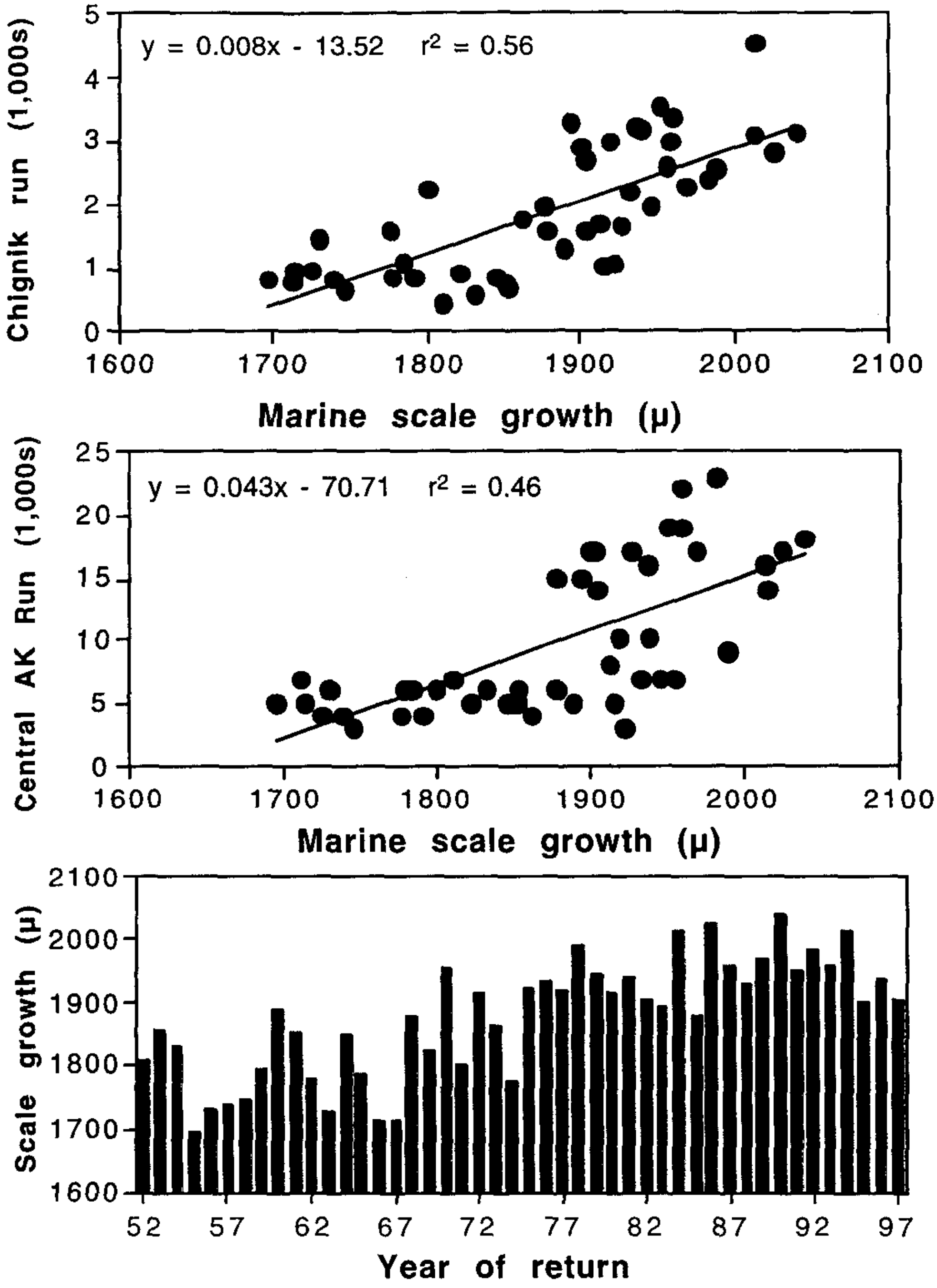

Fig. 25. Relationship between sockeye salmon run size to Chignik lakes and Central Alaska and incremental scale growth during first and second years at sea (upper graphs). Time series of marine growth measurements is shown in bottom graph. Source: Bumgarner 1993 and this study.

