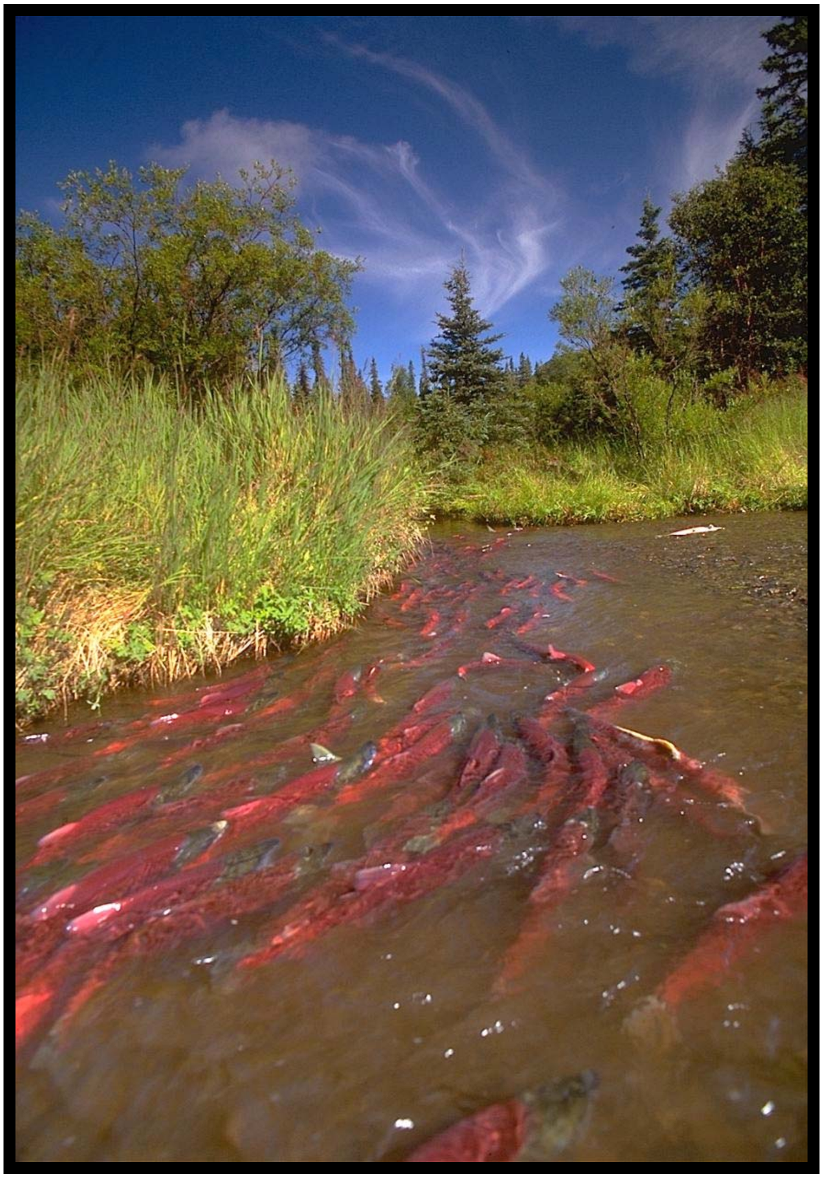
Collapse of Kvichak Sockeye Salmon Production

Brood Years 1991-1999:

Population Characteristics, Possible Factors, and Management Implications



Prepared for:

North Pacific Research Board

and

Bristol Bay Science and Research Institute

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Collapse of Kvichak Sockeye Salmon Production
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Population Characteristics, Possible Factors, and Management Implications

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December 2006

Suggestion format for citation:

Ruggerone, G.T., and M.R. Link. 2006. Collapse of Kvichak sockeye salmon production brood years 1991-1999: Population characteristics, possible factors, and management implications. Unpublished report prepared by Natural Resources Consultants, Inc. and LGL Alaska Research Associates, Inc. for the North Pacific Research Board, Anchorage, AK. xiv + 103p.

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ABSTRACT

Kvichak sockeye salmon, once the largest sockeye stock in the world (up to 50% of world's sockeye production), declined 73% during brood years 1991-1999 compared with previous years. This investigation examined factors associated with the decline and implication for salmon management. Growth and abundance of juvenile sockeye salmon in the Kvichak watershed was density dependent due to cohort abundance and the abundance of previous year's cohorts. Slower growth of juveniles occurred when parent and/or previous spawning escapements were high and fewer smolt per spawner occurred when the previous spawning escapement was high. Adult return per spawner declined with greater parent spawner abundance and with greater abundances of spawners during the previous year, but only after accounting for high interception rates in adjacent fishing districts (Egegik and Ugashik). (An important future task will be to estimate interceptions of Kvichak salmon in adjacent fishing districts using genetic data and population modeling). The significance of density dependence and brood interaction in the lakes stemmed from high densities of salmon in the watershed (spawners per lake area) during peak-cycle years and the lower productivity of the Kvichak stock compared with other Bristol Bay stocks. No evidence for direct depensatory mortality, such as that cause by predators or marine derived nutrients from off-year versus peak-year carcasses, was found. Rather, the Kvichak cycle has likely been maintained by depensatory fishing mortality (some of which is not accounted for in current stock assessments), density-dependent interactions between brood lines, low productivity of the Kvichak watershed, and the fairly constant 5-year age structure of Kvichak salmon.

Reconstruction of Kvichak smolt abundances and survival at sea indicated that approximately 58% of the recent decline was related to the spawner-to-smolt life stage and 42% was related to smolt-to-adult life stage, but other analyses suggested that much of the decline in freshwater may have been related to the condition of spawning adults, which is ultimately related to marine conditions. Mean length-at-age of all Bristol Bay sockeye salmon was low during the period of decline. Growth of juveniles in the lakes tended to be above average during the period of decline, suggesting prey availability in the lakes was not a key factor.

Several other Bristol Bay stocks also declined during the 1991-1999 brood years, but not as much as the Kvichak. The level of decline among Bristol Bay stocks was associated with the ocean age structure of the populations: stocks typically producing ocean age-2 salmon experienced greater declines in abundance than those stocks with significant component of ocean age-3 salmon. The reduction in adult size-at-age, thought to be in response to warm spring ocean conditions experienced by parents, increased abundance of Asian pink salmon (competition for prey) and the 1989 ocean regime shift, may have led to lower reproductive potential and success of adult sockeye salmon, especially ocean age-2 salmon which are smaller and have lower reproductive potential compared with ocean age-3 salmon. We hypothesize that Kvichak salmon were especially vulnerable to reduced growth during late marine stages because they produce the highest percentage of ocean age-2 sockeye salmon in Bristol Bay.

A previously-postulated cause of the Kvichak decline was the change in the escapement goal policy that led to more stable escapement levels beginning in the mid 1980s. The change in policy was made in an attempt to stabilize yield from the Kvichak caused by large fluctuations in

run sizes among years in the 5-year cycle. The previously postulated mechanism is that periodic high escapement levels to the Kvichak are needed in order to provide harvestable surpluses. Analyses here indicate this change in policy was not responsible for the decline and no biological evidence was found to indicate that cyclic spawning escapements are necessary to achieve high productivity of Kvichak salmon.

Comparison of spawning escapement goals of Bristol Bay stocks after standardization by lake surface area revealed that the escapement goal for peak and pre-peak cycle years was high compared with other large stocks in Bristol Bay. This finding was unexpected because the Kvichak stock is the least productive stock in Bristol Bay, suggesting that its escapement goals should possibly be lower per unit of lake area than other stocks.

SUMMARY

The Kvichak River watershed, located in Bristol Bay Alaska, is largest producer of sockeye salmon in world. During peak-cycle years in the 1960s and early 1970s, the Kvichak produced 23-42 million salmon per year and represented up to 80% of Bristol Bay, 62% of North America, and 50% of world sockeye salmon production. However, during 1996-2005, run size declined 74% to only 3.8 million salmon, on average, and salmon harvests declined 84%. The sharp and prolonged decline created considerable economic hardship in the region.

This investigation compared population characteristics of the Kvichak salmon during the decline with its past characteristics and with other Bristol Bay stocks. The goals were to identify potential factors associated with the decline and with the Kvichak cycle, and to examine whether changes to the escapement goal policy during the mid 1980s may have contributed to the decline.

Characteristics of the Decline

The decline in Kvichak salmon began with the 1991 brood year and continued through the 1999 brood year. Adult return per spawner (R/S) and total adult returns declined approximately 73% from 1973-1990 to 1991-1999. R/S averaged 0.79 during the recent period, indicating the return of adult salmon across return ages was considerably smaller than the parent spawning escapement. Spawning escapement declined 18%. Reconstruction of smolt abundances during the recent period of smolt counter error indicated that abundance of smolts declined approximately 64%, on average. The decline of age-2 smolts (83% decline) was greater than the decline in age-1 smolts (43%), largely because Kvichak smolts tended to migrate at an earlier age in response to warmer temperature and smaller escapements. Smolts per spawner declined 48%, on average. In addition to the decline associated with freshwater life history, smolt-to-adult (i.e., marine) survival declined approximately 46%, on average. Thus, the Kvichak decline was related to decreases in survival in both freshwater and marine habitats (see further analyses below).

Comparisons with other Bristol Bay Stocks

The decline in Kvichak productivity was not unique among Bristol Bay salmon stocks. R/S of Egegik and Ugashik stocks declined 47% and 60%, respectively, whereas other Eastside stocks (Naknek and Alagnak) did not decline nearly as much. R/S of most Westside stocks (e.g., Nushagak and Togiak districts) did not exhibit a significant decline (avg. -7%). Residuals (observed – predicted values) from Ricker recruitment curves indicated the productivity of Kvichak salmon declined much more than all other stocks, although productivity of some stocks (Egegik and Ugashik) were consistently below average during brood years 1991-1999. Smolts per spawner and smolt-to-adult survival of both Egegik and Ugashik stocks declined during the recent period, indicating that the decline was not unique to Kvichak. (Smolt-to-adult survival of Kvichak and Egegik salmon were correlated prior to the large Kvichak smolt enumeration error which began in 1995).

The decline in Kvichak salmon was associated with a significant shift in age composition during the freshwater and marine stages. The percentage of age-1 smolts in the adult return

increased 51% and the percentage of ocean age-3 adults increased 41%. Other Eastside stocks also exhibited a change in age composition, although the degree of change was less. Age composition (and productivity) of Westside stocks was relatively stable.

The decline of Kvichak and other Bristol Bay salmon stocks from 1973-1990 to 1991-1999 was positively correlated with the magnitude of change in age composition of the stock. Decline in R/S and total adult return of Bristol Bay stocks were correlated with the percentage decline in numbers of age-2.2 salmon in the adult return, i.e., stocks that lost a large percentage of age-2.2 salmon experienced the greatest decline. Percentage decline in age-2.2 salmon among Bristol Bay stocks explained 58-74% of the variation in R/S and total return. The abundance of age-2.2 Kvichak sockeye salmon declined 85% from 1973-1990 to 1991-1999. This age class typically dominates Kvichak returns (avg. 84% of returns, 1952-1999).

It is noteworthy that the age composition shift among stocks that declined during 1991-1999 followed a similar shift (same direction) in response to the 1976/77 ocean regime shift that led to greater production (i.e., more age-1 smolts and ocean age-3 adults). Thus, age composition of stocks that declined recently is now markedly different from that during 1952-1972. This trend suggests that some stocks are adjusting to new environmental conditions by altering age composition, but that this change in age structure was associated with lower overall productivity. Stocks that did not significantly change age structure did not decline in abundance. The change that began with the 1991 brood year may be related to the reported 1989 climate regime shift.

It has been suggested that the decline in Kvichak productivity was primarily due to the shift toward age-1 smolts. However, Kvichak R/S was not correlated with the percentage of age-1 smolts in the Kvichak smolt migration since the 1952 brood year. In the Kvichak watershed, age-1 smolts produced age-1.x adult returns that exceeded 2.5 million fish in 40% of the years, whereas ocean age-3 sockeye rarely produced more than 2.5 million salmon. This trend highlights the importance of ocean age-2 salmon in the Kvichak return.

The benefit of remaining in Bristol Bay nursery lakes for a second year, as determined by gain in weight and marine survival, was positively correlated with mean percentage of age-2 smolts in the migration across four stocks that have smolt data. In other words, stocks that experienced greatest gain in weight and/or survival at sea after spending two winters in freshwater also tended to stay two years in freshwater. The estimated benefit of Kvichak age-2 smolts was intermediate to that of other Bristol Bay stocks.

Is the Decline Related to Freshwater or Marine Factors?

The relatively high correlation in smolt-to-adult survival of Kvichak and Egegik salmon enabled reconstruction of smolt survival, smolt abundance, and smolts-per-spawner estimates of Kvichak salmon during the recent period when the Kvichak smolt sonar produced erroneously high estimates.

Approximately 58% of the overall decline was attributable to the spawner-to-smolt stage, and 42% of the decline was attributable to the smolt-to-adult stage, a finding that was consistent with observations of Ugashik and Egegik salmon production. Approximately 22% of the decline in smolt production was attributable to the decline in parent spawning escapement. However, as noted below, marine conditions may have contributed to the decline in spawner-to-smolts survival due to smaller spawning adults whose reproductive success may have been compromised by high salmon densities at sea and high metabolic rates in response to relatively warm ocean temperatures. We hypothesize that Kvichak salmon were especially vulnerable to reduced growth during late marine life because they are dominated by ocean age-2 adults, which typically produce fewer eggs and smaller eggs compared with older sockeye salmon.

Density-Dependent Growth, Brood Interaction, and the Kvichak Cycle

The Kvichak cycle is unique among Bristol Bay stocks. Components of the five-year cycle have been described as pre-peak, peak, post-peak, and off-cycle years, which relate to spawning escapement levels and subsequent returns.

Researchers have debated whether the cycle is caused by natural depensatory mechanisms that result in higher survival for fish from high escapement events (predation, biogenic enrichment, parasites in spawning gravels) or simply due to depensatory fishing mortality and a cyclic escapement goal policy. Proponents of the natural depensatory hypotheses argue that large fluctuations in escapement levels should be maintained by management actions in order to sustain high harvest levels from the Kvichak. Knowledge of factors influencing the cycle and whether it is needed to provide surplus yield are critical for establishing escapement goals and for providing economic benefits for the salmon industry and local communities.

Density of Kvichak spawners per lake surface area ranked second among the five Eastside stocks and intrinsic productivity of Kvichak salmon (R/S at low density) was lowest among all nine Bristol Bay stocks, suggesting density-dependence may be an important factor in the Kvichak watershed. Age-1 smolt weight significantly declined with greater parent escapement and previous-year escapement, indicating brood interaction was important. During the 35-year period, 63% of variation in age-1 smolt weight was explained by these two variables. In contrast, age-2 smolt weight was influenced by parent spawners, but not by previous-year spawners. This probably reflects dispersion of rearing age-2 salmon to the west within Lake Iliamna away from spawning areas located in and adjacent to the eastern end of the lake. Residuals (observed - predicted) from the smolt weight models indicated smolt weight was above average during brood years 1991-1996, but below average thereafter. Thus, there was no evidence to suggest that the Kvichak decline or the decline in other eastside stocks was related to slow growth of juveniles in the lakes.

Numbers of smolts produced in the Kvichak watershed increased with parent spawning escapement, brood years 1969-1990. However, abundance of previous-year spawners adversely affected the number of smolts. Approximately 82% of the variation in total smolt abundance was explained by a brood interaction model. The reduction in smolt abundance likely occurred in response to reduced growth during the first year in the lakes because growth during second year was not measurably influenced by previous-year spawners.

A hierarchical series of Ricker spawner recruit models were examined to evaluate the effect on adult recruitment (R_i) of: 1) parent spawners (S_i), 2) previous-year spawners (brood year interaction) (S_{i-1}), 3) a period effect (P) accounting for differential production after the 1972 brood year (i.e., corresponding with smolts influenced by the 1976-77 ocean regime shift), and 4) an interception effect (I) for brood years where the Egegik and Ugashik production was at least twice the Kvichak. All variables contributed significant information to the prediction of Kvichak sockeye returns, based on the Akaike Information Criterion. The following statistical model was developed from brood years 1952-1990:

$$R_i = S_i \exp\left(1.139 - .0000514 S_i - .0000415 S_{i-1} - .964 I + .703 P + \varepsilon\right).$$

This model indicates that interception rates in Egegik and Ugashik fisheries may introduce significant and previously unaccounted for mortality of Kvichak salmon, a finding that is consistent with emerging genetic stock identification results by ADFG. The model also indicates high spawning escapements may suppress R/S of subsequent broods, a finding that is consistent with observations of reduced growth and reduced abundance of smolts in response to large previous-year escapements. It is noteworthy that Kvichak R/S shows no significant density dependence in relation with parent spawners if interceptions in adjacent fishing districts are not accounted for in the model. These analyses indicate density dependent effects on Kvichak R/S are confounded by unaccounted interceptions in the Egegik and Ugashik districts.