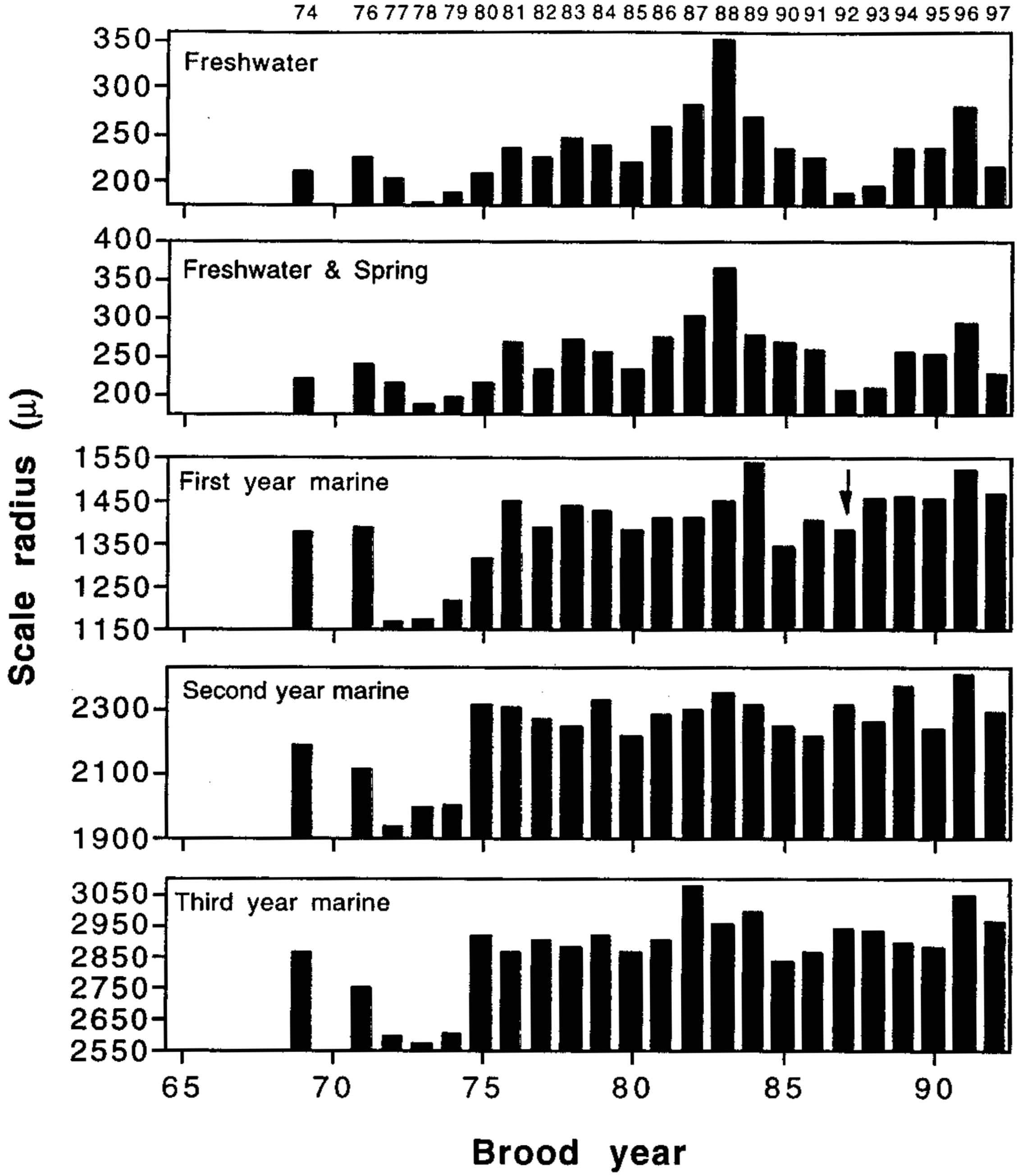

Fig. 26. Mean cumulative scale radii measurements of Coghill Lake sockeye salmon, brood years 1969-1992. Arrow indicates year of interaction with oil. Year of adult return is shown above the top figure. Standard errors were too small to display. No scales were available prior to 1969.

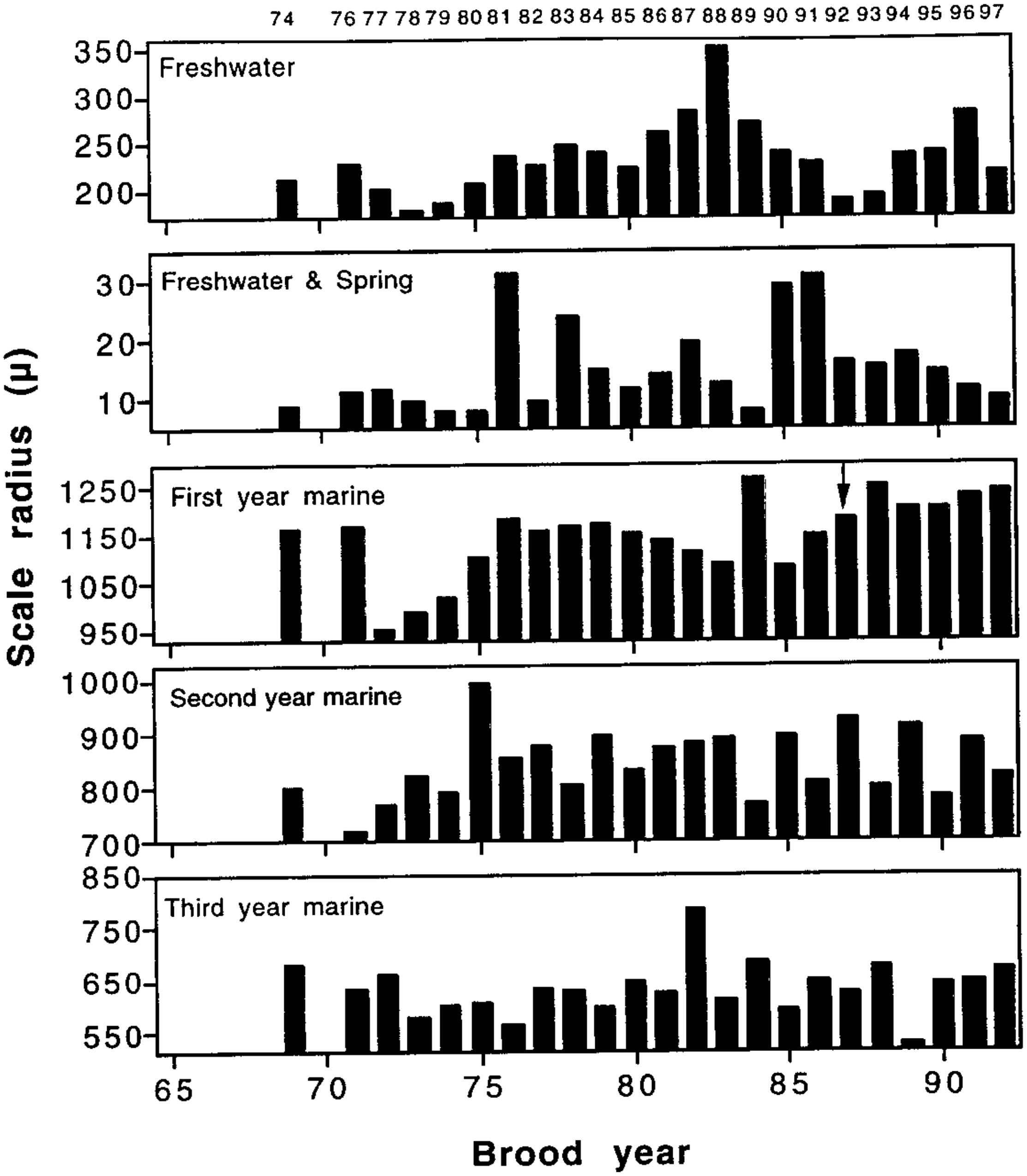

Fig. 27. Mean incremental scale radii measurements of Coghill Lake sockeye salmon, brood years 1969-1992. Arrow indicates year of interaction with oil in Prince William Sound. Year of adult return is shown above the top figure. Standard errors were too small to display. No scales were available prior to 1969.

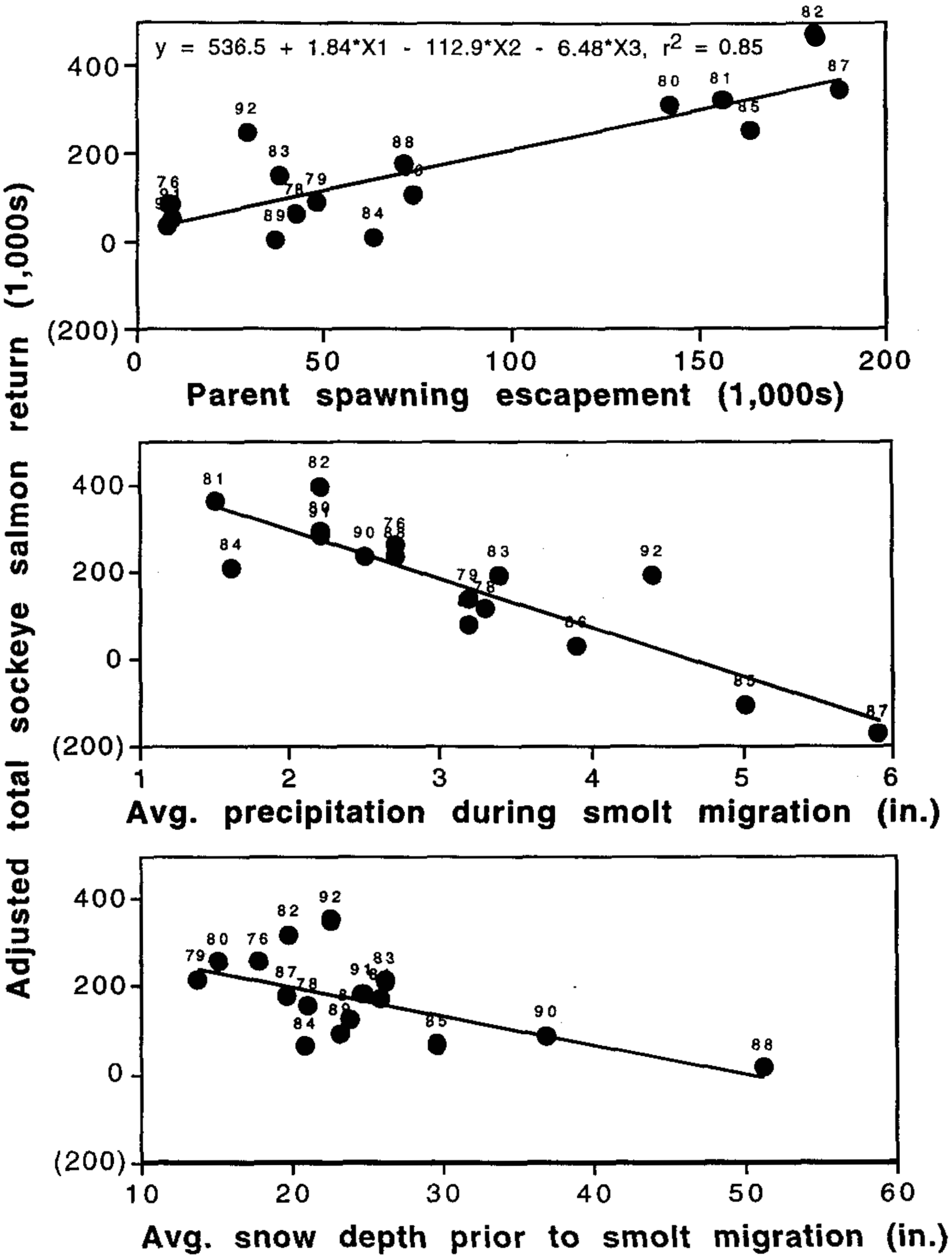

Fig. 28. Regression corrected plots showing the effect on Coghill Lake sockeye return of parent spawning escapement, average precipitation during smolt migration (May and June), and average snow depth prior to smolt migration (Nov. - May). Brood year (1976-1992, excl. 1977) is shown above each value.

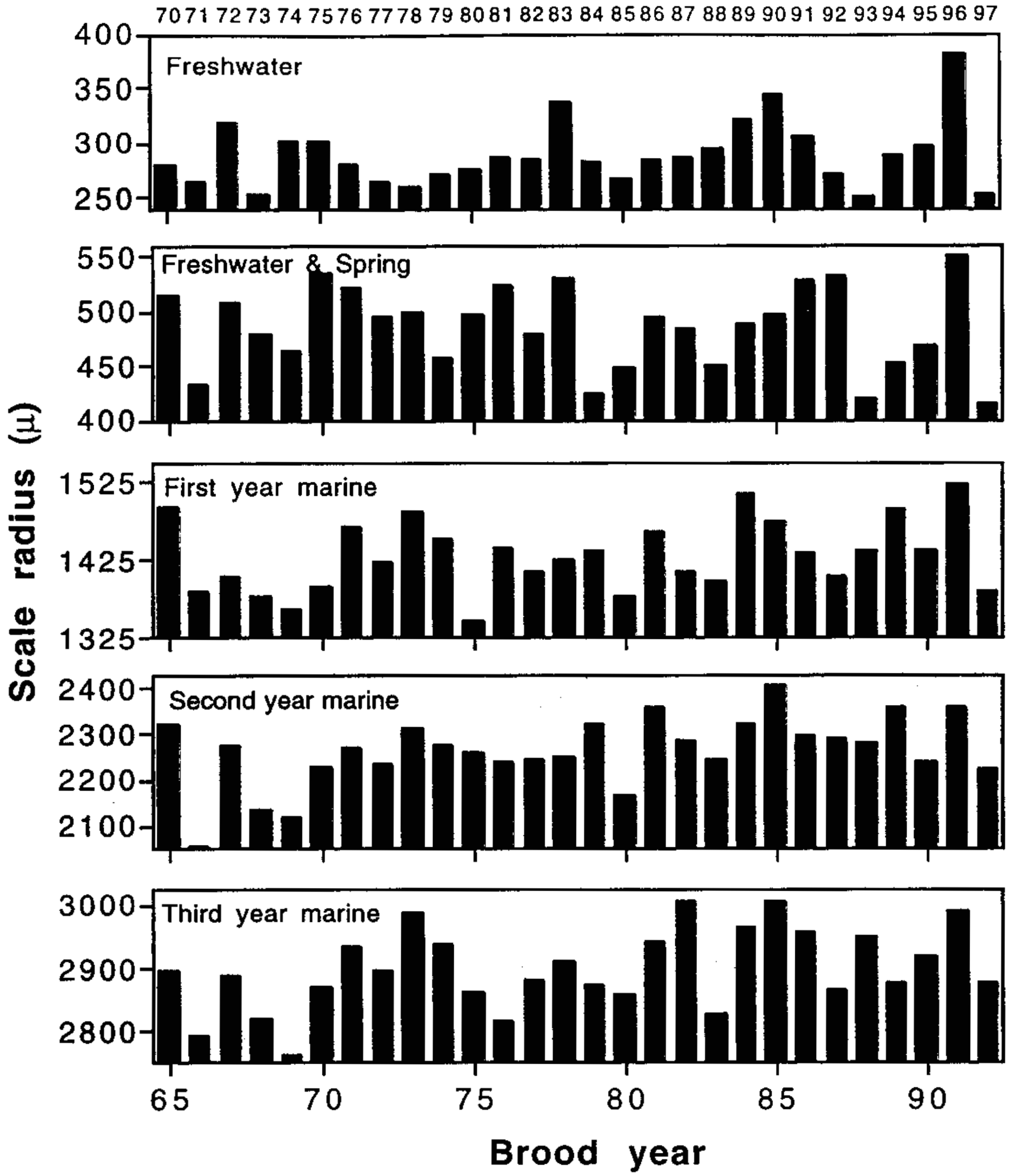

Fig. 29. Mean cumulative scale radii measurements of Black Lake sockeye salmon, brood years 1965-1992. Year of adult return is shown above the top figure. Standard errors were too small to display.