Characteristics of Kvichak cycle years were examined to determine whether post-peak and off-cycle years had lower productivity, as suggested by the hypothesis of cyclic dominance, which involves natural mechanisms such as depensatory predation. We found the opposite pattern in productivity among years of the cycle than would be expected from previous hypotheses used to explain the Kvichak cycle. Large spawning escapements during peak-cycle years had a negative effect on growth of post-peak progeny, leading to higher percentages of age-2 smolts and lower smolts per spawner in post-peak years. Growth of off-cycle smolts rebounded following low escapements during the post-peak cycle. Further improvement in growing conditions following several years of low escapement was apparent from relatively large smolts produced by pre-peak cycle years in relation to parent spawning escapement. Smolts per spawner and smolt biomass per spawner were relatively high during off-cycle and pre-peak cycle years. Cycle-year patterns were consistent with statistical models, which show that density-dependence and brood interaction suppressed juvenile growth and adult R/S. There was no evidence for depensatory mortality that might be caused by predation or marine derived nutrients from peak year carcasses (model residuals indicated no benefit in smolt weight, smolt abundance or R/S during peak cycle broods). Rather, characteristics of cycle years followed expected patterns established by parent escapement and previous-year spawning escapements. These findings have important implications for setting Kvichak escapement goals.

Adult R/S was highest for pre-peak cycle (2.6), followed by peak cycle (2.3), off-cycle (1.9) and post-cycle years (1.2). This pattern fits the pattern of negative interaction between peak and post-cycle years followed by partial recovery in off-cycle years and full recovery in pre-cycle years. However, unaccounted interceptions of Kvichak salmon in Egegik and Ugashik fisheries likely influenced R/S statistics especially for off-cycle and post-cycle years. Returns from post-peak (44% of years) and off-cycle years (53% of years) often occurred when returns to Egegik and Ugashik were large relative to Kvichak returns, whereas high potential interception rates were less frequent during pre-peak (20% of years) and peak years (9%). The low R/S of post-peak cycle years was consistent with its low smolt biomass per spawner, whereas the low R/S of off-cycle years was not (off-cycle years experienced the highest smolts per spawner and highest smolt biomass per spawner). R/S of off-cycle years was probably biased low because some fish were intercepted in adjacent fishing districts and not tallied in the Kvichak return. R/S of pre-peak cycle years was the highest of all cycle years, and it reflects high smolt per spawner, high biomass per spawner, and high smolt-to-adult survival. Hence, overall production from pre-peak years rebounded four years after the previous peak-cycle.

Factors Associated with Reduced Productivity and Production, 1991-1999

Residuals of the Kvichak spawner-recruit model indicated that LN R/S was unusually low during brood years 1991-1999. Three variables (age-specific length of parents (+), Kamchatka pink salmon abundance (-), SST during June of parent return (-)) were significantly correlated with residuals of the Kvichak brood interaction model developed with years 1952-1990 and applied to 1974-1999. A multivariate model was developed that incorporated length-at-age of parents and an index of Kamchatka pink salmon abundance. This model explained 44% of the variability in LN R/S residuals (after density-dependence and brood interaction effects in lakes had been removed). Inclusion of SST during the parent return improved the variability explained by the model to 51%, but the SST variable was marginally significant (partial $P = 0.057$).

These findings suggest that relatively small length-at-age of parents and relatively high SST may have resulted in lower reproductive success of escapements during the 1990s than in previous years. Previous research on interactions between sockeye and pink salmon indicated pink salmon significantly reduced size of returning sockeye salmon and reduced survival of Bristol Bay sockeye salmon (avg. 36% reduction), especially ocean age-2 adults and age-1 smolts. The observed 79% decline in abundance of ocean age-2 sockeye salmon during the decline is consistent with this observation. Eastside stocks may be more susceptible to interactions with Asian pink salmon compared with Westside stocks because Eastside stocks have greater spatial overlap with Asian pink salmon. The greater R/S decline associated with stocks having numerous ocean age-2 adults may reflect the greater susceptibility of smaller, younger spawning salmon to environmental conditions that favor slower growing and older salmon (i.e., age-x.3). We hypothesize that Kvichak salmon were especially vulnerable to reduced growth at sea because they are dominated by ocean age-2 adults which typically produce fewer eggs and smaller eggs compared with older sockeye salmon. Further research is needed on the potential effects of relatively high SST and small size at age on the fecundity and reproductive condition of sockeye salmon by ocean age.

Kvichak Escapement Goals

Escapement goals of Bristol Bay sockeye stocks were compared after standardizing the values by lake surface area. Kvichak spawner density produced by the peak and pre-peak escapement goal was higher than that of other large Bristol Bay stocks except Ugashik. This finding was unexpected because Kvichak sockeye is the least productive of all Bristol Bay stocks. (A high spawner density implies high lake productivity unless the spawning grounds are limiting production). An escapement density comparable to other Bristol Bay stocks is equivalent to 5.4 million Kvichak sockeye salmon, which is similar to the mean historical escapement (5.3 million salmon). However, a goal of 5.4 million salmon is less than the existing mean escapement goal of 6.8 million spawners (weighted by cycle year), i.e., escapement goals of 2-10 million spawners during off-cycle years and 6-10 million spawners during pre-peak and peak-cycle years.

Recommendations and Conclusions

A key to further refining our understanding of past and future changes in the abundance of Kvichak salmon will be to accurately index the abundance, age, and size of smolts produced over time. These estimates can help partition changes in productivity between marine and freshwater factors and to facilitate the evaluation of escapement goals. Although the smolt program on the Kvichak system produced large erroneous estimates as far back as 1995, it once worked well as evidenced by the improvements it made to preseason forecasts, and progress has been made to correct the problems introduced then with new sonar equipment. We recommend the reintroduction of a smolt program that can provide abundance estimates comparable to those obtained prior to 1995.

Estimating smolt abundance on the Kvichak is technically challenging and more difficult than doing so for the Egegik River. Kvichak and Egegik smolt-to-adult survival estimates were highly correlated prior to 1995 indicating each acoustic system provided an accurate estimate of the relative abundance of smolts and that Egegik survival rates are a good surrogate for tracking changes in marine survival for Kvichak smolts. At least while technical challenges associated with estimating smolt abundance on the Kvichak are overcome, we recommend an Egegik program also be reintroduced. In addition to tracking Kvichak survival, such a program would improve preseason forecasts of ocean age-2 returns to Egegik.

Unaccounted interceptions of Kvichak salmon in Egegik and Ugashik districts have long complicated interpretation of the stock dynamics of Kvichak salmon and provided some erroneous support for the concept of enhanced productivity (marine survival) during peak years. We recommend these interceptions of Kvichak fish be carefully reconstructed for past years, especially during years of high Egegik and Ugashik returns relative to Kvichak returns. In addition, we recommend that stock composition of catches from eastside districts be a standard component of the annual assessment program. ADFG has begun to re-analyze past interceptions of Kvichak salmon in the Egegik District using genetic stock identification and population modeling. This task is key to developing an unbiased recruitment relationship, which is needed to estimate spawner escapement goals for the Kvichak watershed. Multiple methods should be undertaken to estimate a range in Kvichak spawning escapement that will enable the potential for sustained high harvests. Brood interaction should be considered in the evaluation, especially if high densities of spawners are recommended in some cycle years.

Findings presented here indicate that the relatively low R/S of post-peak and off-cycle years was caused by unaccounted interceptions of adult salmon in Egegik and Ugashik fishing districts and by brood interactions in the nursery lake, rather than cyclic dominance associated with direct depensatory mortality, as has been previously postulated. Our findings are generally in agreement with those of Rogers and Poe (1984) and Eggers and Rogers (1987) who, using less data than presented here, also found no evidence of direct natural depensatory mortality. There was no evidence that biogenic enrichment of salmon carcasses provided a boost to growth and/or survival of peak-cycle progeny.

The Kvichak decline does not appear to have been caused by a change in the stock's escapement goals made in 1984. Production from the first four brood years following the policy change to relatively stable escapement levels across the cycle averaged 2.9 returns per spawner, which was higher than the average of 2.5 R/S from the previous 10 brood years. Subsequent declines in productivity and yield from the Kvichak during brood years 1991-1999 were also observed in other Bristol Bay stocks (e.g., Egegik and Ugashik) in response to lower smolt-to-adult survival (marine factors) and fewer smolts produced per spawner (freshwater factors). The substantial decline in production from eastside stocks beginning with the 1991 brood year coincides closely with the 1989 ocean regime shift, which produced generally warmer freshwater and marine conditions. These data and others presented here suggest that changes to the Kvichak escapement goal policy in 1984 was not a major factor leading to the stock's decline. Rather, multiple factors involving climate, growth at sea, population age structure, and density-dependent interactions appear to have contributed to the decline.

The results from our analysis do not support the existing escapement goal policy of higher escapement levels (6 to 10 million fish) during peak and pre-peak return years compared to other return years (2 to 6 million). Maintenance of the Kvichak cycle through management does not appear necessary for high salmon productivity and harvestable surpluses, a conclusion also made by Rogers and Poe (1984). However, shifting away from the cycle by stabilizing spawning escapement levels is made difficult because of a desire to harvest Kvichak salmon each year, the low productivity of Kvichak salmon, and the propensity of the Kvichak stock to experience cyclic patterns in response to relatively constant age at maturation, brood interaction, and interception of salmon in adjacent Bristol Bay fishing districts. We recommend further work to evaluate and define escapement goal policies for the Kvichak in light of the results provided here.

INTRODUCTION

The Kvichak River watershed, located in Bristol Bay Alaska (Fig. 1), is largest producer of sockeye salmon in world. During peak-cycle years in the 1960s and early 1970s, the Kvichak watershed produced 23-42 million salmon per year and represented up to 80% of Bristol Bay, 62% of North American and 50% of world sockeye salmon production (Fig. 2). The contribution of Kvichak salmon to world production has decline steadily over the past 40 years, in part because the Kvichak stock did not respond as favorably to the 1976/77 ocean regime shift that led to greater salmon production throughout northern areas of the Pacific Rim. Nevertheless, the Kvichak stock remained a major producer of sockeye salmon throughout the 1980s and early 1990s. Runs during 1978-1995 averaged 14.8 million salmon per year (range: 2.0 to 35 million).

Beginning in 1996, relatively few sockeye salmon returned to the Kvichak River (avg. 3.8 million). On average, run size declined 74% from the periods 1978-1995 to 1996-2005. The sharp decline in run size produced an even greater decline in harvest (84% decline) as harvest managers attempted to restrict fishing and allow nearly all of the run to escape to the spawning grounds. The average value of the Kvichak harvest (in 2005 dollars) declined from $65 million per year during 1978-1995 to just $7 million per year during 1996-2005. The loss of the Kvichak contributions to fishing operations created significant hardship for the Bristol Bay salmon industry and the region's communities.

Speculation about factors causing the collapse grew as the series of low salmon runs continued from 1996 into the late 1990s and early 2000s. Initially, the decline was unexpected because pre-season forecasts indicated large runs and the decline was very abrupt. Although the University of Washington had conducted studies in the Kvichak watershed since the 1950s, no obvious factors of decline surfaced from these data, although field research had been limited in the recent decade. Speculation was further fueled by the exceptionally large smolt migrations estimated by sonar beginning in 1995 that produced relatively few adults. Although the sonar counts had been used to successfully forecast adult returns for many years, recent studies indicate that the sonar greatly overestimated Kvichak smolt abundance beginning in the mid 1990s, apparently due to changes in hardware and operation (see appendix). The inaccuracy of the smolt enumeration program was untimely because smolt data are important for identifying whether the decline was related to freshwater or marine factors and whether management (i.e., changes to the escapement goal policy for the Kvichak) contributed to the decline.

The unexpected decline in Kvichak salmon also fueled speculation that high seas salmon fishing had removed most of the Kvichak run. However, since the mid 1970s these fisheries have been restricted to western areas near Asia where previous tagging data indicated few Bristol Bay salmon (Myers et al. 1996). New genetic information also indicates Bristol Bay sockeye salmon, especially those originating from east side stocks (i.e., Kvichak, Egegik), extend westward to the Kamchatka Peninsula. Asia produces relatively few sockeye salmon (Rogers 2001) and no spike in sockeye salmon was apparent in Asian markets. It seems unlikely that interceptions of Kvichak salmon near Asia were responsible for the dramatic decline in the adult returns to Bristol Bay.

The Kvichak sockeye salmon stock is unique among Bristol Bay sockeye salmon stocks in many characteristics. The Kvichak run is known for its cyclic production, which typically occurs every 5 years, or 4 years when smolts grow rapidly and leave freshwater after one winter in the lake instead of two winters (Rogers and Poe 1984). The five-year cycle reflects the dominant age of Kvichak salmon. The cycle has been described as having a pre-peak, peak, post-peak, and two off-cycle years. Peak cycle years receive large spawning escapements that typically produce large returns. Post-peak and off-cycle years experience much smaller parent spawning escapements and produce smaller runs. The pre-peak cycle is intermediate in size. Considerable effort has been expended to determine whether the cycle is caused by depensatory fishing (Eggers and Rogers 1987) or whether natural factors also cause depensation and influence the cycle (Mathisen and Poe 1981).

Knowledge of factors affecting the cycle is important because it has implications for harvest management and economic yield from the fishery. Eggers and Rogers (1987) found that fishing exerted significant depensatory mortality and was largely responsible for the cycle, although they also detected density dependence and somewhat reduced productivity following large spawning escapements (i.e., brood interaction). The findings of Rogers and Poe and Eggers and Rogers led to changes in spawning escapement goal policy for the Kvichak in 1984 whereby the pre-peak and peak escapement goals were reduced from 6 to 14 million, to 6 to 10 million and escapement goals for other cycle years were increased from 2 million to “4 to 6” million (point goal of 5 million). The impetus for this change was from fishery scientists and from the fishing industry where it was believed that the change would reduce large fluctuations in run sizes and reduce interannual variation in catches, thereby having a stabilizing effect on income and improving the overall economic performance of the fishery.

The primary objective of this report was to describe characteristics of the Kvichak sockeye salmon decline in relation to previous characteristics and to other Bristol Bay stocks in an attempt to identify potential factors of the decline. Particular emphasis was placed on factors that might be influenced by management, namely the magnitude and pattern of escapement levels. This report builds upon earlier Kvichak studies by Roger and Poe (1984) and Eggers and Rogers (1987). An important goal of the study was to determine whether the decline in Kvichak salmon production (total return) and productivity (adult return per spawner, R/S) was unique to the Kvichak stock and whether factors of decline were related to freshwater habitats, marine habitats, and/or management. Current Kvichak escapement goals were compared with those of other Bristol Bay stocks after standardizing the goals by escapement salmon per lake surface area.

METHODS

Parent escapement and return by age (brood tables) and smolt data were obtained from databases initially developed by D.E. Rogers, University of Washington. Catch and return data were collected by the Bureau of Commercial Fisheries, Fisheries Research Institute (FRI), and Alaska Department of Fish and Game (ADFG). These databases were updated in recent years using statistics provided by L. Fair, ADFG, and statistics in annual ADFG smolt reports (Crawford 2001). The brood table statistics used in this investigation include catches from Bristol Bay districts only ("inshore returns"). Salmon catches that occurred in Area M fisheries and in high seas fisheries (mostly prior to mid-1970s) were not included because they are subjected to greater allocation error between salmon regions and among Bristol Bay stocks. Total return estimates reported by ADFG include all sockeye salmon captured in the False Pass, Unimak Island, and Shumagin Island areas even though other stocks of salmon are known to mix in these fisheries (D. Eggers, ADFG, pers. comm.). Ultimately, use of the inshore versus total return brood table probably had little or no effect on qualitative conclusions about Bristol Bay salmon population dynamics drawn from brood table data.

Recently reconstructed escapement and brood table data for the Alagnak River stock were provided by D. Eggers, ADFG, and obtained from Clark (2005). This reconstruction led to significant changes in the Alagnak brood table compared with the previous table maintained by ADFG. A greater proportion of the Naknek-Kvichak District catch was assigned to Alagnak. Re-allocation of Naknek-Kvichak catch had a negligible effect on Kvichak brood table statistics.

Ricker recruitment curve equations (Ricker 1954) were developed using the linearized relationship unless noted otherwise:

1) Ln R/S = a + b (spawner escapement) + residual.

Spawner-recruit (SR) indices of productivity after removing density-dependence were calculated as residuals (observed – predicted) from the linearized recruitment curve (Peterman et al. 1998). SR indices were used to examine commonality in productivity trends among Bristol Bay stocks after removing the effects of density dependence.

Stepwise and multiple regression analyses were used to test a number of hypotheses. Overall P values were used to judge the significance of the overall regression, and partial P values were used to determine the significance of each variable in the multiple regression. P values identify the probability of incorrectly rejecting a null hypothesis. In most tests, the level of acceptable error (α) was 0.05.

RESULTS

Population Characteristics of Kvichak Sockeye Salmon

Adult sockeye Salmon Production

Kvichak sockeye salmon runs exhibit a cyclic pattern that is unique among Bristol Bay stocks. Peak runs tend to occur every five years (Fig. 3), although early age of smoltification (e.g., runs in 1979 and 1983) can cause many fish to return at age four instead of age five. Cyclic patterns of abundance led to highly variable annual run size and catch since at least 1950 (coefficient variation (c.v.) = 101% and 113%, respectively).

During 1952-2005, Kvichak run size (catch plus escapement) averaged 9.6 million ± 9.8 (SD) million sockeye salmon and catch averaged 4.7 million ± 5.4 million salmon (Fig. 2). However, run size declined in 1996 and remained relatively low through 2005, averaging only 3.8 million salmon, a 74% decline compared with runs during 1978-1995. During this period, runs during peak-cycle years (1999 and 2004) also remained small compared with previous cycle years. Preseason forecasts of Kvichak sockeye salmon were typically much higher than observed runs beginning in 1996, although the 1999 peak run was slightly higher than the preseason forecast (Fig. 4).