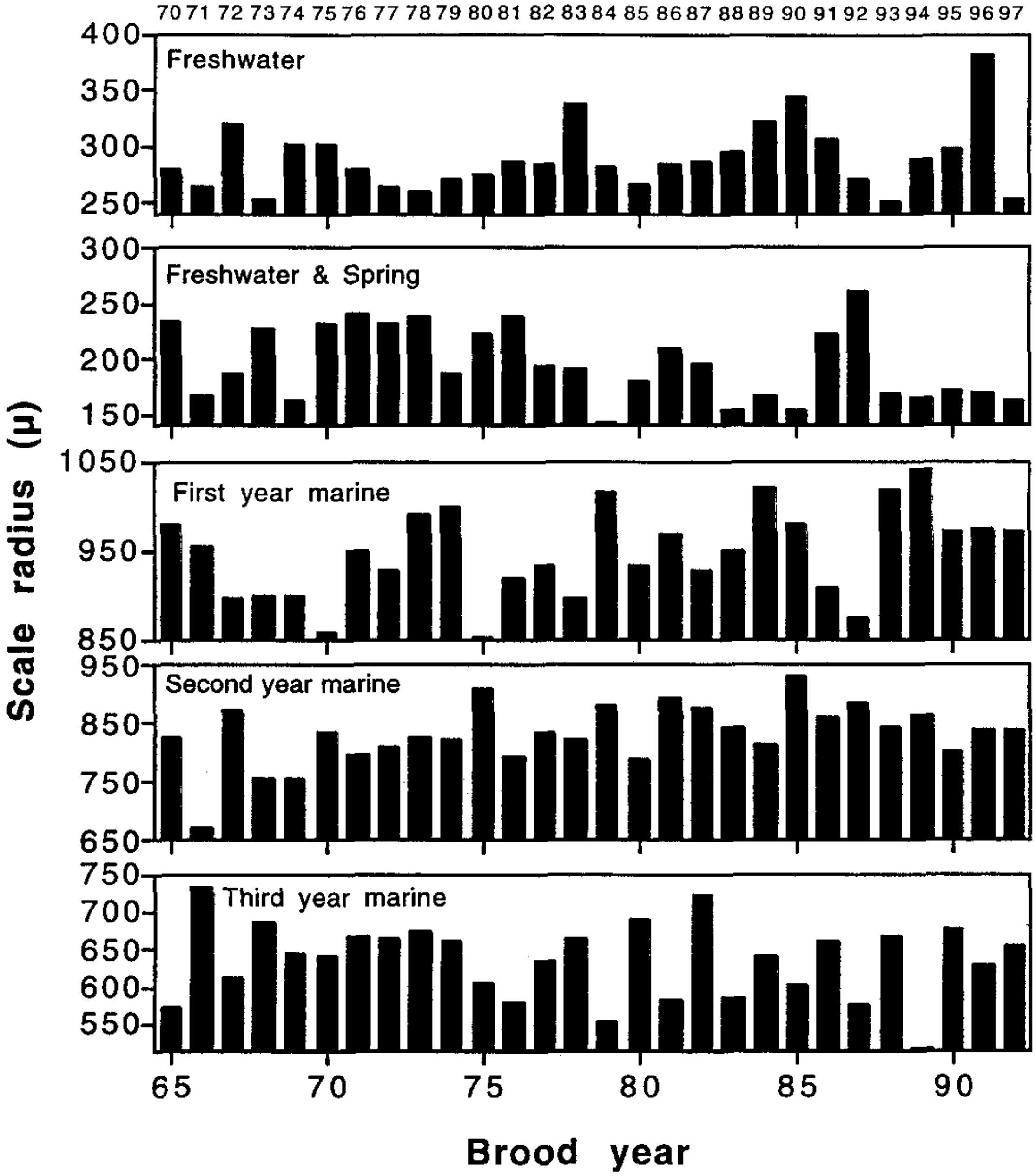

Fig. 30. Mean incremental scale radii measurements of Black Lake sockeye salmon, brood years 1965-1992. Year of adult return is shown above the top figure. Standard errors were too small to display.

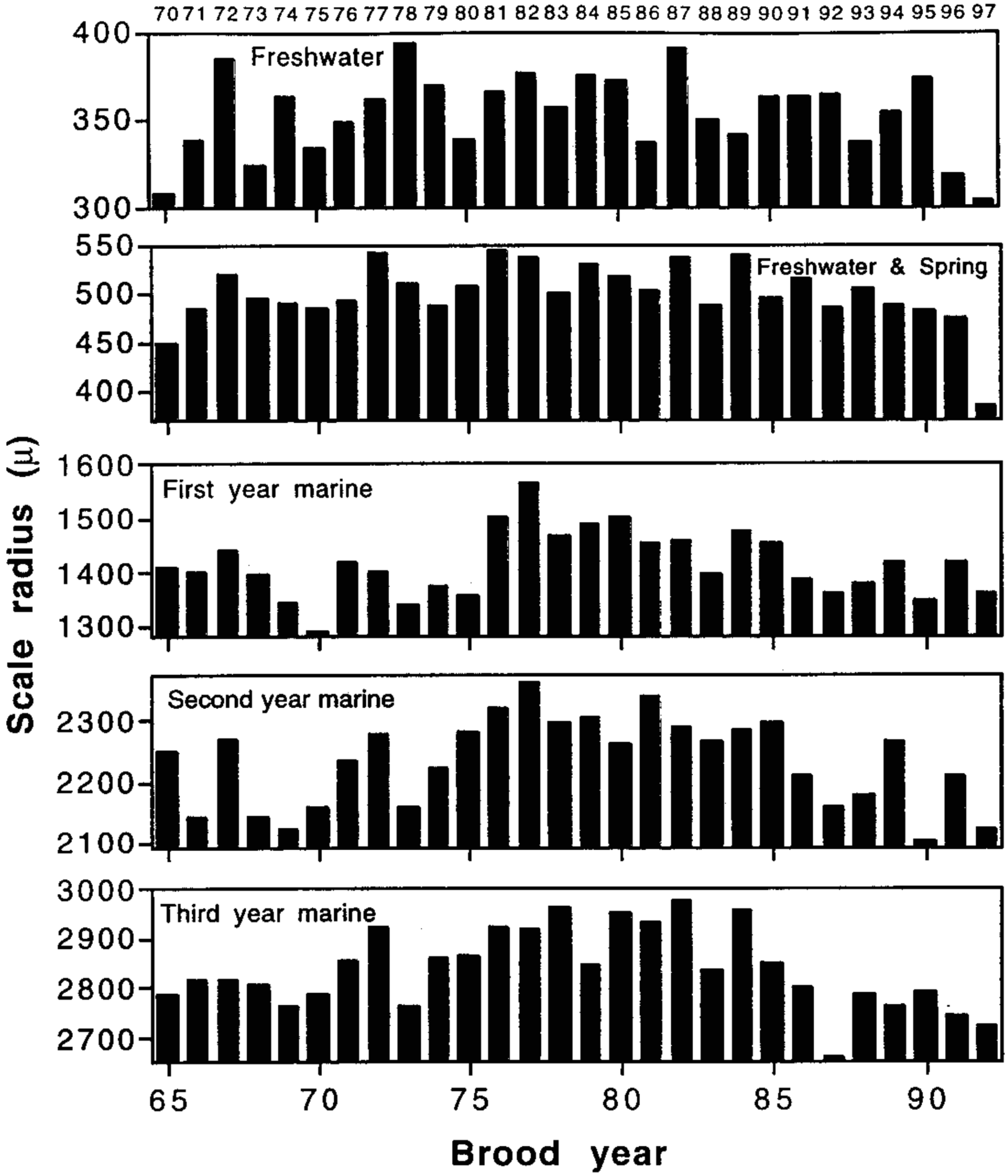

Fig. 31. Mean cumulative scale radii measurements of Nushagak Bay sockeye salmon, brood years 1965-1992. Year of adult return is shown above the top figure. Standard errors were too small to display.

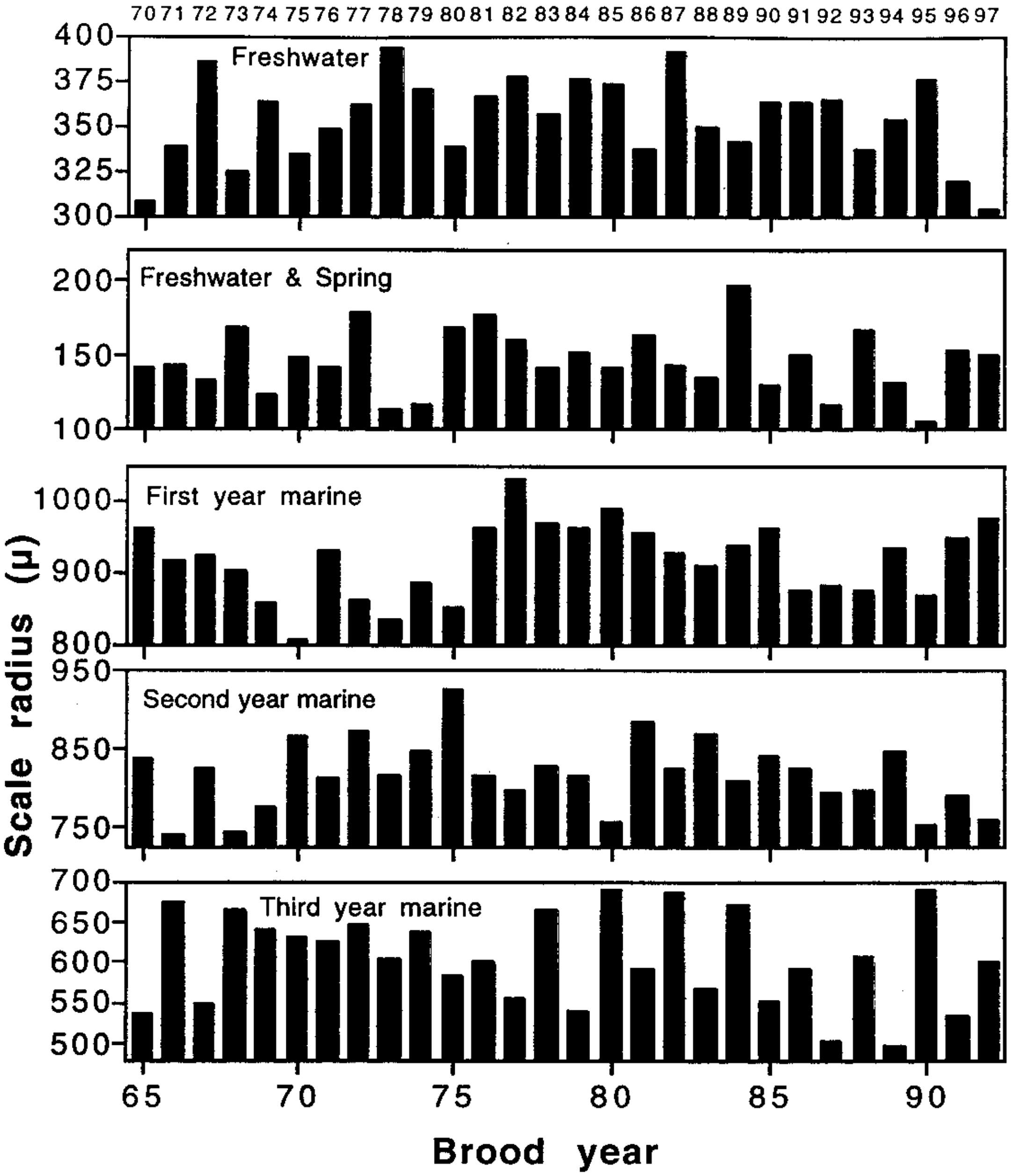

Fig. 32. Mean incremental scale radii measurements of Nushagak Bay sockeye salmon, brood years 1965-1992. Year of adult return is shown above the top figure. Standard errors were too small to display.