Harvests of Kvichak sockeye salmon declined, on average, from 8.4 million ± 5.7 million (SD) fish during 1978-1995 to 1.4 million ± 1.9 million fish during 1996-2005, an 84% decline in catch. Harvest rates declined 53% during 1996-2005, including almost no harvests during 1997, 2002, and 2003. Nevertheless, spawning escapements declined 62%, on average, from 6.4 million during 1978-1995 to 2.5 million during 1996-2005.

Low Kvichak run size in 1996 was produced primarily by the 1991 brood year (i.e., parent spawning year; Fig. 3). Return per spawner and total return of Kvichak sockeye salmon were consistently low during brood years 1991-1999 (Fig. 5). Return per spawner during this period averaged 0.75 ± 0.3 (SD) adults per spawner and 6 of 9 brood years failed to reproduce themselves (less than 1 R/S). Total adult return and return per spawner during 1991-1999 were 74% and 73% smaller, respectively, compared with those during 1973-1990 (Table 1). Preliminary data indicates 2.3 adults returned per spawner from a relatively small parent escapement in 2000 (1.8 million), i.e. a modest increase compared with the previous 10 years.

Kvichak productivity trends were examined after removing the potential effect of salmon density (i.e., siblings) in freshwater on subsequent adult returns. Density-dependent effects were removed by calculating residuals from the Ricker recruitment curve. The recruitment curve was developed for brood years 1973-1990, a period of relatively high productivity throughout Bristol Bay. Residuals from the recruitment curve were strongly negative during brood years 1991-1999 (Fig. 5), indicating low productivity of Kvichak salmon after accounting for potential density-dependent effects in the lakes or on the spawning grounds. Recruitment residuals were significantly higher during 1973-1990 compared with 1991-1999 ($P < 0.001$) and 1952-1972 ($P = 0.013$). Recruitment residuals during 1991-1999 tended to be lower compared with those during 1952-1972 ($P = 0.088$), i.e., brood years prior to the 1976/77 ocean regime shift.

The low productivity of Kvichak salmon during 1991-1999 was not unique but the duration of the decline was unique. Brood years 1965-1972 also produced consistently low return per spawner (Fig. 5). However, this period included two relatively large peak cycle returns (15-40 million salmon) that were produced by large spawning escapements (14-24 million salmon). The series of low productivity from brood years 1965-1972 was explained, in part, by exceptionally large spawning escapements. Thus, the nine-year period of low productivity and total production (1991-1999) is unique among the 50-year time series because it is not explained, in part, by exceptionally large spawning escapements and associated density-dependent effects.

On average, 58% ± 27% of Kvichak adult returns spent two winters in freshwater (age-2.x) during 1952-1999. However, age composition in the adult returns was not consistent over time. During 1952-1975, approximately 71% of the adults spent two years in freshwater, declining significantly to 55% during 1976-1990, and to only 33% during 1991-1999 (Fig. 6; ANOVA: df = 2, 44; overall $P = 0.001$, P (period) < 0.05). Productivity during these three periods were low, high, and low, respectively. If annual mean age composition is weighted by salmon abundance, then age-2 smolts contributed 65% of the total salmon return during 1952-1999, i.e., larger runs tended to be associated with numerous age-2 smolts.

Approximately 75% ± 15% of Kvichak adult returns spent two winters at sea (age-x.2), indicating that the Kvichak is dominated by ocean age-2 sockeye salmon (Fig. 6). The percentage of ocean age-2 sockeye salmon was exceptionally low only during brood years 1973, 1986, and 1996. The percentage of ocean age-2 sockeye was significantly greater during 1952-1972 (81%) compared with 1991-1999 (64%; $P = 0.006$), whereas the percentage during 1973-1990 (74%) was intermediate compared with adjacent periods and not significantly different. If annual mean age composition is weighted by salmon abundance, then ocean age-2 sockeye salmon contributed 84% of the total salmon return during 1952-1999. During 1991-1999, the weighted average percentage of ocean age-2 sockeye salmon declined to 76%. These data indicate ocean age-2 sockeye salmon is the dominant age group produced in the Kvichak watershed and that broods rarely produced numerous ocean age-3 salmon. As noted below, the exceptionally high percentage of ocean age-2 sockeye salmon in the Kvichak is unique among Bristol Bay sockeye salmon.

Juvenile Sockeye Salmon Production

Kvichak smolts have been monitored since the mid 1950s. Initially, smolts were enumerated with a fyke net, then sonar was deployed in 1971. Sonar count data provided relatively accurate preseason forecasts of Kvichak salmon during the 1980s and early 1990s. However, smolt counts in the mid-to-late 1990s were exceptionally large leading to erroneously large adult forecasts. Subsequently, studies have shown that sonar greatly overestimated smolts beginning with the 1995 smolt year (see Appendix). Two methods were used to estimate smolt abundances during 1995 to 2003 based on forward and backward reconstructions of annual smolt abundances. First, a statistical model was developed to predict age-specific smolt abundances from historical estimates of parent escapement, previous spawning escapement, and temperature during the rearing period (see Appendix for “escapement model”). Second, it was discovered that Kvichak smolt abundances could be back calculated from Kvichak smolt-to-adult survival estimates and adult returns because survival rates of Egegik and Kvichak smolts were correlated (see subsequent section for details on "Egegik model"). There was no evidence to suggest Kvichak smolt length and weight data were less accurate during the recent period and no adjustments were made.

Numbers of age-1 smolts declined from 76 million ± 16 million (SE) smolts during brood years 1974-1990 to 58 million ± 11 million smolts during 1991-1998[1], a 23% decline based on the escapement model after 1994 (Table 2). Numbers of age-2 smolts declined from 83 million ± 21 million smolts during brood years 1974-1990 to 39 million ± 9 million smolts during 1991-1998, a 54% decline. Overall smolt production declined 39%. These estimates assumed average spawner-to-smolt and environmental relationships, which were used to predict annual smolt abundance after 1994. The corresponding percentage of age-2 smolts in the annual migration declined from 49% to 39% during the recent period.

Smolt production trends were also calculated using the Egegik model for smolt years after 1994. Numbers of age-1 smolts declined from 76 million ± 16 million (SE) smolts during brood years 1974-1990 to 43 million ± 11 million smolts during 1991-1998, a 43% decline (Fig. 7). Numbers of age-2 smolts declined from 83 million ± 21 million smolts during brood years 1974-1990 to 14 million ± 3 million smolts during 1991-1998, a 83% decline. Overall smolt production declined 64% and the corresponding percentage of age-2 smolts in the annual migration declined from 49% to 38% during the recent period. The Egegik-based smolt models indicated a greater reduction in smolt production compared with the escapement-based models. As discussed below, the Egegik model likely captured year-to-year variation in smolt production more accurately than the escapement model.

Length of age-1 and age-2 smolts averaged 87.1 ± 4.3 mm and 106.8 ± 6.7 mm, respectively, during 1955-2003 smolt years (Fig. 7). Age-1 and age-2 smolt weights averaged 5.8 ± 0.9 g and 10.3 ± 2.0 g during 1955-2003 smolt years, indicating smolts gained at least 78% more body weight by staying in freshwater for a second year. Age-specific lengths of smolts were significantly smaller during 1977-2003 compared with those during 1955-1976 (Fig. 7; df = 47, $P < 0.01$). The cause for the relatively abrupt decline in smolt size at age is unknown, but it corresponds with an increase in the percentage of age-1 smolts and with the 1976-77 ocean regime shift. The decline in size at age coupled with an increase percentage age-1 smolts is unusual because slower growing smolts typically remain in the lakes for a second year (Burgner 1991). Scale growth measured from returning adults did not exhibit the shift in smolt size (Ruggerone, unpublished analysis). Smolt length and weight associated with the 1991-1999 brood years were slightly smaller than long-term averages, but were similar to smolt sizes during 1974-1990.

Smolt-to-adult survival of age-1 and age-2 smolts averaged 7.6% and 13.0%, respectively, during brood years 1956-1998 (Figs. 8 and 9). Survival tended to be low until increasing in the mid-1970s. However, low survival began again with the 1991 brood year and remained relatively low through the 1998 brood year. Estimated survival of age-1 smolts declined from 9.1% during brood years 1974-1990 to 7.4% during 1991-1999, an 18% decline. Survival of

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[1] Kvichak smolts produced by the 1998 brood were the last that could be estimated from Egegik smolt counts, which terminated in the 2001 smolt year.

age-2 smolts declined from 14.0% to 7.9%, a 44% decline. Total survival declined from 10.8% to 5.8%, a 46% decline[2]. Reduced survival began with the 1994 smolt year (Fig. 9). As discussed above, smolt estimates beginning with the 1995 smolt year (brood years 1992 and 1993) were based on predictions of Kvichak smolt survival from Egegik smolt survival.

Smolts produced per spawner averaged 22.8 smolts during 1956-1998 (Fig. 8). Smolt production was low during 1956-1973 brood years and then appeared to increase substantially beginning in 1977. This change coincides with a significant ocean regime shift indicating climate change likely influenced freshwater productivity. Smolt abundance prior to 1971 was based on expanded fyke net catches rather than sonar counts (Rogers and Poe 1984). Smolts produced per spawner declined from 28.7 ± 3 smolts during brood years 1974-1990 to 14.9 ± 5 smolts during 1991-1998, a 48% decline. Smolt biomass per spawner declined 50%.

In summary, the decline in Kvichak productivity and production began with the 1991 brood year and continued through the 1999 brood year, corresponding with salmon runs observed from 1995 through the 2005 season. The decline was associated with lower smolt-to-adult survival (based on the Egegik smolt model) and a 76% decrease in ocean age-2 sockeye salmon. The decline was not associated with a reduction in smolt size at age, but the percentage of age-1 smolts in the migration increased. Smolts per spawner declined nearly 50% even though juvenile sockeye salmon spent less time, on average, in the lakes. Thus, lower Kvichak productivity during brood years 1991-1999 was related to both freshwater and marine life stages.

Comparison of Kvichak with Other Bristol Bay Stocks

Adult Return per Spawner

An important question to address is whether the decline in Kvichak salmon productivity (R/S) during 1991-1999 was unique to the Kvichak watershed or whether other Bristol Bay stocks also declined. This question was examined by comparing time series of return per spawner and residuals from recruitment curves of each Bristol Bay stocks, and by correlating recruitment curve residuals between Kvichak and other stocks.

Return per spawner of Kvichak sockeye salmon was consistently less than other stocks in Bristol Bay, 1952-1999 (Fig. 10). Kvichak return per spawner averaged 2.2 ± 1.8 (SD) salmon, whereas return per spawner of other stocks averaged 3.6 adults and ranged from 3.0 adults (Togiak) to 5.1 adults (Egegik) during the 48-year period. Coefficient of variation in Kvichak return per spawner (82%) was intermediate to highly variable stocks (Igushik and Ugashik: 102-126%) and less variable stocks (Wood and Togiak: 50-57%).

Ricker recruitment curves were calculated for each Bristol Bay stock during the period of high productivity, 1973-1990. Regressions of several of the stocks (Kvichak, Egegik, Naknek) were not statistically significant (Table 3), suggesting density dependence was not detectable within the range of spawning escapements during this time period[3]. Density dependence, as

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[2] The low total survival estimate is based on weighted mean survival of age-1 and age-2 smolts. During the recent period, the more abundant age group tended to have low survival.

[3] The question of density dependence is examined in greater detail in the Kvichak cycle section of this report.

indicated by the regression slope, was inversely related to the mean density of spawning escapements in Bristol Bay watersheds (Fig. 11). Stocks having large lake surface areas tended to have low densities of spawners per lake area and less evidence of density dependence.

The average intrinsic productivity of Kvichak sockeye salmon (3.4 adult return per spawner (R/S)), as measured by the slope of the Ricker recruitment curve when density is near zero, was considerably lower than all other Bristol Bay stocks (mean: 6.7 R/S; range: 4.1-9.8 R/S) (Table 3). Mean return per spawner of Bristol Bay stocks during 1973-1990 could be explained by the following multivariate equation involving intrinsic productivity of the stock and escapement density (spawners per km^2 lake area):

2) Mean R/S = 1.485 + 0.985 (Productivity) – 1.207 (Escapement density),

$R^2 = 0.74$, n = 8 watersheds, overall P = 0.033, P (productivity) = 0.013, P (spawner density) = 0.036. This statistical model shows that mean R/S of Bristol Bay sockeye salmon could be explained by the intrinsic productivity of each stock and the density of spawners. Higher spawner density and lower productivity led to lower mean R/S, as expected. The low mean R/S of Kvichak salmon stems from its relatively low productivity and its high spawner density, especially during peak-cycle years.

Residuals from the stock-specific recruitment regressions (SR index) were calculated for further comparisons of productivity between Kvichak and other Bristol Bay stocks. Recruitment curve residuals indicate that productivity of all Bristol Bay stocks was consistently low prior to the 1973 brood year, then productivity increased in the mid-1970s (Figs. 10 and 12), corresponding with the 1976/1977 ocean regime shift. In contrast to other Bristol Bay stocks, productivity and production of Kvichak sockeye salmon increased relatively little following the regime shift (also see Table 1). Productivity of major Eastside stocks (Kvichak, Egegik, Ugashik, Naknek) tended to be relatively low during brood years 1991-1999 (Fig. 12), although the decline in productivity was not as high as in Kvichak salmon. On average, R/S of Eastside stocks (excluding Branch) declined 44% from 1973-1990 to 1991-1999 (Table 1). R/S of Kvichak salmon declined 73% compared to 60% for Ugashik, 47% for Egegik, and 24% for Branch[4]. Naknek R/S declined relatively little (5%).

In contrast, most Westside stocks, except Igushik, did not show a marked decline in R/S beginning with the 1991 brood year (Figs. 10 and 12). On average, R/S of Westside stocks decreased 7% whereas total return increased 18% from 1972-1990 to 1991-1999 (Table 1). Only Igushik salmon declined markedly, but its values may be less accurate due to its small size in the mixed stock fishery. R/S of Wood River salmon increased 16% and total return increased 57% during 1991-1999. These data show that productivity and production of Eastside stocks tended to decline in 1991 and thereafter whereas Westside stocks were relatively stable. For most Eastside stocks, the decline in R/S was associated with slightly greater parent escapements, a trend that typically occurs in salmon populations in response to competition for resources. However, the Kvichak decline in R/S was associated with an 18% decrease in parent escapement.

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[4] Return per spawner of Branch River sockeye increased significantly with the 2000 brood year.

Kvichak SR indices (residuals from Ricker recruitment curve) were compared with those of each Bristol Bay stock and Westside and Eastside aggregate stocks (excluding Kvichak) during brood years 1952-1990, i.e., prior to the recent decline. Kvichak SR indices were positively correlated with those of each Bristol Bay stock ($n = 39$, $P < 0.05$) except for Nushagak. Correlations were low ($r < 0.64$). Igushik, a Westside stock, had the highest correlation with Kvichak (Fig. 13c; $r = 0.64$). This correlation is apparent from R/S time series (Figs. 8 and 10) where Kvichak and Igushik stocks show similar cycles of abundance. The high correlation between Igushik R/S and Kvichak R/S is peculiar but may only be an artifact of suspected large measurement error for catch estimates for this stock. Positive correlations between most stocks were largely in response to the positive response of all Bristol Bay stocks to the 1976/77 ocean regime shift (only Wood River was significantly correlated with Kvichak during 1973-1990: $n = 18$, $P = 0.028$; $r = 0.51$).

Kvichak SR Index was weakly correlated with that of aggregate Eastside stocks ($R^2 = 0.18$, excluding Kvichak) and aggregate all Bristol Bay stocks ($R^2 = 0.28$, Fig. 13), suggesting some factors affecting Kvichak productivity were unique to Kvichak. It is noteworthy, for example, that previous-year spawning escapements to the Kvichak watershed ($P = 0.047$) added significant information ($P = 0.047$) to the relationship between Kvichak and Bristol Bay productivity (overall $R^2 = 0.36$, $P < 0.001$). This relationship suggests that large Kvichak spawning escapements have a negative effect on productivity of the following brood year (this finding was also observed with aggregate Eastside stocks; see analysis of Kvichak cycle for more analyses of density dependence and brood interactions).

Time series of residuals from the SR Index correlations of Kvichak on other stocks (see Fig. 13) were plotted to determine whether the Kvichak productivity deviated from other Bristol Bay stocks during 1991 and thereafter (Fig. 14). Beginning in 1991, these plots show that the Kvichak SR Index was consistently below expectations based on SR indices for aggregate Eastside stocks, aggregate Westside stocks, aggregate Bristol Bay stocks, and Igushik stock, which had the highest correlation with Kvichak. Thus, even though R/S of other Eastside stocks declined in 1991 and thereafter (see Table 1), Kvichak productivity declined the most.

SR Indices for aggregate Eastside and Westside stocks were compared to determine whether these large aggregations responded similarly to environmental factors. Prior to the 1991 brood year, SR index of Eastside and Westside stocks were positively correlated ($R^2 = 0.51$; Figs. 15 and 16). R/S (i.e., productivity uncorrected for density dependence) of aggregate Eastside and Westside salmon were also correlated ($R^2 = 0.40$). However, these correlations failed to be maintained during 1991-1999 when productivity of Eastside salmon under performed expectations based on performance of Westside salmon (Fig. 16). Only Eastside production from the 1997 brood year achieved expected production. However, production from this brood year was low for both Eastside and Westside stocks. Parents that produced the 1997 brood year experienced exceptionally warm sea surface temperatures and low prey production, as shown by numerous emaciated and dying seabirds during summer 1997 (Kruse 1998).

In summary, productivity of two other major Eastside stocks (Egegik, Ugashik) declined significantly beginning in 1991, but their decline was not as great as Kvichak. Most Westside stocks and two Eastside stocks (Naknek and Alagnak (Branch)) did not decline. Kvichak R/S was correlated with R/S of other Bristol Bay stocks prior to 1991, although productivity of Kvichak salmon was much lower than that of other stocks. These findings indicate that the decline in Kvichak salmon was not unique to the Kvichak watershed. As discussed below, this finding has important implications for management because the decline cannot be attributed solely to changes in escapement goal policy, which was not changed for these other stocks.

Kvichak Spawning Escapement Density

During 1973-1999, spawning densities of Kvichak salmon (spawners per km^2 lake area) were not statistically different from most Bristol Bays stocks; only Togiak and Igushik stocks had statistically higher densities but these lakes are quite small (Fig. 17). However, Kvichak adult returns per km^2 (catch plus escapement) were significantly less than Egegik, Ugashik, Wood River, Togiak, and Igushik (ANOVA multiple range test, $P < 0.001$). On average, Kvichak experienced the lowest adult return per km^2 of lake surface area of all Bristol Bay stocks (Fig. 17). Kvichak also produced the lowest R/S (2.2 adults) and lowest catch per spawner (1.2 adults) among Bristol Bay stocks.

It is noteworthy that Egegik had the lowest escapement per km^2 of lake area, the highest R/S, and the highest catch per spawner in Bristol Bay during 1973-1999. The low escapement density of Egegik salmon likely contributed to low competition for resources and exceptionally high productivity.

Salmon Age Composition and Population Decline

Age composition of Kvichak salmon produced by brood years 1991-1999 was significantly different compared with that during 1973-1990. The percentage of age-1.x adults (age-1 smolts) increased 39%, on average, and the percentage of age-x.3 adults increased 29% (Table 1). However, the shift in age composition of smolts and adults returning from the ocean was not unique to Kvichak salmon. The percentage of age-1.x and age-x.3 also increased in other Eastside stocks, such as Egegik and Ugashik (Table 1). In contrast, age composition of Westside stocks changed little.

The decline of Kvichak and other Bristol Bay salmon stocks from 1973-1990 to 1991-1999 was associated with the degree of change in age composition of the stock. Decline in R/S and total adult return of Bristol Bay stocks were highly correlated with the percentage decline in numbers of age-2.2 salmon in the adult return (Fig. 18), i.e., stocks that lost a large percentage of age-2.2 salmon experienced the greatest decline. Percentage decline in age-2.2 salmon explained 58-74% of the variation in the decline of Bristol Bay salmon populations.

The decline in R/S was correlated with changes in both freshwater and ocean age composition of salmon stocks. Stocks experiencing large declines in R/S also experienced a relatively large shift from age-2 to age-1 smolts and a large shift from ocean age-2 to ocean age-3 salmon (Fig. 19). Shifts in freshwater and ocean age composition explained 73% and 84% of the variation in R/S, respectively. Ocean age composition was influenced by freshwater age composition, i.e., the shift to age-1 smolts was correlated with the shift to ocean age-3 adults (R^2

= 0.71). However, as described below, change in age composition in response to the 1976-77 regime shift led to an increase rather than decrease in R/S.

Age composition of Bristol Bay stocks also shifted in response to the 100% increase in Bristol Bay R/S and 140% increase in adult returns from brood years 1952-1972 to 1973-1990. The percentage of age-1.x adults in Eastside returns increased 34% (Kvichak age-1.x increased 55%). The percentage of x.3 salmon increased 32% among Westside stocks and 18% among Eastside stocks (Kvichak age-x.3 increased 31%). These data show that the tremendous increase in Bristol Bay sockeye salmon production associated with the mid 1970s ocean regime shift was also associated with a shift in age composition of Bristol Bay salmon stocks. Furthermore, the change in age composition during the salmon production increase was in the same direction as shown in the recent salmon decline, i.e., greater percentages of age-1 smolts and ocean age-3 sockeye salmon. Thus, the recent shift in age composition has led to a more extreme age composition relative to that of the 1952-1972 period. Conditions associated with these extreme age compositions were unfavorable for most Eastside salmon stocks. Stocks that did not experience change in age composition during the recent period (i.e., most Westside stocks) did not decline.

Age-1 smolt Hypothesis

Lew (2003) proposed that the decline of Kvichak salmon was caused by a shift from age-2 to age-1 smolts: age-1 smolts, which are smaller, experienced lower survival than age-2 smolts, therefore fewer adults returned. As shown above, the decline in Kvichak production was associated with a 51% increase in age-1.x adults and an increase in the percentage of age-1 smolts. This hypothesis assumed that greater mortality associated with spending an extra year in the lakes was much less than the difference in marine survival of age-1 and age-2 smolts.

The age-1 hypothesis is not supported by data since 1952. Regression of Ln R/S on percentage of age-1 smolts in the smolt migration, brood years 1952-1998, shows no correlation between R/S and smolt age composition (Fig. 20; $R^2 = 0.05$, n = 44, P = 0.14). The lack of a relationship is related to large age-1.2 adult returns and high R/S during 1956, 1965, 1974-1976, 1979, and 1983 brood years. This analysis indicates productivity of Kvichak salmon did not significantly vary with freshwater age composition and hence the recent shift to greater proportion age-1 smolts cannot explain the large decline by itself. Production of age-1 and age-2 smolts varies tremendously from year-to-year and adult returns would be much lower if few adults returned from age-1 smolts. It is more plausible that the recent low production of adults was related to low numbers of both age-1 and age-2 smolts.

Benefit of Migrating as Age-2 smolt

The tradeoff between mortality in the lake versus mortality in the ocean was examined by comparing weight gain and survival benefit of age-2 versus age-1 sockeye salmon smolts in the Kvichak, Egegik, Ugashik, and Wood river watersheds (Table 4). Egegik smolts experienced the greatest weight gain and greatest marine survival benefit by staying a second year in the lake, and Egegik salmon had the highest percentage of age-2 smolts in the migration (Fig. 21). Weight gain and survival benefit of Kvichak and Ugashik stocks were intermediate and the associated percentage of age-2 smolts in the migration was intermediate. Wood River experienced the least gain by staying an additional year in freshwater and the percentage of age-2 smolts in the migration was small. Thus, the benefit of staying in freshwater for an additional year, as measured by increased body weight of smolts and survival at sea, was positively correlated with mean smolt age of Bristol Bay stocks (Fig. 21).

Ocean Age-2 Sockeye Salmon

The ocean age composition of Kvichak salmon is dominated by ocean age-2 salmon and this is unique among Bristol Bay stocks. The percentage of ocean age-2 salmon varies little from brood year to brood year as indicated by the low coefficient of variation (C.V.) during 1952-1990 (16.9%). In contrast, the C.V. of other Bristol Bays stocks averages 37.4% and ranges from 23.3% (Egegik) to 53.5% (Nushagak). Comparison of adult returns to the Kvichak River from each brood year with the percentage of ocean age-2 in the returns shows that large returns (> 5 million salmon) have never occurred when the percentage of ocean age-3 salmon exceeded 35% of the total return from a brood (Fig. 20). The number of years when the return of ocean age-3 salmon exceeded 2.5 million fish was only 23% during 1952-1999. In contrast, freshwater age-1 salmon (age-1.x) exceeded 2.5 million fish in 40% of the years.

These analyses indicate that production of ocean age-2 sockeye salmon has been important to the productivity of Kvichak salmon during the past five decades. Production of ocean age-2 salmon is more important to the Kvichak stock than appears to be the case for other Bristol Bay stocks, based on the historically low C.V. of age composition of Kvichak relative to other stocks. The biological reason for a high proportion of ocean age-2 salmon is unknown, but some potential factors are discussed below.

Mean age composition of Bristol Bay sockeye salmon appears to be a genetic trait (Rogers 1987) and ocean age-2 could be strongly selected for in the Kvichak. Small streams tend to produce smaller and younger adults that are more suitable for shallow water (Bishop 1991, Wetzel 1993) and less susceptible to predation by size-selective bears (Ruggerone et al. 2001), whereas larger rivers tend to produce older and larger adults. Factors influencing the age of beach spawning stocks are relatively unknown (Rogers 1987), although Ruggerone (1989) hypothesized that the dominance of ocean age-3 sockeye salmon in Chignik beach spawning salmon was associated with size-selective predation by juvenile coho salmon on sockeye fry because larger, older salmon produce large fry. In Iliamna Lake, ocean age-2 salmon may be favored, in part, because younger adult salmon produce smaller eggs which can better absorb oxygen (greater surface area: volume ratio) when broadcast among large boulders of island beaches where water flows are lower than in riverine habitats. Island beach spawning, where eggs rely upon wind-generated currents to supply oxygen, is unique to Iliamna Lake. Stocks from island beaches are a major component of peak cycle runs. However, as discussed below, reduced growth at sea in recent years may have disproportionately reduced the reproductive potential of ocean age-2 salmon compared with ocean age-3 salmon.

Is Decline Related to Freshwater or Marine Factors?

Enumeration of smolt abundance is important when attempting to determine whether the decline in salmon production is related to freshwater or marine factors. Unfortunately, the decline of Kvichak salmon was also associated with obvious over estimates of annual smolt abundances in during the decline. Analyses of historical data suggested that significant smolt counting error began in the 1995 smolt year (see Appendix), which corresponds with the 1992 (age-2 smolt) and 1993 (age-1 smolt) brood years[5].

Correlation of Kvichak, Egegik, and Ugashik Smolt Survival

Smolt abundance and associated survival at sea was estimated for Egegik and Ugashik during 1982-2001 smolt years. These data, especially Egegik, were used to examine trends in survival at sea and to determine whether Kvichak smolt survival was correlated with other stocks. If correlated, then marine survival of Kvichak smolts could be estimated for the period of sonar error using Egegik or Ugashik marine survival estimates and new estimates of Kvichak smolt abundance and smolts per spawner could be back calculated from observed adult returns.

Survival of Kvichak sockeye salmon smolts was correlated with survival of Egegik smolts leaving freshwater during the same year, 1982-1994, excluding 1985[6]. Correlation was significant among age-1 smolts ($n = 12$, $R^2 = 0.59$, $P = 0.029$) and age-2 smolts ($n = 12$, $R^2 = 0.61$, $P = 0.014$) (Fig. 22). Survival of total Kvichak smolts was correlated with survival of total Egegik smolts ($n = 12$, $R^2 = 0.59$, $P = 0.002$), but Kvichak total survival was highly correlated with that of age-2 Egegik smolts ($n = 12$, $R^2 = 0.90$, $P < 0.001$). Survival of age-1 Kvichak smolts was correlated with survival of age-1 Ugashik smolts ($n = 12$, $R^2 = 0.59$, $P = 0.002$), but Kvichak survival was not correlated with age-2 and total Ugashik survival ($P > 0.05$). Survival of Kvichak age-1 and age-2 smolts was not correlated ($n = 12$, $R^2 = 0.00$, $P > 0.05$). These data indicate Kvichak smolt survival can be predicted from Egegik smolt survival, and can be used to back calculate Kvichak smolt abundances (see below).

Survival of Egegik Smolts, 1980-1998

Survival of Egegik smolts was examined because it is correlated with that of Kvichak smolts. Survival of Egegik salmon smolts declined 34%, on average, from brood years 1980-1990 (24.6% survival) to 1991-1998 (16.2% survival). On average, survival of age-1 and age-2 smolts declined 22% and 31%, respectively. Survival of age-2 smolts was not statistically greater than that of age-1 smolts. These data indicated that smolt survival of Kvichak salmon also declined in recent years.

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[5] Recent examination of the sonar equipment suggests the counter may have produced erroneous information as far back as 1993. However, as described in the Appendix, counting error was exceptionally large beginning in 1995.

[6] The 1985 smolt year was excluded because it was an obvious outlier. The unusual values were likely related to low smolt counts and mis-allocation of adult returns to this smolt year, leading to unusually high survival of Kvichak salmon, e.g., age-1: 47% survival; age-2: 32% survival.

Hindcasts of Kvichak Smolt Abundances and Survival

The Kvichak/Egegik smolt survival regressions were used to hindcast survival of Kvichak smolts during 1995-2001, i.e., the period when sonar over-estimated Kvichak smolts. Based on this approach, survival averaged 6.6 ± 2.1%, 7.9 ± 3.3%, and 5.8 ± 2.6%[7] for age-1, age-2 and total Kvichak smolts (Fig. 23), respectively, during smolt years 1994-2001, i.e., years approximately corresponding with brood years 1991-1999. These values represent a 20%, 41%, and 42% decline in survival, on average, compared with years 1982-1993. ANOVA indicated survival at sea of Kvichak smolts was significantly lower during the recent period (df = 1, 36; F = 6.031, P = 0.019).

Revised Kvichak Smolt abundances

Kvichak marine survival estimates based on Egegik survival regressions were considerably greater than those based on the escapement-based model (see Appendix) to predict smolt abundances (Fig. 23). As previously noted, the escapement-based smolt models could not capture unique sources of mortality in freshwater because they were based on spawning escapement and temperature. In contrast, back-calculations of smolt abundances from the Egegik marine survival estimates and observed adult returns would likely captured unique freshwater mortality factors, assuming marine survival predictions were reasonably accurate among years.

Comparison of age-specific smolt abundances based on sonar counts during 1982-1993 smolt years (when counts were believed to be relatively accurate) with abundances back-calculated from Egegik-based marine survival shows that the Egegik method produced values similar to the sonar-based estimates (Fig. 24a). During 1982-1993 smolt years, age-1 smolt abundances based on the Egegik method were 45% greater, on average, compared with reported abundances. Age-2 smolt abundances based on the Egegik method were 11% lower, and total smolt abundances were 12% higher. Thus, the Egegik method provided reasonably accurate estimates of total Kvichak smolt abundances during 1982-1993 and it is reasonable to assume that the Egegik-based approach provided more plausible estimates of smolt abundance during 1995-2001 compared with the statistical model that utilized parent escapement.

Egegik-based estimates of smolt abundances were considerably less than estimates produced by the escapement-based smolt models during 1994-2001 (Fig. 24b). This finding implies that spawner-to-smolt production during 1994-2001 was below average because the smolt models provided mean estimates of smolt abundances that were based on earlier relationships between smolt abundances and spawning escapement and temperature. Thus, Kvichak production during the recent decline was low in response to both freshwater and marine factors.

Kvichak, Egegik, and Ugashik Smolts per Spawner

Smolts produced per spawner in the Kvichak watershed were estimated from reported smolt abundance estimates when the sonar counts were reasonably accurate (prior to 1995), and by

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[7] Lower mean survival for total smolts compared with age-1and age-2 smolts is related to differences in regression relationships.

estimates based on the escapement-based method and the Egegik-based method after 1994. Normalized plots of smolts per spawner during brood years 1980-1999 indicate smolt production was typically below average during brood years 1991-1998 (Egegik method; Fig. 25b). Plots based on the escapement-based model indicate annual smolts per spawner were low during 1991-1995, but relatively high during 1996-1999 (Fig. 25a). Given the observed low adult returns from the 1996-1999 broods, the escapement-based smolt estimates imply exceptionally low marine survival. As noted above, the escapement-based model likely overestimated smolt production and underestimated survival at sea, especially for brood years 1996-1999.

Smolts produced per spawner in the Egegik and Ugashik watersheds were examined during 1980-1999 in order to explore whether stocks other than Kvichak experienced reduced smolt production. Normalized plots indicate Egegik smolts per spawner were typically below average during brood years 1989-1998 (Fig. 25c). Ugashik smolts per spawner were also below average during brood years 1989-1999. These data suggest the modest decline in production of Egegik and Ugashik adult salmon during 1991-1999 was related in part to reduced survival in freshwater. Like Kvichak salmon, these stocks also experienced reduced survival at sea during this period. Thus, available data suggest the decline in Kvichak, Egegik, and Ugashik adults was associated with factors affecting survival in both freshwater and the ocean.

Contribution of Freshwater vs. Marine Factors to Kvichak Collapse

Available data were used to estimate the proportion of the decline that was attributable to spawner-to-smolt survival (largely freshwater) versus smolt-to-adult survival (largely marine). Kvichak adult returns and R/S declined 77% and 74%, respectively, from brood years 1974-1990 to 1991-1998 (Table 2)[8]. Estimated smolt production, based on the Egegik method after 1994, declined 64%, on average. The decline in smolt production was greater for age-2 (83%) compared with age-1 smolts (43%). Density of juvenile sockeye salmon in upper Lake Iliamna declined 50% from brood years 1974-1990 to 1992-1999 (townet data provided by D. Rogers, University of Washington). Smolts per spawner declined 48%, and smolt-to-adult survival declined 46%, on average. The decline in marine survival of age-2 smolts (44%) appeared to be greater than that of age-1 smolts (18%).