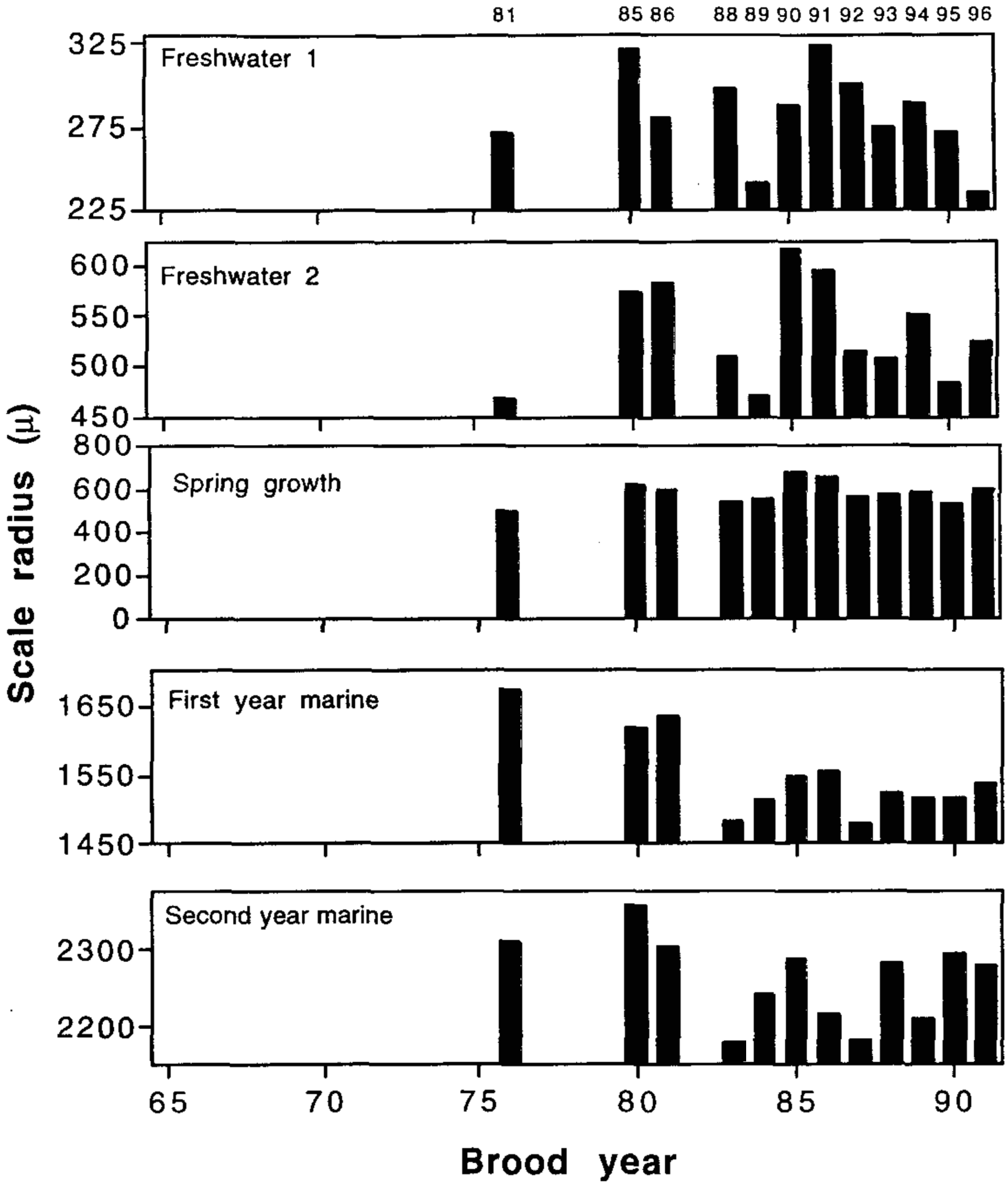

Fig. 33. Mean cumulative scale radii measurements of early Bear Lake sockeye salmon, brood years 1976-1991. Year of adult return is shown above the top figure. Standard errors were too small to display.

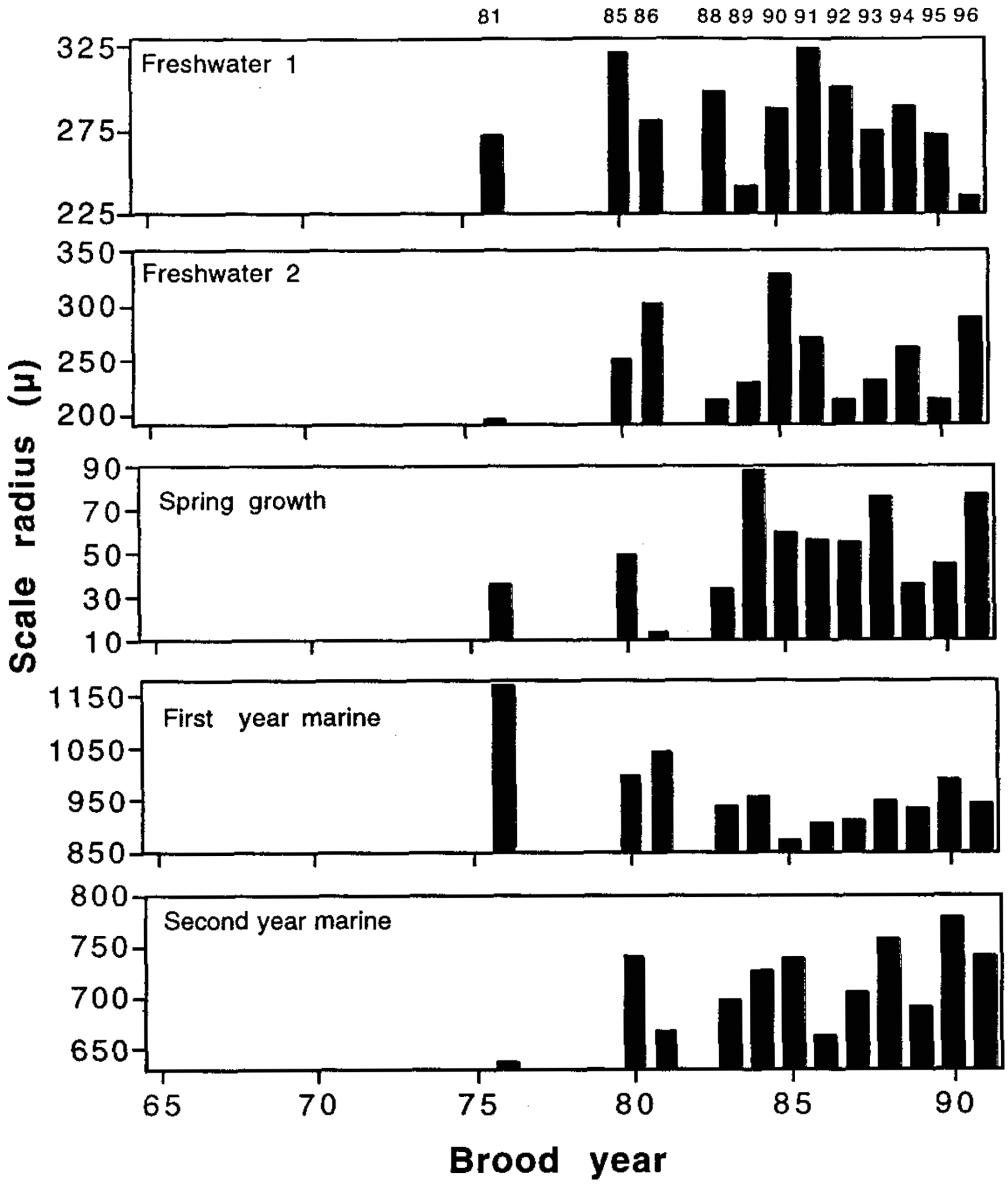

Fig. 34. Mean incremental scale radii measurements of early Bear Lake sockeye salmon, brood years 1976-1991. Year of adult return is shown above the top figure. Standard errors were too small to display.