These data indicate that the decline in Kvichak salmon production was related to factors associated with spawner-to-smolt life stages (freshwater) and to survival at sea. Approximately 58% of the overall decline was attributable to the spawner-to-smolt stages, and 42% of the decline was attributable to the smolt-to-adult stage (Table 2). This finding is consistent with changes in Ugashik and Egegik salmon production during the decline period. Approximately 22% of the decline in Kvichak smolt production was attributable to the decline in spawning escapement after accounting for the reduction in smolts per spawner. However, as noted below, marine conditions may have contributed to the decline in spawner-to-smolt survival through smaller-than-average spawning adults whose reproductive success may have been additionally compromised by high salmon densities at sea and high metabolic rates associated with relatively warm ocean temperatures during their return migration.

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[8] 1998 is the last available brood year for which Kvichak smolt counts can be estimated from Egegik smolt counts.

Kvichak Cycle, Density-Dependence, Marine Derived Nutrients, and Depensatory Mortality

Factors influencing the five-year Kvichak population cycle have been investigated for decades. Mathisen and Poe (1981) hypothesized that the cycle was important to the stability of sockeye production in this system and in fact was *needed* to produce high yield from the stock. They suggested that the cycle was initiated by depensatory predation of char and trout, biogenic enrichment of lakes during peak-cycle years, and/or increased parasitic fauna in spawning gravels following peak-cycle years (Mathisen 1966). The "need" for the cycle to provide large surplus yield was based on the assumption that regular periods of very low fry abundance were needed (2 or 3 out of every 5 years) to reduce the abundance of predators. With predators regularly reduced in abundance or fitness, the sockeye stock could provide higher yields than would stable escapement and production. The mechanism for higher yields being that stable escapement supports much higher levels of predation on juvenile sockeye than cyclic production.

Burgner et al. (1969) assumed that the Kvichak cycle was caused by either depensatory predation or marine derived nutrients transported by peak cycle spawners, but no evidence was provided. However, Rogers and Poe (1984) concluded that the cycle was created by weather (shifts on smolt age) and low spawning escapements and was maintained by high fishing mortality in off cycle years. Rogers and Poe concluded that there is no evidence for inequality in cycle year productivity and therefore large returns could be produced by large escapements regardless of cycle year. They estimated "optimal" escapement to be approximately 6-10 million salmon, but noted that it would take considerable time to rebuild off-cycle years.

Eggers and Rogers (1987) examined population statistics of Kvichak sockeye salmon to determine whether the Kvichak cycle was influenced by depensatory fishing and/or a depensatory agent independent of the fishery. Depensatory mortality occurs when mortality is relatively high at low abundances. The cause of depensatory mortality is key to setting escapement goals for the Kvichak. If caused by entirely natural mechanisms, then a cyclic escapement goal policy is probably warranted; if created or maintained by simply managing the fishery to achieve cyclic escapements, then stabilizing escapement goals among years will lead to more stable and possibly higher yield from the stock.

Cyclic sockeye runs are common in the Fraser River, British Columbia, but the Kvichak run is the only stock in Bristol Bay that exhibits the strong, typically five-year cycle. Eggers and Rogers (1987) found little evidence of direct depensatory mortality independent of the fishery. However, they observed that production was depressed following large escapement events (brood year interaction). They found that fishing mortality on the Kvichak stock was highly depensatory: a much higher percentage of the return was harvested from smaller returns. Eggers and Rogers (1987) and Rogers and Poe (1984) concluded that the management policy should be altered. During this period ADFG reduced the peak and pre-peak escapement goal from 8 to 12 million to 6-10 million salmon and to raise the goals for off-cycle escapement to 4-8 million (up from 2 million). In 1996, the off cycle goal was reduced to 4-6 million and in 1998 the lower end of the goal was reduced (2 million) and a sliding harvest rate was introduced where the goal would be a function of the return size in which harvest rate would be 50% when the return was more than twice the lower end of the escapement range (applied to both off cycle and peak year ranges). Thus, past and current escapement goals for the Kvichak watershed help to maintain the Kvichak cycle.

The dominance of age-2.2 sockeye salmon in the Kvichak return is a key factor contributing to the cyclic returns because the majority of returns from a brood occur five years later rather than spread across four, five and six years later. Adult returns from the Kvichak River are dominated by ocean age-2 adults (84% of total abundance, 1952-1999) and there is relatively little variation in ocean age (coefficient of variation = 16.9%) compared with that of other Bristol Bay stocks (C.V. mean = 37.4%; range: 23.3-53.5%). The coefficient of variation of smolt age is also relatively low (39.8%) compared with that for other stocks (C.V. mean = 67.5%; range: 23.3-126.2%). The low variability in age structure could be the result of the Kvichak stock experiencing relatively little environmental variability that affects age of smoltification and marine age or that natural selection for the dominant age is high, i.e., age-2.2 salmon. Environmental variability in terms of lake temperatures and marine conditions over the last century has not been constant suggesting the latter mechanism may be more plausible.

<u>Density-Dependent Growth and Brood Interaction of Juveniles</u>

The expected average density of juvenile sockeye in the Kvichak watershed (based on spawners per lake surface area) is high even though Iliamna Lake and Lake Clark are exceptionally large lakes (Table 3). Inferred juvenile density of Kvichak salmon[9] is second highest among Eastside stocks and 5th highest among all nine Bristol Bay stocks (assuming even distribution in lakes), even though productivity of Kvichak salmon (R/S at when few spawners) is lowest among all Bristol Bay stocks (Table 3). Given the relatively high juvenile densities in the Kvichak lakes, it is not surprising that weight of age-1 and age-2 smolts declined with greater parent spawning escapement, 1954-1999 (Fig. 26). Age-1 smolt weight from post-peak broods tended to be below average at a given spawning escapement, providing initial evidence of interaction between brood lines.

The relationship between age-1 smolt weight and spawning escapement (millions of fish) can be described by the following multivariate equation (years 1955-1990):

3) Age-1 wt (g) = 6.71 - .554 (Ln parent spawners) - .052 (previous-year spawners),

n = 35, $R^2 = 0.63$, overall $P < 0.001$, P (parent spawners) < 0.001, P (previous-year spawners) < 0.01), serial autocorrelation = 0.28 ($P > 0.05$). This finding indicates that large spawning escapements (and the resulting numerous fry) can reduce the growth of progeny of subsequent brood years. The adverse effect of large spawning escapements on progeny of following year's brood has been documented in several other Alaskan lakes (Ruggerone and Rogers 2003). Spring, summer, and winter air temperature did not add information to the model ($P > 0.33$).

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[9] Density data for Bristol Bay juvenile sockeye salmon are only consistently available for the Wood River and Kvichak watersheds where the University of Washington has long-term salmon programs. Standardized 10 minute surface tow-net catches averaged 57.1±10.3 juvenile sockeye salmon in the upper end of Iliamna Lake (1961-1999) compared with 49.6 ± 8.0 juvenile sockeye salmon in Lake Aleknagik (1958-1998). Annual geometric mean catch data provided by D. Rogers, University of Washington.

Age-2 smolt weight was influenced by abundance of parent spawners (proxy for juvenile abundance), but not by abundance of previous-year spawners. The lack of a relationship with previous-year spawners may be related to dispersal of juvenile salmon away from the major spawning areas and toward the lower end of Iliamna Lake during the second year (Burner et al. 1969) and to fewer age-2 salmon remaining in the lakes. Age-2 smolt weight declined in response to greater parent spawning escapement and warmer air temperature during winter through summer of their second year in the lake ($n = 36$, $R^2 = 0.72$, overall $P < 0.001$). The negative relationship with air temperature may be a spurious correlation due to greater reported mean growth prior to the mid-1970s when air temperature was consistently colder. A higher percentage of age-2 smolts occurred during the earlier period (Table 1) suggesting growth was lower rather than higher during the early period.

Residuals (observed - predicted) from the smolt weight models show that age-1 smolt weight was above average during brood years 1991-1996, but below average thereafter (Fig. 27). Residuals of age-2 smolt weight followed a similar pattern of relatively high growth followed by low growth during the period of low salmon productivity. The magnitude of smolt weight residuals during 1991-1998 were somewhat extreme compared with previous years.

<u>Brood Interaction Effect on Smolt Age</u>

The influence of density dependence, brood interaction and air temperature (winter, spring, or summer during each season) on the percentage of age-2 smolts produced by brood year was examined, 1953-1990. The arcsine transformed percentage of age-2 smolts in the migration could be explained by the following multivariate model:

4) $$\text{AS \% age-2 smolt} = 0.829 + .081\,(\text{Ln spawners}) + .017\,(\text{previous-year spawners}) - .076\,(\text{temperature}),$$

$n = 36$, $R^2 = 0.40$, overall $P < 0.001$, P (LN spawners) = 0.023, P (previous-year spawners) = 0.031), P (April, May temperature) < 0.002, serial autocorrelation = 0.048 ($P > 0.05$). Spring air temperature during emergence had the greatest effect on smolt age. Residuals during 1991-1998 varied considerably and tended to be negative (fewer age-2 smolts than predicted) during 1993-1996 when smolt size was great and positive during 1997-1998 when smolt size was relatively small.

<u>Brood Interaction Effect on Smolt Abundance</u>

Numbers of smolts produced in the Kvichak watershed increased with parent spawning escapement (Fig. 28). However, high abundances of previous-year spawners adversely affected the number of smolts produced by brood years 1969-1990 (Fig. 29). Years with fewer smolts were associated with reduced growth, which was caused by numerous spawners and fry during the previous year (Fig. 27). The reduction in smolts likely occurred in response to reduced growth during the first year in the lakes because growth during second year was not influenced by previous-year spawners. The number of smolts produced by a brood year can be explained by the following multivariate equation:

5) Ln Smolts (millions) = 3.725 + .879 (Ln parent spawners) – .263 (Ln previous-year spawners),

n = 20, $R^2 = 0.82$, overall $P < 0.001$, P (parent spawners) < 0.001, P (previous-year spawners) = 0.004), serial autocorrelation = -0.13 ($P > 0.05$).

Brood Interaction Effect on Return per Spawner

Analyses of Kvichak smolt weight, smolt age, and smolt abundance indicates significant interaction between sockeye salmon originating from adjacent brood years. Therefore tests were conducted to determine whether brood year interaction significantly influenced adult returns. Furthermore, Eggers and Rogers (1987) provided evidence that return per spawner of Kvichak salmon was reduced by interceptions of Kvichak salmon in Egegik and Ugashik district fisheries. They suggested that interceptions had the greatest effect when the combined adult return to Egegik and Ugashik was at least twice that of the Kvichak return.

A series of Ricker type spawner recruit models were examined to evaluate the effect on adult recruitment (R_i) of 1) parent spawners (S_i), 2) previous-year spawners (brood year interaction) (S_{i-1}), 3) a period effect (P) accounting for differential production after the 1972 brood year (i.e., corresponding with smolts influenced by the 1976-77 ocean regime shift), and 4) an interception effect (I) for brood years where the Egegik production was at least twice the Kvichak. The interception variable was coded as “1” when Egegik and Ugashik production was more than twice that of Kvichak and “0” when it was less. The period effect was coded as “1” when brood year was 1973 or greater and “0” when it was less. The models have multiplicative error (i.e., log normal) which is typical for spawner recruit data. The series of models are:

Linear Model:

$$R_i = S_i \exp(\alpha + \varepsilon)$$

Ricker:

$$R_i = S_i \exp(\alpha - \beta S_i + \varepsilon)$$

Ricker + Interception:

$$R_i = S_i \exp(\alpha - \beta S_i + \gamma I + \varepsilon)$$

Ricker + Period:

$$R_i = S_i \exp(\alpha - \beta S_i + \delta P + \varepsilon)$$

Ricker + Period + Interaction:

$$R_i = S_i \exp(\alpha - \beta S_i + \gamma I + \delta P + \varepsilon)$$

Ricker + Brood Year Interaction:

$$R_i = S_i \exp\left(\alpha - \beta_1 S_i - \beta_2 S_{i-1} + \varepsilon\right)$$

Ricker + Brood Year Interaction + Period:

$$R_i = S_i \exp\left(\alpha - \beta_1 S_i - \beta_2 S_{i-1} + \delta P + \varepsilon\right)$$

Ricker + Brood Year Interaction + Interception:

$$R_i = S_i \exp\left(\alpha - \beta_1 S_i - \beta_2 S_{i-1} + \gamma I + \varepsilon\right)$$

Ricker + Brood Year Interaction + Interaction + Period:

$$R_i = S_i \exp\left(\alpha - \beta_1 S_i - \beta_2 S_{i-1} + \gamma I + \delta P + \varepsilon\right)$$

These models were fit to the Kvichak brood table data, brood years 1952 to 1990. Brood years 1991 to 1999 were excluded from the models because aforementioned analyses demonstrated that production from these broods was anomalous (non-stationary). Brood years 1967 and 1968 were also excluded because these fish experienced exceptionally cold sea surface temperatures in 1971 as smolts and during the first year at sea and experienced exceptionally low survival. Nevertheless, sample size remained high after removing these two years (i.e., 37 years). Brood tables were constructed from inshore returns and did not include estimates of interceptions of Bristol Bay fish in the South Peninsula June fishery or high seas salmon fisheries. The models were fit using maximum likelihood (log normal errors) and an Excel Solver template provided by D. Eggers, ADFG. All of the models provided significant fits (relative to the mean).

Akaike Information Criterion (AIC; Akaike 1974) and associated P-values indicated that the Ricker model was significantly improved with the addition of Egegik interception, Period, and brood year interaction (Table 5):

6) $R_i = S_i \exp\left(1.139 - .0000514 S_i - .0000415 S_{i-1} - .964 I + .703 P + \varepsilon\right)$

A plot of observed and predicted adult returns in relation to parent spawning escapement is shown in Fig. 30. Mean residual (absolute) was 4 million sockeye salmon, or approximately 34% of the mean annual return of Kvichak sockeye salmon (11.6 million salmon) (Fig. 31). Residuals of the five variable model (equation 6) were 1.3 million fish less per year compared with the Ricker model. The statistical model indicates that R/S of Kvichak sockeye salmon declined with greater parent spawner escapement and greater spawner escapement during the previous year. This finding is consistent with the observation of reduced growth and reduced smolt abundance in relation to parent escapement and previous-year escapement.

The Egegik and Ugashik interception index was highly significant in the model, supporting the hypothesis that Kvichak sockeye salmon are harvested in adjacent districts. Interceptions are especially important in years when Kvichak returns are low because they mask density-dependent relationships if not accounted for in the model (e.g., Fig. 29). However, one problem with this model is that it tends to identify those years when productivity is relatively low, i.e. when Kvichak returns were much less than Egegik and Ugashik returns.

These analyses show that the density-dependent effect of parent escapement on adult recruitment only became apparent after incorporation of the interception index or after excluding years of potentially high interceptions. Without incorporation of the interception index, many years with low parent escapement had relatively low R/S, leading to a statistically insignificant recruitment curve. Lack of density-dependence in Kvichak R/S data is unrealistic given the high density of juvenile salmon that inhabit the lakes in some years. Thus, interceptions of Kvichak salmon likely mask the R/S relationship. Interceptions provide a strong form of depensatory mortality (when not accounted for) and likely contributed to the Kvichak cycle because the percentage of Kvichak run intercepted in other districts was likely high in years when Kvichak run size was small.

An important future task will be to estimate numbers of Kvichak salmon harvested in Egegik and Ugashik fishing districts, especially during years of low Kvichak returns when interception effects on R/S can be great. ADFG has collected genetic samples in the Egegik District and has begun testing for interceptions of Kvichak salmon in the Egegik District (D. Eggers, ADFG, pers. comm.).

Marine Derived Nutrients and Depensatory Predation

Smolt weight, smolt abundance, and the spawner recruit model (6) were examined to evaluate whether marine derived nutrients and/or depensatory predation influenced Kvichak salmon.

Residuals from the age-1 and age-2 smolt weight models were examined to determine whether residuals during peak-cycle years were significantly higher than those during other cycle years, as might be expected if they benefited from marine derived nutrients produced by parent carcasses. ANOVA did not reveal significant difference in age-1 (df = 3, 31, F = .415, P = 0.74) and age-2 smolt (df = 3, 31, F = .509, P = 0.679) weight residuals by cycle years. In both tests, mean residual from peak-cycle years was negative whereas mean residual during pre-peak years was positive. Thus, there is no evidence that growth of progeny from peak-cycle years significantly benefited from marine derived nutrients delivered by their parents. Instead, the findings were consistent with density-dependent growth.

Equation 5, which predicts smolt abundance from spawning escapement, was used to evaluate whether smolt abundance residuals during peak-cycle years were higher than those during other cycle years, as would be expected if salmon carcasses provided a survival benefit to peak cycle progeny and/or if predation in the lakes was depensatory and significant. Residuals did not differ by cycle year indicating little or no effect in response to marine derived nutrients and/or depensatory predation in the lakes (ANOVA, n = 31, df = 3, 27; F = 0.131, P = 0.940).

The spawner recruit model (equation 6) was used to evaluate whether adult return residuals during peak-cycle years were higher than those during other cycle years, as would be expected if salmon carcasses provided a survival benefit to peak cycle progeny and/or if predation was depensatory and significant. Residuals during 1953-1990 did not differ by cycle year indicating little or no effect in response to marine derived nutrients and/or depensatory predation in the lakes or marine environment (e.g., beluga whales) (ANOVA, n = 36, df = 3, 32; F = 1.616, P = 0.205). Inclusion of data during 1991-1999 in the ANOVA produced a similar finding of non-significance (P = 0.331). These findings are consistent with analyses of smolt weight and smolt abundances by cycle year in which there was no significant benefit associated with peak-cycle years.

Thus, neither smolt weight nor smolt abundance trends were consistent with the hypothesis that marine derived nutrients provides a significant benefit to progeny and contributes to the Kvichak cycle.

Population and Productivity of Kvichak Cycle Years

Population characteristics of juvenile sockeye salmon produced by each cycle year support the aforementioned analyses of density-dependence and brood interaction. As described below, large escapements led to reduced juvenile growth and greater percentages of age-2 smolts in the migration and in the adult return. Large escapements also affected growth and age composition of subsequent broods. For the analyses described below, smolt abundance and survival data were limited to brood years 1969 to 1991, i.e., the period of relatively accurate sonar smolt counts (smolt years 1971-1994).

Parent spawning escapement was exceptionally high during peak-cycle years (median: 10 million fish) and mean smolt weight of age-1 and age-2 progeny (6.6 g) was significantly lower compared with all other cycle years (7.9-8.5 g; Fig. 32; Table 6). The percentage of age-2 smolts in the migration (89%) and in the adult return (79%) was highest for the peak-cycle year, a pattern consistent with density-dependent growth (Burgner 1991). Peak cycle years produced the fewest smolts per spawner (14 smolts vs. 17-30 smolts), which likely stems in part from production of relatively more age-2 smolts and additional mortality of overwintering fish in the lakes. Biomass per spawner of total smolt production from peak-cycle years (115 g) was similar to post-peak (126 g) but much lower than pre-peak years and off-cycle years (180-206 g; Fig. 32).

Spawning escapement of post-peak cycle years was the smallest of all years (median: 2.2 million), yet mean weight of smolts (7.9 g) was less than that of off-cycle years (Fig. 32). This finding probably reflects the negative effect of numerous progeny from the peak cycle on growth of post-cycle progeny. Post-peak years produced the second highest percentage of age-2 smolts in the migration (69%), reflecting the slow growth during the first year in the lake (5.6 g) when they interacted with numerous peak cycle salmon. Growth of post-peak fish experienced relatively great weight increase during the second year in the lake (86%) compared with other cycle years (avg. 75%). This increase likely reflected relaxation of density-dependence one year after migration of peak cycle age-2 smolts. Smolt per spawner (17 smolts) and smolt biomass per spawner of post-cycle fish was low (126 g) compared with that of pre-peak and off-cycle years.

Spawning escapement of off-cycle years was relatively small (median: 2.6 million fish) and off-cycle progeny interacted little with peak and pre-peak progeny. Mean smolt weight of off-cycle years was highest of all cycle years (8.5 g v. 6.6-7.9 g), as expected if density-dependent growth was significant (Fig. 32, Table 6). Off-cycle broods also produced the highest percentage of age-1 smolts in the migration (77%) and in the adult return (51%). The relatively rapid growth and early age-at-smoltification of off-cycle salmon influenced the highest abundance of smolts per spawner (30 smolts) and highest smolt biomass per spawner (207 g). Thus, freshwater productivity of off-cycle years was not less than peak-cycle years, as had been previously assumed. This is an important finding because it provides evidence that depensatory mortality in freshwater, as might be caused by marine derived nutrients or predation, was insignificant. Instead, smolt weight and smolts per spawner increased and age decreased when salmon density was low.

Pre-peak cycle years experienced relatively high spawning escapements (median: 6.4 million salmon) but mean smolt weight (7.9 g) was similar to that of off-cycle and post-peak cycle years (Fig. 32). The percentage of age-2 smolts in the migration was moderately low (48%), likely reflecting the relatively high weight of age-1 smolts (5.8 g; Table 6). Smolts per spawner (28 smolts) was considerably higher than that of peak and post-peak cycle years (14 – 17 smolts), probably because approximately 52% migrated as age-1 smolts and experienced less mortality in the lakes compared with fish rearing in the lakes for a second year. Smolt biomass per spawner of pre-peak cycle years (180 g) was higher than that of peak and post-peak cycle years (115 g – 126 g), but slightly less than that of off-cycle years.

These analyses support the hypothesis that large spawning escapements during peak-cycle years had a negative effect on growth of post-peak progeny, leading to higher percentage of age-2 smolts and lower smolts per spawner (Fig. 32). Growth of off-cycle smolts rebounded following low escapements during the post-peak cycle. Further improvement in growing conditions following several years of low escapement was apparent from relatively large smolts produced by off-cycle and pre-peak cycle years in relation to parent spawning escapement (Table 5). The patterns described here are consistent with the statistical models described above, which show density-dependence and brood interaction effects on juvenile growth and adult R/S. The finding also suggest that density-dependence had the greatest effect during the first rather than second year in the lakes. The reduction in density dependence during the second year in the lakes provides a benefit for remaining in the lakes for two rather than one year and may have influenced moderately high percentage of age-2 smolts in most years.

Adult return per spawner was highest for pre-peak cycle (2.6), followed by peak cycle (2.3), off-cycle (1.9) and post-cycle years (1.2; Fig. 32). This pattern fits the pattern of negative interaction between peak and post-cycle years followed by partial recovery in off-cycle years and full recovery in pre-cycle years. However, as noted previously, interceptions in Egegik and Ugashik fisheries likely influenced R/S relationships. Returns from post-peak (44% of years) and off-cycle years (53% of years) often occurred when returns to Egegik and Ugashik were large relative to Kvichak returns, whereas high potential interception rates were less frequent during pre-peak (20% of years) and peak years (9%). The low R/S of post-peak cycle years was consistent with its low smolts per spawner and low smolt biomass per spawner, whereas the low R/S of off-cycle years was not (off-cycle years experienced the highest smolts per spawner and highest biomass per spawner). R/S of off-cycle years was probably biased low because some fish were intercepted in adjacent fishing districts and not tallied in the Kvichak return, as indicated by the exceptionally high interception index for off-cycle years (53% of years where Kvichak return was less than 2x Egegik and Ugashik return).

R/S of pre-peak cycle years was the highest of all cycle years. The high R/S of pre-peak years reflects high smolts per spawner, high biomass per spawner and high smolt-to-adult survival. This pattern supports analyses indicating that large escapements during peak years suppressed productivity of subsequent years, but that productivity recovered to relatively high levels after several years of low escapement. As shown previously, R/S residuals from peak-cycle years was not significantly greater than that from other cycle years after removing years of large Egegik and Ugashik returns. Thus, there was no evidence of a survival benefit during peak cycles in response to marine derived nutrients or depensatory predation in the lakes or marine environment, a finding that is consistent with aforementioned analyses (Marine Derived Nutrients section).

Several patterns emerge from the analysis of Kvichak population data by cycle year. Smolts per spawner increased with greater mean age-1 and age-2 smolt weight, reflecting the importance of growth on survival in the lakes (Fig. 33). Smolts per spawner decreased with greater percentage of age-2 smolts in the migration or adult return because age-2 smolts experienced additional mortality in the lakes. Smolt-to-adult survival increased with greater percentage of age-2 smolts, as expected because age-2 smolts are larger and older than age-1 smolts. Thus, Kvichak smolts experience a tradeoff between additional mortality when spending an extra year in the lakes versus going to sea as age-1 smolts and experiencing somewhat higher mortality at sea (because they are smaller and tend to spend three rather than two years at sea) (see Table 4, Fig. 21). One advantage of staying in the lakes for a second year is the relaxation of density dependence during the second year. It is noteworthy that R/S increased with greater percentage of ocean age-2 salmon in the spawning escapement, but this trend may have been an artifact of fewer age-2 salmon during off-cycle years and higher interception rates in Egegik District..

Summary

In contrast with previous hypotheses about Kvichak cycle production, the analyses presented here do not suggest peak-cycle years have innately greater productivity than off-cycle years. Instead these analyses suggest productivity in freshwater of off-cycle years was relatively high and that its low smolt-to-adult survival and moderate R/S are related to high interception rates in Egegik and Ugashik fishing districts. There was no evidence that progeny of peak-cycle years benefited from increased nutrients provided by parent spawners or that progeny of off-cycle years were adversely affected by depensatory predation in the lakes. Rather, smolt weight and smolt abundance were influenced by density dependence and brood interaction. High interception rates of Kvichak salmon during years of small Kvichak returns (produced by small parent escapements) is a major source of depensatory mortality, leading to the impression that off-cycle years have innately low productivity because interceptions are not presently tallied in the Kvichak return statistics.

Factors Associated with Reduced Productivity and Production

The previously described brood interaction model,

$$R_i = S_i \exp\left(1.139 - .0000514S_i - .0000415S_{i-1} - .964I + .703P + \varepsilon\right)$$

did not explain the consistently low adult returns and exceptionally low productivity of Kvichak salmon produced by broods in the 1990s (Fig. 31). Thus, factors that might explain or correlate with low productivity of Kvichak salmon during the 1990s were examined. The following analysis focused on years after the 1976-77 regime shift. Prior to the regime shift, the 1967 and 1968 broods experienced exceptionally low productivity (Fig. 31), apparently in response to low SST encountered by these fish in early marine life in 1971 and 1972.

Residuals of Kvichak productivity (LN R/S) during 1974-1999 were positively correlated with parent length at age ($r = 0.60$), and negatively correlated with SST experienced by parents ($r = -0.51$), an index of Kamchatka pink salmon abundance based on a running 3-year mean ($r = -0.51$) (see Table 7), and the 1989 regime shift ($r = -0.63$). All correlations were statistically significant ($P < 0.05$). SST during smolt entry to the southeastern Bering Sea was not correlated with productivity ($P > 0.05$). Annual pink salmon abundance associated with the second year at sea of sockeye salmon was not significantly significant ($r = -0.22$, $P = 0.26$), but the correlation was significant when abundance was averaged over three years (see Table 7).

Residuals of Kvichak productivity (LN R/S) could be explained by the following multivariate equation, brood years 1974-1999:

7) Recruitment residual = 0.611+ .424 (parent length Z) - 0.014 (pink salmon index),

$n = 26$, $R^2 = 0.44$, overall $P < 0.001$, P (parent length) = 0.003, P (pink index) = 0.02, serial autocorrelation = 0.25 ($P > 0.05$) (Fig. 34). This model suggests that productivity of Kvichak sockeye salmon was reduced by consistently high Kamchatka pink salmon abundance since the early 1990s. Previous analyses indicated that Asian pink salmon significantly affected growth and survival of Bristol Bay salmon (Ruggerone et al. 2003). Kvichak productivity was positively correlated with parent length-at-age. Adult length at age of Bristol Bay sockeye salmon was consistently small beginning in 1990 (Ruggerone et al., in review), and may be an indicator of reduced reproductive potential of Kvichak salmon, especially ocean age-2 salmon that typically have low fecundity and small egg size.

Recruitment residuals may have also been influenced by relatively warm SST during the year of homeward migration:

8) Recruitment residual = 0.444+ 0.374 (parent length Z) – 0.011 (pink salmon index)
- 0.232 (SST parents),

n = 26, $R^2 = 0.51$, overall P = 0.001, P (parent length) = 0.006, P (pink index) = 0.059, P (SST parents) = 0.057, serial autocorrelation = 0.12 ($P > 0.05$). This model suggests that high SST during the homeward migration may have contributed to lower productivity, but the model is less preferred because the P-value slightly exceeds 0.05.

The direction of these linear and multivariate relationships makes biological sense. However, corroborating field data are not available to determine whether the reproductive potential and success of Kvichak spawners was unusually low beginning in 1991. Length-at-age of returning adults was consistently small during this period (Ruggerone et al., in review) and it is known that smaller adults produce smaller and fewer eggs (Groot and Margolis 1991, Quinn 2005). Rogers and Poe (1984) noted that weight of female Kvichak salmon provided a better index of reproductive potential than did numbers of fish.

During 1997, returning adults experienced unusually warm and calm ocean conditions that led to starvation of sea birds along the Alaska Peninsula and the Bering Sea (Kruse 1998). Surface waters appeared to have lower prey availability and a vast region of the Bering Sea was affected by an unusual bloom of plankton. D. Rogers, University of Washington, suggested that the unexpectedly low returns of adult salmon in 1997 may have been in response to these unusual conditions. Bioenergetic modeling has suggested that warmer than average temperatures during El Nino years can lead to significantly reduced fecundity of marine fish (Harvey 2005). Residuals from Equation 7 (LN R/S) were exceptionally low in 1997 and in other years in the 1990s.

Alagnak (Branch) Sockeye Salmon

Alagnak River discharges into Kvichak Bay at the confluence with Kvichak River. Unexpectedly, adult runs to the Alagnak system increased to 3.7 - 6.57 million salmon during 2003-2005. Prior to this recent period, Alagnak was considered to be a minor producer in the Naknek/Kvichak District and management did not develop a biological escapement goal. Spawning escapements were largely based on aerial surveys that underestimated total escapement. Clark (2005) reconstructed spawning escapements from historical aerial survey and tower counts. Eggers (unpublished analysis, ADFG) reconstructed the brood table for the Alagnak system, based on the upwardly revised escapement estimates provided by Clark (2005). The new brood table for Alagnak system indicates it was more productive than previously thought.

The large returns in recent years were produced by increasingly greater spawning escapements in response to harvest restrictions in Kvichak Bay to protect the Kvichak sockeye run. Alagnak R/S has been relatively stable in recent years compared with other Eastside stocks (Table 1), declining from approximately 3.1 to 2.4 during 1973-1990 to 1991-1999. The smaller than average decline in R/S may be related to the relatively high percentage of ocean age-3 sockeye salmon (84%), which were less affected during the decline in productivity during 1991-1999 (see previous analyses). Preliminary data indicate that the 2000 brood year experienced exceptional productivity (R/S) even though parent escapement was relatively great (1.2 million spawners). Greater production in recent years in response to larger spawning escapements suggests that Alagnak escapement may have been too low during earlier years. However, the exceptionally large escapements during 2003-2005 (3.7 to 5.4 million spawners) will likely lead to low productivity (R/S) in the near future.

Kvichak Spawning Escapement Goals

Given the current cyclic nature and wide range of Kvichak escapement goals[10], the potential impact of fishery interceptions on data quality, and the lack of evidence for nutrient- and predation-related depensatory mortality, it is worthwhile to compare Kvichak escapement goals with those of other Bristol Bay stocks.

Adult salmon returns and spawning escapements of each Bristol Bay stock were standardized by lake surface area, 1973-1999. Approximately 73% of all annual spawning densities in Bristol Bay were less than 3,000 spawners per km^2, with most falling between 1,000 to 2,000 spawners per km^2.

The mid-point of Bristol Bay escapement goals translates to a spawner density of 2,250 spawners per km^2 (excluding Igushik and Togiak: 4000-4400 spawners per km^2; Kvichak value weighted by cycle years; Table 8). The upper end of Bristol Bay escapement goals translates to a spawner density of 3,320 spawners per km^2, on average.

The mid-point peak-cycle (and pre-peak cycle) escapement goal for the Kvichak stock (2,770 spawners per km^2, or 8 million salmon) is the upper end of all large systems in Bristol Bay (Table 8) and it is approximately 124% greater than that of Egegik, 46% greater than Naknek, and 7% greater than Wood River. The upper goal spawner density for pre-peak and peak-cycle years (3,460 spawners per km^2 or 10 million fish) is higher than or equal to the upper goal of all large Bristol Bay stocks. Comparison of spawner densities among Bristol Bay stocks suggests that pre-peak and peak-cycle escapement goals for Kvichak salmon are high and this is particularly noteworthy given that the Kvichak is the least productive stock (R/S) in Bristol Bay (Fig. 17). Assuming that spawning habitat isn't a limiting factor (Burgner et al. 1969), yields from lower productivity stocks, such as the Kvichak, would be maintained at lower spawning densities.

Mid-point escapement goals of Bristol Bay stocks were plotted against lake surface area. This relationship assumes that the escapement goals are determined primarily from the capacity of the watershed to support salmon rather than the productivity of watershed. Stocks having relatively high productivity were expected to have above average residuals. However, measures of productivity (Ricker a) did not add significant information to the models ($P > 0.17$), suggesting that measurement errors in the goal and/or the productivity measurement confounded the relationship.

The initial model utilized all Bristol Bay stocks except Kvichak and Alagnak. Stock escapement goals were highly correlated with lake surface area (Fig. 35). Approximately 90% of the variability in the goal was explained by Log lake surface area. However, the predicted Kvichak goal was exceptionally low: only 1.9 million spawners were needed to produce

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[10] Off-cycle goal of 2 to 10 million spawners and peak and pre-peak goal of 6 to10 million spawners; harvest rate of 50% on returns above twice the lower bound of the escapement goal; Baker et al. (2006).

sustained harvests in the Kvichak watershed. This low predicted value was caused by the significant effect of Egegik on the model. The escapement goal for Egegik is exceptionally low in relation to its relatively great lake surface area[11]. Removal of Egegik from the model and use of a linear model produced more reasonable results (Fig. 35):

9) Escapement goal = .201 + .0018 (lake area (1000 km^2)),

$n = 6$, $R^2 = 0.90$.

The Kvichak goal predicted by this model is 5.4 ± 2.7 million sockeye salmon (± 95% CI). The predicted goal is similar to the revised mean goal for off-cycle years (mean: 6 million spawners) but it is considerably lower than the goal for peak and pre-peak cycle years (mean: 8 million spawners; Fig. 35). Given the low productivity of Kvichak salmon compared with other Bristol Bay stocks, one would expect the established Kvichak goal to be lower rather than higher than that of other stocks.