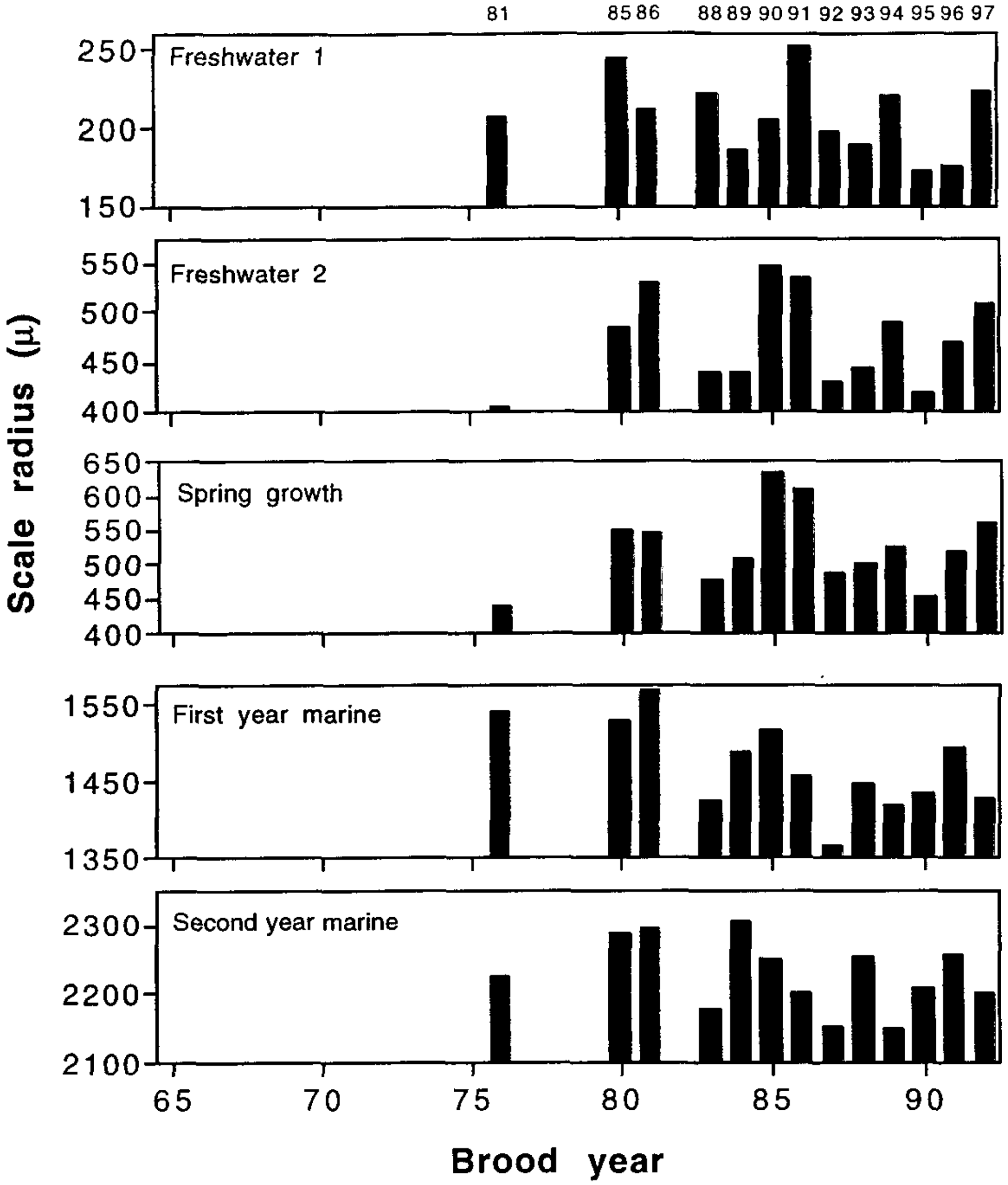

Fig. 35. Mean cumulative scale radii measurements of late Bear Lake sockeye salmon, brood years 1976-1992. Year of adult return is shown above the top figure. Standard errors were too small to display.

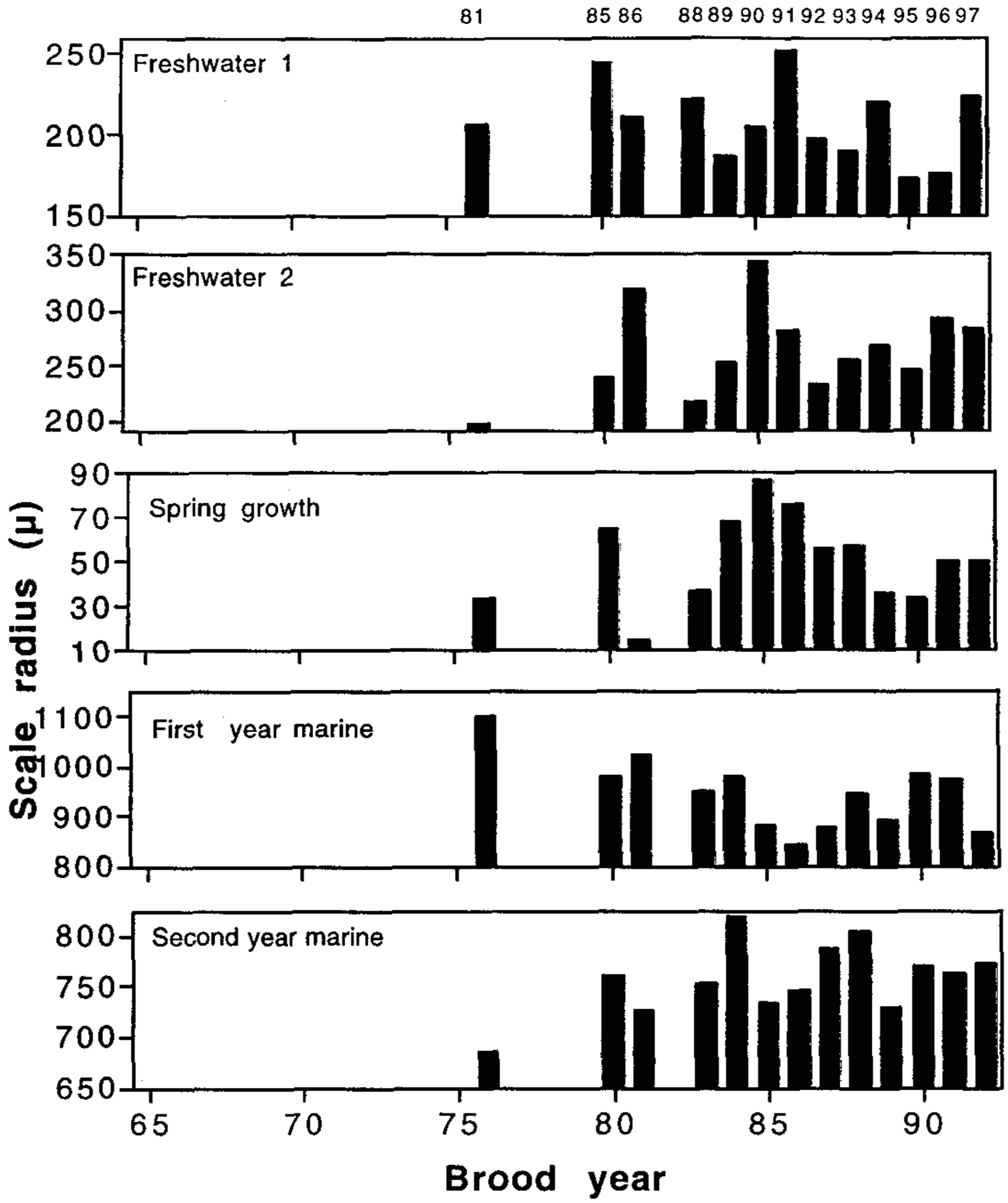

Fig. 36. Mean incremental scale radii measurements of early Bear Lake sockeye salmon, brood years 1976-1992. Year of adult return is shown above the top figure. Standard errors were too small to display.