This analysis offers a different view of Kvichak spawning escapements compared with the analysis based on Kvichak spawner and return data (Fair et al. 2004, Baker et al. 2006). Spawning escapement during peak and pre-peak years has averaged 8.8 million salmon, whereas escapement during off-cycle years has averaged only 2.4 million salmon (Table 6). Mean escapement (5.3 million fish) is similar the mean escapement level suggested by the meta analyses (5.4 million fish). Mean spawning densities in the Kvichak watershed (per lake area) relative to other Bristol Bay watersheds are very high during peak and pre-peak years and very low during off-cycle years, leading to a mean observed escapement level that is consistent with that of other Bristol Bay stocks. However, the existing mean escapement goal of 6.8 million spawners (weighted by cycle year) is higher than the historical mean escapement and the mean escapement goal that is comparable to other Bristol Bay stocks.

A key question is whether managers should continue to maintain the Kvichak cycle by maintaining cyclic spawning goals. The evidence presented in this report suggests there is little or no direct depensatory mortality within the Kvichak watershed in response to either marine derived nutrients (carcasses) or predators. Instead, growth of juvenile sockeye and smolts per spawner *increased* when salmon abundance was low. Progeny from post-peak spawners were somewhat small and less productive (smolts per spawner) because of apparent brood interaction with progeny from peak spawning years. A depensatory relationship was observed in adult R/S (low R/S from post-peak and off-cycle years), but this was most likely caused by unaccounted interceptions in Egegik and Ugashik fisheries, especially during years of small Kvichak returns.

Thus, there does not appear to be compelling evidence that a strong Kvichak cycle should be maintained in order to provide high yields. The Kvichak stock has a propensity to cycle, in part, because ocean age is relatively constant (ocean age-2 fish), large spawning escapements adversely affect subsequent brood production, and because a high percentage of small Kvichak returns have been harvested in the Egegik and Ugashik districts in the past.

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[11] The relationship between escapement goal and lake area provides evidence that the current goal for Egegik is too low. Egegik is one of the most productive stocks in Bristol Bay (Ricker a), therefore its escapement goal should be above rather than below the linear regression.

DISCUSSION

The decline in Kvichak salmon was not unique among Bristol Bay populations, although the magnitude of its decline was greater than all other Bristol Bays stocks. Both Egegik and Ugashik stocks declined significantly. Peterman et al. (2003) also noted that productivity of Kvichak, Egegik, and Ugashik salmon was low in the early 1990s. Corrected smolt data for these stocks indicated the decline was related to factors affecting survival in both freshwater and the ocean. When comparing productivity of all Bristol Bay stocks, it was apparent that stocks having greater percentages of ocean age-2 salmon in their adult returns experienced the greatest decline. The Kvichak stock, whose return in the past has been composed of 84% ocean age-2 salmon, experienced the greatest decline of the eastside stocks. Numbers of Kvichak ocean age-2 salmon declined 79% and ocean age-3 salmon declined 60%, on average. Adults in the dominant age group of Kvichak salmon (age-2.2) declined 91%.

Juvenile growth in the lakes was not likely a direct factor of the Kvichak decline. Smolt size was above model predictions during 1991-1996, then below average through 2002. Potentially, some factor affecting survival in the egg-to-early-fry stage could have led to greater than expected growth if density dependence was reduced; this potential factor was not examined here. Scouring of redds is an unlikely cause of the decline in freshwater because aerial survey data did not indicate an obvious shift in spawner distribution among beach spawners versus tributary spawners, which is what would be expected if riverine spawners were differentially affected[12]. Instead it appears that all Kvichak populations declined, indicating major factors of decline were common to all populations.

Reproductive Success of Kvichak Adult Salmon

Factors affecting the condition of spawning adults were examined as a potential cause of the decline. Length at age of parents was low from brood years 1990 to 1998 (Ruggerone et al., in review). Also, SST during June of the homeward migration was typically above average during 1990-1998. These changes may be linked to the reported ocean regime shift in 1989 (Hare and Mantua 2000) that was associated with smaller adult size at age. Major changes in the marine environment were observed in 1997, leading to numerous dead and weakened seabirds, and low salmon returns to Bristol Bay (Kruse 1998). Higher SST may alter the energetic demand of maturing fish and affect female fecundity (Harvey 2005). Smaller salmon typically produce smaller and fewer eggs (Burgner 1991, Quinn 2005). Previous analyses of Kvichak R/S indicated female body weight provided a better index of reproductive potential than did numbers of salmon (Rogers and Poe 1984). Furthermore, stocks having the greatest decline typically produced the highest percentage of ocean age-2 salmon. The combined lower fecundity of ocean age-2 salmon relative to ocean age-3 salmon, relatively small size at age, and greater susceptibility of ocean age-2 salmon to above average SST during the homeward migration may have contributed to the decline in salmon. Additional research is needed to examine the

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[12] Examination of aerial survey data from 1961-1990 to 1991-1996 indicated a 5% increase in the relative spawning contribution by creek and pond spawner populations (on average), a 2% increase in the contribution by five river populations, a 4% decrease in the contribution by island beach populations, and a 3% decrease in the contribution by five mainland beach populations. Data provided by D. Rogers.

relationships between high SST, smaller salmon size, ocean age, and reproductive potential and success of salmon.

Competition with Pink Salmon

Relatively little is known about factors affecting salmon survival at sea, although it is generally believed that greater growth leads to greater survival (Pearcy 1992, Ruggerone et al. 2005; in review). Growth of Bristol Bay sockeye during the second and third years at sea (scale pattern analysis) and in adult returns (length at age) was reduced in response to greater Asian pink salmon abundance, 1955-2000 (Ruggerone et al. 2003, 2005). Furthermore, smolt-to-adult survival was reduced by approximately 26% (age-2 smolts) to 46% (age-1 smolts) when competing with pink salmon for prey during their second year at sea. This mortality corresponded with 22% fewer adult returns among adults produced by even-year smolts that competed with pink salmon during the following odd-numbered year. The reduction in adult returns during 1977-1997 was estimated to be 92 million adult salmon (Ruggerone and Nielsen 2005).

The effect of pink salmon on Bristol Bay sockeye salmon was previously unknown because the multiple ages of sockeye maturity mask the effect unless adult return data are organized by year of smolt migration. A recent study of 53.5 million coded-wire-tagged Chinook salmon in Puget Sound documented a 59% decline in release-to-adult survival when juveniles interacted with numerous pink salmon in their first year at sea (Ruggerone and Goetz 2004). This study also documented a reduction in growth and delayed maturation in response to competition with pink salmon. Although further research is needed to document interactions between pink salmon and other salmonids, numerous studies show distinct odd-even patterns in survival and growth that implicate pink salmon as a dominant competitor in the North Pacific Ocean (Ruggerone and Nielsen 2005).

A recent large increase in Kamchatka pink salmon abundance may have influenced the recent decline of Kvichak salmon. The even-year line of Western Kamchatka pink salmon increased dramatically beginning in 1994 (Bugaev 2002, Ruggerone and Nielsen 2005). These fish would have interacted with age-1 smolts produced by the 1991 brood of Kvichak salmon, i.e., the first year in which R/S was consistently low. Kamchatka pink salmon abundance was consistently high from 1994-2000, declined from 2001 to 2003, then increased in 2004 to 2005. High abundances of Kamchatka pink salmon would have first interacted with the 1991 Kvichak brood, which is the first year of significant decline. The consistently high abundance of Asian pink salmon may have inhibited recovery of prey species thought to occur when pink salmon abundance exhibits a strong odd-even pattern in abundance (Ruggerone et al. 2005). This hypothesis is supported by the significant negative correlation between the three-year running mean of pink salmon abundance and Kvichak productivity, 1974-1999.

The observation of reduced adult returns and productivity among Bristol Bay stocks having larger ocean age-2 components (see Figs. 18 and 19) is consistent with the hypothesis that competition with pink salmon contributed recent decline in Kvichak and other Bristol Bay stocks. On average, 1.04 million fewer ocean age-2 and 0.44 million fewer ocean age-3 Bristol

Bay salmon per stock (avg. 31.5% reduction) returned from even-year smolt migrations compared with odd-year migrations, 1977-1997 (Ruggerone et al. 2003).

The observation that pink salmon have greater effect on ocean age-2 salmon compared with ocean age-3 salmon is consistent with findings based on smolt-to-adult survival estimates, in which pink salmon had its greatest effects on age-1 smolts and ocean age-2 adults. Thus, it is possible that the continually high abundance of Kamchatka pink salmon during 1994-2000 may have adversely affected adult salmon returning to Kvichak, Egegik and Ugashik watersheds. These stocks also appear to have greater overlap with Asian pink salmon compared with Wood River and other Nushagak District stocks (Myers 1997) that experience little or no decline. Stocks that experienced little or no decline in productivity also had greater percentages of ocean age-3 salmon, which were affected less by pink salmon.

Kvichak Cycle

Factors influencing the Kvichak cycle have been a mystery for decades. Mathisen and Poe (1981) postulated that the cycle may be caused by depensatory predation and/or improved growing conditions for peak cycle progeny in response to nutrient enrichment provided by carcasses of their parents and that the cycle was needed to produce high yields. They speculated that maintenance of the Kvichak cycle may be critical to high salmon production and stable escapement levels will produce little surplus yield from the stock.

Several sockeye salmon stocks returning to the Fraser River, British Columbia, undergo a four year cycle, which is consistent with their four year life span (age-1.2). A variety of natural and human-induced factors affecting the cycle have been hypothesized (Levy and Wood 1992). Recently, Ricker (1997) concluded that interaction between brood lines is the likely source of Fraser River cycles. However, Myers et al. (1997) found only weak interactions between brood lines in Fraser River sockeye salmon and suggested these interactions may not be sufficient to cause the observed cycles.

The results presented here do not support the hypothesis of cyclic dominance of the peak-cycle year. Smolt biomass per spawner and smolt per spawner tended to be *greater* during pre-peak and off-cycle years than during peak and post-peak cycle years, as would be expected if density dependence and brood interaction were important to growth and survival in the lakes. There was no evidence that progeny of peak-year spawners benefited significantly from marine derived nutrients provided by parent carcasses. Instead, growth and abundance of smolts were predictably related to parent spawning escapement and previous escapement (brood interaction).

Despite a lack of quantitative estimates of predation rates, the hypothesis of entirely natural mechanisms causing cyclic dominance has been supported over the years because R/S of peak and pre-peak cycle years has been higher than during post-peak and off-cycle years. The findings presented here and by Eggers and Rogers (1987) indicate that R/S during post-peak and off-cycle years is biased low because numerous Kvichak salmon are intercepted in Egegik and Ugashik districts and these fish are not tallied as Kvichak salmon. Interceptions have a much greater effect on R/S of post-peak and off-cycle years because, like a depensatory predator, they remove a larger percentage of the population when the Kvichak population is relatively small.

Post-peak and off-cycle adult returns are small because their parent spawning escapements are small and because progeny of post-peak broods are adversely affected reduced prey availability caused by peak-year progeny.

The Kvichak cycle is likely maintained by combination of human-induced and natural factors: 1) depensatory fishing mortality in the Naknek/Kvichak District, 2) unaccounted depensatory fishing mortality in adjacent fishing districts, 3) negative interaction between juvenile salmon originating from adjacent brood lines, and 4) the propensity of the Kvichak salmon to mature at a relatively constant age (i.e., five years). There is no evidence of direct depensatory mortality such as that caused by predators (e.g., beluga whales (Markowitz and Link 2006) and predatory freshwater fishes) or by positive effects of periodic influx of marine derived nutrients, as shown by analysis of model residuals.

Although part of the cause appears due to natural age composition features of the stock and brood interaction in the lake, these do not in themselves require a cyclic escapement goal policy to produce surplus yields. Instead, knowledge of these features suggest that *periodic* very large escapement events create or reinforce otherwise unnecessary cyclic production.

Kvichak Escapement Goal

Managing for very high densities of spawners in the Kvichak relative to other Bristol Bay stocks is not consistent with the fact that the Kvichak is a relatively low productivity stock. Peak-cycle and off-cycle escapement goals of Kvichak sockeye salmon were compared with those of other Bristol Bay stocks after standardizing the goals by lake surface area (i.e., juvenile rearing habitat). Spawner density calculated from the mid-point escapement goal during pre-peak and peak-cycle years was greater than all other Bristol Bay stocks, except for Ugashik, Togiak and Igushik, which are small systems. This finding is opposite of what is expected because the Kvichak stock has lower productivity compared with other stocks and therefore juvenile densities should be lower than that of other stocks (based on spawners per lake area).

Egegik and Kvichak Production After 1976/1977 Regime Shift

The tremendous increase in R/S and total return of Egegik sockeye salmon relative to other Bristol Bay stocks following the 1976/77 ocean regime shift has raised speculation about factors causing this increase. Egegik salmon productivity (R/S) increased 230% and total return increased 350% from 1952-1972 to 1973-1990 (Table 1). The analysis presented here shows that the relatively high productivity of this stock was likely influenced by its relatively low density of spawners per lake surface area (Table 8). Low spawner density allowed great growth of juveniles (Table 4) and presumably high survival in freshwater even after spawning escapements increased in the late 1970s. Numerous large smolts and favorable ocean conditions contributed to the very high productivity of Egegik sockeye salmon. Greater harvests rates during large Egegik returns probably led to greater interceptions of Kvichak salmon, thereby inflating estimates of already high productivity of Egegik salmon and deflating productivity estimates for Kvichak salmon.

The high productivity and low spawning density (per lake area) of Egegik salmon is opposite that of Kvichak salmon. The relatively small response of Kvichak salmon to the 1976/77 ocean regime shift was likely related to relatively high density of juveniles in the lake prior to the regime shift, low productivity of the watershed, and interceptions of Kvichak salmon in the Egegik District.

Recommendations and Conclusions

A key to further refining our understanding of past and future changes in the abundance of Kvichak salmon will be to accurately index the abundance, age, and size of smolts produced over time. These estimates can help partition changes in productivity between marine and freshwater factors and facilitate the evaluation of escapement goals. Although the smolt program on the Kvichak system produced large erroneous estimates as far back as 1995[13], it once worked well as evidenced by the improvements it made to preseason forecasts, and progress has been made to correct the problems introduced then with a new piece of equipment. We recommend the reintroduction of a smolt program that can provide abundance estimates comparable to those obtained prior to 1995.

Estimating smolt abundance on the Kvichak is technically challenging and more difficult than doing so for the Egegik River. Kvichak and Egegik smolt-to-adult survival estimates were highly correlated prior to 1995 indicating each acoustic system provided an accurate estimate of the relative abundance of smolts and that Egegik survival rates are a good surrogate for tracking changes in marine survival for Kvichak smolts. At least while technical challenges associated with estimating smolt abundance on the Kvichak are overcome, we recommend an Egegik program also be reintroduced. In addition to tracking Kvichak survival, such a program would likely improve preseason forecasts of returns to Egegik.

Unaccounted interceptions of Kvichak salmon in Egegik and Ugashik districts have long complicated interpretation of the stock dynamics of Kvichak salmon and provided some erroneous support for the concept of enhanced productivity (marine survival) during peak years. We recommend these interceptions of Kvichak fish be carefully reconstructed for past years, especially during years of high Egegik and Ugashik returns relative to Kvichak returns. In addition, we recommend that stock composition of catches from eastside districts be a standard component of the annual assessment program. ADFG has begun to re-analyze past interceptions of Kvichak salmon in the Egegik District using genetic stock identification and population modeling. This task is key to developing an unbiased recruitment relationship, which is needed to estimate spawner escapement goals for the Kvichak watershed. Multiple methods should be undertaken to estimate a range in Kvichak spawning escapement that will enable the potential for sustained high harvests. Brood interaction should be considered in the evaluation, especially if high densities of spawners are recommended.

Findings presented here indicate that the relatively low R/S of post-peak and off-cycle years was caused by unaccounted interceptions of adult salmon in Egegik and Ugashik fishing districts and by brood interactions in the nursery lake, rather than cyclic dominance associated with direct

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depensatory mortality, as has been previously postulated. Our findings are generally in agreement with those of Rogers and Poe (1984) and Eggers and Rogers (1987) who, using less data than presented here, also found no evidence of direct natural depensatory mortality. There was no evidence that biogenic enrichment of salmon carcasses provided a boost to growth and/or survival of peak-cycle progeny.

The Kvichak decline does not appear to have been caused by a change in the stock's escapement goals made in 1985. Production from the first four brood years following the policy change to relatively stable escapement levels across the cycle averaged 2.9 returns per spawner, which was higher than the average of 2.5 R/S from the previous 10 brood years. Subsequent declines in productivity and production from the Kvichak during brood years 1991-1999 were also observed in other Bristol Bay stocks (e.g., Egegik and Ugashik) in response to lower smolt-to-adult survival (marine factors) and fewer smolts produced per spawner (freshwater factors). The dramatic decline in production from the 1991 brood year coincides closely with the 1989 ocean regime shift, which produced generally warmer freshwater and marine conditions. These data and others presented here suggest that changes to the Kvichak escapement goal policy in 1987 was not a major factor leading to the stock's decline. Rather, multiple factors involving climate, growth at sea, salmon age structure, and density-dependent interactions appear to have contributed to the decline.