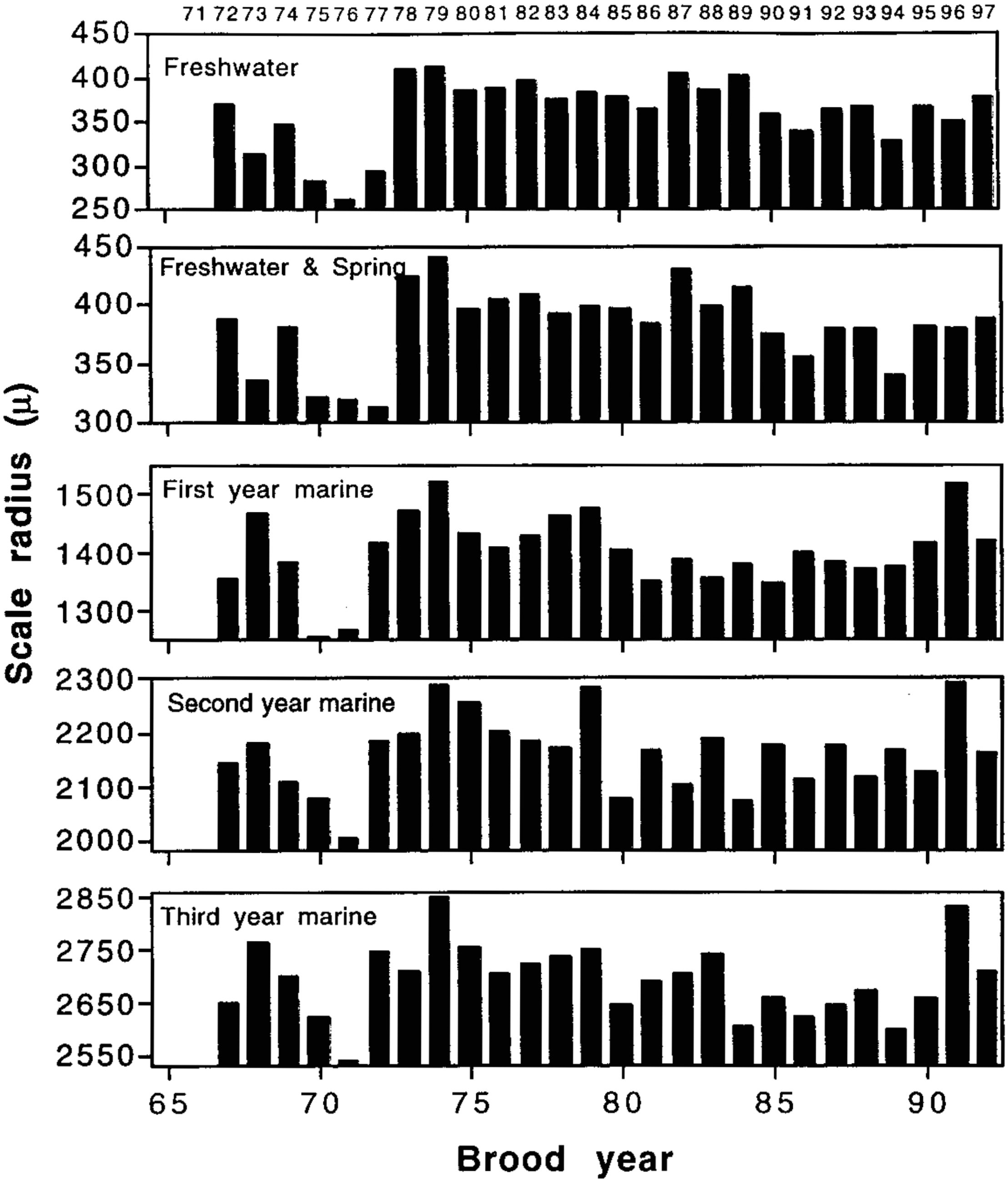

Fig. 37. Mean cumulative scale radii measurements of Kasilof River sockeye salmon, brood years 1966-1992. Year of adult return is shown above the top figure. Standard errors were too small to display.

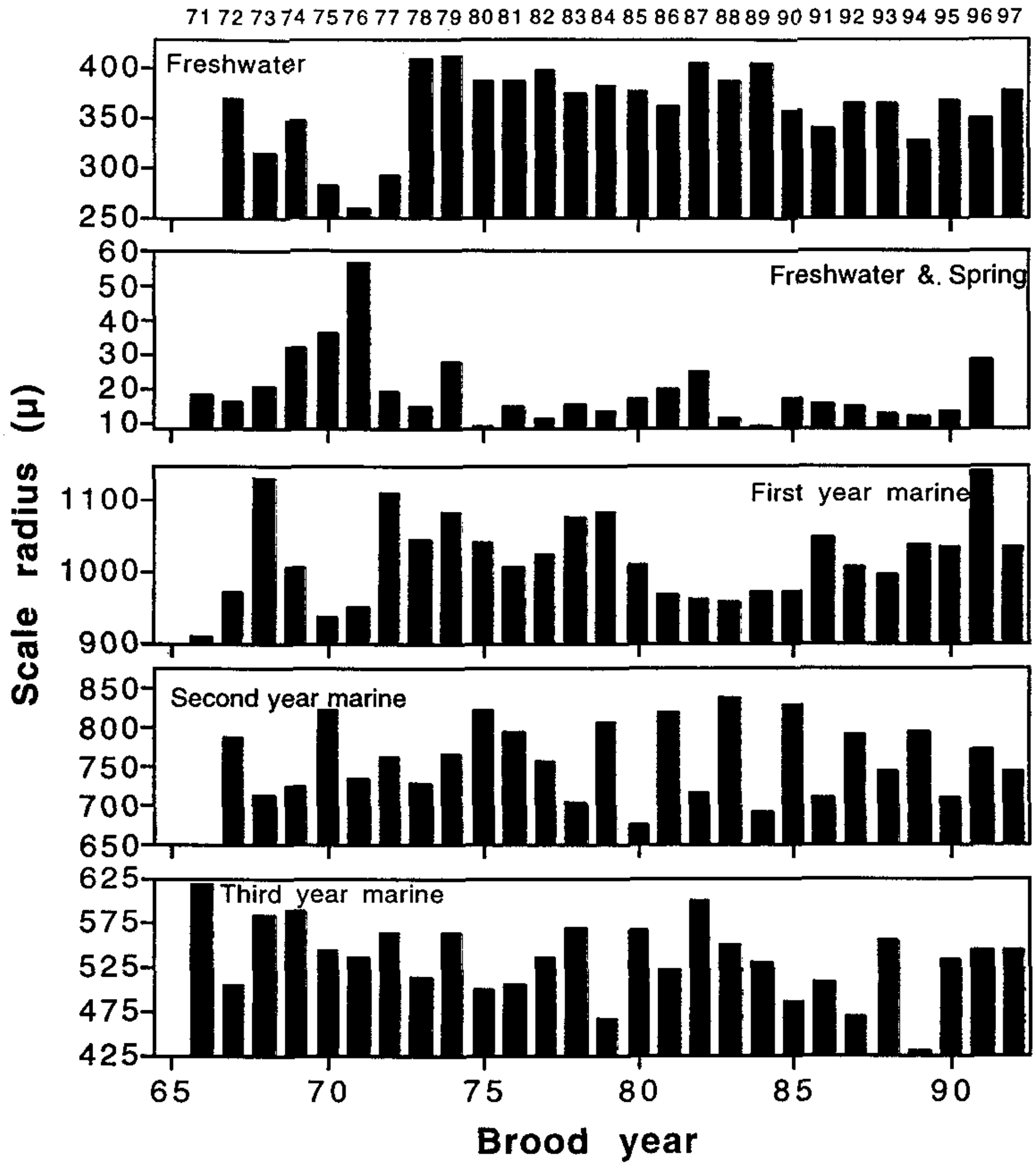

Fig. 38. Mean incremental scale radii measurements of Kasilof River sockeye salmon, brood years 1966-1992. Year of adult return is shown above the top figure. Standard errors were too small to display.