The results from our analysis do not support the existing escapement goal policy of higher escapement levels (6 to 10 million fish) during peak and pre-peak return years compared to other return years (2 to 6 million). Maintenance of the Kvichak cycle through management does not appear necessary for high salmon productivity and harvestable surpluses, a conclusion also made by Rogers and Poe (1984). However, shifting away from the cycle by stabilizing spawning escapement levels is made difficult because of a more immediate desire to harvest Kvichak salmon each year, the low productivity of Kvichak salmon, and the propensity of the Kvichak stock to experience cyclic patterns in response to relatively constant age at maturation, brood interaction, and interception of salmon in adjacent Bristol Bay fishing districts. We recommend further work to evaluate and define escapement goal policies for the Kvichak in light of the results provided here.

ACKNOWLEDGEMENTS

This investigation was funded by a grant from the North Pacific Research Board and by funding from the Bristol Bay Science and Research Institute. Ideas presented in this report benefited from earlier collaborations with D. Rogers, University of Washington, to whom this investigation is dedicated. D. Eggers (ADFG) provided constructive comments on the report. This investigation could not have been possible without the considerable forethought and tremendous effort by biologists who collected data on Bristol Bay sockeye salmon during the past 50 years.

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TABLES AND FIGURES

Table 1. Mean return per spawner, total adult return, spawning escapement, and age composition of adult returns during brood years 1952-1972, 1973-1990, and 1991-1999. Percentage change in values is from 1973-1990 to 1991-1999.

Period	Togiak	Igushik	Wood	Nushagak	Total Westside	Kvichak	Naknek	Egegik	Ugashik	Branch	Total Eastside W/O Brch	Bristol Bay W/O Brch
	Return per spawner											
1952-72	2.3	2.0	1.9	2.6	1.9	1.5	2.2	2.6	1.8	1.1	1.8	1.7
1973-90	3.5	5.8	2.8	3.4	3.5	2.8	3.2	8.5	5.6	3.1	3.9	3.8
1991-99	3.2	2.5	3.3	3.7	3.2	0.8	3.0	4.5	2.2	2.4	2.1	2.3
% change	-9%	-57%	16%	8%	-7%	-73%	-5%	-47%	-60%	-24%	-48%	-39%
	Return of salmon											
1952-72	0.26	0.4	1.5	0.44	2.47	9.1	1.8	2.0	0.8	0.4	13.8	16.2
1973-90	0.64	1.3	3.0	1.76	6.77	14.7	4.4	9.1	4.1	1.4	32.3	39.1
1991-99	0.65	1.0	4.7	1.58	7.98	3.9	4.1	7.3	2.8	1.6	18.1	26.0
% change	1%	-24%	57%	-11%	18%	-74%	-7%	-20%	-31%	15%	-44%	-33%
	Escapement											
1952-72	0.12	0.2	0.8	0.13	1.30	4.9	0.8	0.8	0.5	0.3	7.0	8.3
1973-90	0.22	0.4	1.2	0.71	2.47	5.8	1.4	1.1	0.9	0.4	9.2	11.7
1991-99	0.21	0.4	1.4	0.48	2.43	4.8	1.5	1.6	1.4	0.7	9.3	11.7
% change	-7%	-3%	16%	-32%	-2%	-18%	12%	48%	48%	74%	1%	0%
	Percentage age 1.											
1952-72	81.7	74.6	86.3	91.6	84.1	28.8	42.1	16.9	39.9	74.2	29.2	43.0
1973-90	86.8	89.3	91.2	95.4	91.7	44.7	51.7	23.8	41.4	76.9	39.0	48.4
1991-99	87.6	86.2	90.5	94.7	91.1	61.9	66.1	29.1	59.5	73.8	49.2	61.8
% change	1%	-3%	-1%	-1%	-1%	39%	28%	22%	43%	-4%	26%	28%
	Percentage age .3											
1952-72	61.8	63.8	41.5	84.7	51.2	19.4	53.7	41.9	31.8	81.9	33.0	35.7
1973-90	72.9	76.5	53.3	84.8	67.8	25.5	63.2	42.6	43.6	82.7	38.8	44.2
1991-99	77.9	76.4	50.3	84.3	62.6	32.8	70.7	50.5	50.0	83.4	51.5	54.1
% change	7%	0%	-6%	-1%	-8%	29%	12%	19%	15%	1%	33%	22%

Table 2. Estimated change in total return, return per spawner, smolt per spawner, and smolt survival of Kvichak sockeye salmon from brood years 1974-1990 to 1991-1998 (mean ± 1 SE). See text for description of methods to estimate smolt abundance and survival during 1995-2001 smolt years when smolt sonar was in error. The Egegik model provided more accurate estimates of smolt abundance and survival. Brood years based on availability of smolt data.

	Brood years		
	1974-1990	1991-1998	% change
Adult return (millions)	15.5 ± 2.9	3.9 ± 1.2	-75%
Return per spawner	2.7 ± 0.3	0.8 ± 0.1	-72%
Parent escapement (miilions)	6.1 ± 1.1	4.6 ± 1.1	-26%
Values based on smolt model after 1990:			
No. age-1 smolt (millions)	76 ± 16	58 ± 11	-23%
No. age-2 smolt (millions)	83 ± 21	39 ± 9	-54%
Total smolt (millions)	159 ± 28	97 ± 15	-39%
Smolt per spawner	29 ± 3	29 ± 6	0%
Survival: age-1 smolt (%)	9.1 ± 1.4	5.1 ± 2.1	-44%
Survival: age-2 smolt (%)	14.0 ± 2.6	2.8 ± 0.9	-80%
Survival: total smolt (%)	10.8 ± 1.4	3.6 ± 1.0	-67%
Values based on Egegik-based method after 1990:			
No. age-1 smolt (millions)	76 ± 16	43 ± 11	-43%
No. age-2 smolt (millions)	83 ± 21	14 ± 3	-83%
Total smolt (millions)	159 ± 28	57 ± 12	-64%
Smolt per spawner	29 ± 3	15 ± 4.5	-48%
Survival: age-1 smolt (%)	9.1 ± 1.4	7.4 ± 1.9	-18%
Survival: age-2 smolt (%)	14.0 ± 2.6	7.9 ± 3.0	-44%
Survival: total smolt (%)	10.8 ± 1.4	5.8 ± 1.0	-46%

Approximate % change in adult production (Egegik-based method) assocated with life stages:

		Corrected for reduced survival:		
Spawners to smolt: (based on reduction in total smolt)				58%
Escapement:	35%	22%	13%	
Smolt per spawner:	65%	78%	45%	
		100%	58%	
Smolt to adult (based on reduction in total survival at sea)				42%
				100%

Methods to approximate % change associated with life stage:

1) Spawner-to-smolt stage (58%) = (% smolt decline)/(% smolt decline + % decline smolt survival).
2) Smolt-to-adult stage (42%) = (% decline smolt survival)/(% smolt decline + % decline smolt survival).
3) Spawners-to-smolt stage decline associated with escapement (35%) = (% escapement decline)/(% smolt per spawner decline + % escapement decline).
4) Spawners-to-smolt stage decline associated with escapement after correcting for reduced survival (22%): ((early spawners x recent smolt per spawner) - (recent spawners x recent smolt per spawner))/(reduction in smolts abundance).

Table 3. Salmon productivity, density-dependence, and characteristics of Bristol Bay sockeye salmon lakes. Escapement values and Ricker recruitment curve values based on production during brood years 1973-1990, a period of high and somewhat stable productivity. Salmon productivity is based on slope of Ricker curve at origin. Regression slope is that of linear model to describe Ricker curve parameters (LN R/S = a + b(S) + residual). Mean density was also adjusted for the number of juveniles that spent two summers in lakes (based on adult age composition). Lake morphometrics from Burgner et al. (1969).

	Number	Surface	Mean	Escapement (1,000s)		Esc. density (1000s/km^2)		Mean density	Productivity	Regression	Regression
Watershed	of lakes	area (km^2)	depth (m)	Mean	Range	Mean	Maximum	adj. for FW age	(low density)	Slope	P-value
Eastside stocks											
Kvichak	2	2889	49	5820	227, 17510	2.0	6.1	3.1	3.4	-0.047	0.148
Pre-peak & peak		2889	49	8799	250, 17510	3.0	6.1	5.0			
Off		2889	49	2403	227, 6070	0.8	2.1	1.3			
Egegik	1	1132		1090	328, 2190	1.0	1.9	1.7	7.2	0.022	0.940
Naknek	4	791	41	1370	357, 2645	1.7	3.3	2.6	4.1	-0.235	0.286
Ugashik	2	385		920	39, 3321	2.4	8.6	3.8	9.1	-0.582	0.013
Alagnak	4	297		406	35, 804	1.4	2.7	1.7	14.8	-3.122	0.001
Westside stocks											
Wood	5	425	47	1250	330, 2969	2.9	7.0	3.2	6.2	-0.728	0.001
Nuyakuk	3	279	94	710	390, 3320	2.5	11.9	2.7	5.2	-0.944	0.001
Igushik	2	74	26	410	60, 1987	5.5	26.9	6.1	9.8	-2.363	0.001
Togiak	2	49		220	74, 462	4.5	10.8	5.1	9.2	-5.283	0.001

Table 4. Relationship between growth in freshwater, geometric mean survival at sea, and benefit of staying extra year in lakes as indicated by the increase in growth and survival of age-2 smolts. Values based on maximum number of years available after the ocean regime shift in mid-1970s and prior to smolt counting error in mid-1990s.

Stock	Smolt yrs	Smolt age	Survival (%)	Wt (g)	% age 2 smolt (±SE)
Kvichak	1976-93	Age 1	7.5	5.6	47% ±26
		Age 2	11.9	9.4	
		Difference	4.4	3.8	
Egegik	1982-93	Age 1	18.4	9.8	71% ±19
		Age 2	28.6	14.3	
		Difference	10.2	4.5	
Ugashik	1982-93	Age 1	4.9	7.1	49% ±23
		Age 2	10.0	11.5	
		Difference	5.1	4.4	
Wood River	1975-90	Age 1	6.0	7.0	7% ±7
		Age 2	6.9	9.3	
		Difference	0.9	2.36	

Table 5. Summary of alternative stock recruitment models with log-normal errors, brood years 1952-1990. Akaike Information Criteria (AIC) and the P-value were used to evaluate the best recruitment model. The analysis indicated the best model was a Ricker model modified by Egegik interception index, time period (1953-1972, 1973-1990), and brood year interaction (BYI). Brood years 1967 and 1968 were excluded from the analysis because SST was exceptionally cold for smolts.

Model	Number of Parameters	- Log L	Likelihood Ratio	p-value	AIC	Model Comparison	New Variable
Linear	1	38.10			40.1		
Ricker	2	37.56	1.081	0.298	41.6	Linear	
Ricker + Period	3	35.67	3.784	0.151	41.7	Ricker	Period
Ricker + Interception	3	34.10	6.917	0.009	40.1	Ricker	Interception
Ricker + BYI	3	35.71	3.709	0.157	41.7	Ricker	BYI
Ricker + BYI + Period	4	33.38	4.578	0.032	41.4	Ricker + Period	BYI
Ricker + BYI + Interception	4	31.52	8.369	0.004	39.5	BYI	Interception
Ricker + Interception + Period	4	28.69	10.831	0.001	36.7	Ricker + Interception	Period
Ricker + BYI + Interception + Period	5	24.35	8.682	0.003	34.3	Ricker + Interception + Period	BYI
Ricker + BYI + Interception + Period	5	24.35	18.068	0.000	34.3	Ricker + BYI + Period	Interception
Ricker + BYI + Interception + Period	5	24.35	14.352	0.000	34.3	Ricker + BYI + Interception	Period

Table 6. Summary of Kvichak productivity and production statistics by cycle year. Values relying on smolt data before 1971 and after 1994 smolt years were excluded from mean and median values (fyke net catches or sonar overestimated smolt abundances). Values after 1995 smolt year were based on the Egegik method of estimating smolt abundance. Years when interception rates of Kvichak salmon were likely high are underlined.

Cycle Year	Brood year	Escapement (millions)	Escapement % age x.2	Return (millions)	Return per spawner	% x.2 return	% 2.x+ return	Smolts per spawner	Biomass per spawner	age 1 wt (g)	age 2 wt (g)	% age 2 smolt	Survival at sea	Age 1 survival	Age 2 survival
Pre-peak	55	0.3	72	1.3	5.1	61.5	74.3			7.3		66.7			
Cycle	59	0.7	94	0.5	0.7	75.8	42.1			6.8	9.9	66.7			
	64	1.0	94	4.9	5.1	82.4	56.5			7.4	14.2	44.8			
	69	8.4	97	5.1	0.6	83.6	92.2	16.7	123.8	5.8	10	38.6	3.6	0.5	8.6
	74	4.4	91	25.5	5.8	88.4	68.4	50.1	400.9	5.8	10.1	51.4	11.5	7.5	15.3
	79	11.2	92	40.2	3.6	86.2	50.8	27.5	180.1	5.5	9.1	28.8	13.0	9.0	22.9
	84	10.5	91	23.1	2.2	81.4	81.3	39.5	264.3	5.5	7	79.7	5.6	5.2	5.7
	89	8.3	92	25.4	3.1	80.6	85.9	17.8	125.7	5.5	9.3	41.2	17.2	4.1	35.8
	94	8.3	94	6.9	0.8	79.2	57.7	13.8	96.7	6.5	10.6	31.1	6.0	2.9	27.2
	98	2.3	78	0.9	0.4	35.5	33.6	7.9	59.5	5.8	8.5	74.7	4.9	9.2	1.5
	mean	5.5	90	13.4	2.7	75.5	64.3	30.3	218.9	6.2	9.9	52.2	10.2	5.2	17.7
	median	6.4	92.0	6.0	2.6	81.0	63.0	27.5	180.1	5.8	9.9	48.1	11.5	5.2	15.3
Peak-	52	6.0		17.3	2.9	73.3	14.4								
Cycle	56	9.4	99	33.1	3.5	81.1	18.1			4.6	7.6	45.9			
	60	14.6	100	48.8	3.3	87.3	96.6			4.3	7.5	78.4			
	65	24.3	99	40.1	1.6	95.2	76.6			5.9	9.2	65.5			
	70	13.9	98	15.0	1.1	95.8	99.7	13.9	114.7	4.2	8.3	99.5	7.8	5.1	7.6
	75	13.1	96	35.7	2.7	94.3	81.3	22.1	159.1	5.5	7.8	73.2	12.3	8.6	13.6
	80	17.5	96	12.5	0.7	84.9	65.6	12.9	80.6	5.1	8.5	33.6	5.5	2.9	10.8
	85	7.2	68	16.9	2.3	83.5	86.7	13.6	107.0	4.5	8.3	88.8	17.2	20.4	16.8
	90	7.0	91	24.5	3.5	90.0	89.2	31.7	253.4	5.6	8.2	91.9	11.0	14.7	10.7
	95	10.0	87	9.8	1.0	81.4	6.4	8.7	72.6	6.8	11.9	44.5	11.3	15.3	2.3
	99	6.2	87	7.8	1.3					4.2	7.5	58.1		2.4	
	mean	11.8	92	23.8	2.2	86.7	63.5	18.8	142.9	5.1	8.5	77.4	10.8	10.3	11.9
	median	10.0	96.0	17.3	2.3	86.1	78.9	13.9	114.7	4.9	8.3	88.8	11.0	8.6	10.8
post-peak	53	0.3		0.5	1.6	76.9	76.9								
	57	2.8	34	3.6	1.3	88.1	89.2				10.3	87.2			
	61	3.7	64	3.1	0.8	75.6	85.2			4.8	9.8	92.5			
	66	3.8	33	5.5	1.5	78.7	76.0			5.5	10.6	44.6			
	71	2.4	72	2.3	1.0	89.8	85.9	10.9	125.9	5.1	13.1	80.8	9.0	6.6	9.6
	76	2.0	82	9.9	5.1	89.5	41.6	29.5	234.0	6	10.3	44.8	17.1	18.1	15.9
	81	1.8	18	2.1	1.2	81.6	51.9	25.7	236.7	4.9	10	84.4	4.6	14.1	2.8
	86	1.2	74	4.3	3.6	46.7	60.0	16.9	125.8	5.6	10.8	35.0	21.4	13.2	36.7
	91	4.2	77	4.7	1.1	70.1	17.9	12.4	99.3	6	9.5	57.7	8.9	17.4	2.8
	96	1.5	40	1.6	1.1	22.9	2.2	45.4	304.9	6.7	10.3	18.2	2.4	2.3	11.2
	mean	2.4	55	3.8	1.8	72.0	58.7	19.1	164.3	5.6	10.5	65.9	12.2	13.9	13.6
	median	2.2	64.0	3.4	1.2	77.8	68.0	16.9	125.9	5.6	10.3	69.2	9.0	14.1	9.6
other	54	0.2		0.8	3.1	90.7	86.7				14.4				
	58	0.5	43	0.3	0.5	76.0	56.0			6.3	13.1	20.0			
	62	2.6	68	4.8	1.9	89.9	95.2			5.2	11.3	79.1			
	63	0.3	58	0.9	2.5	68.0	90.6			6.8	12.6	20.0			
	67	3.2	87			78.6	59.9			5.7	11	33.3			
	68	2.6	88			67.4	41.3			6	11.1	35.3			
	72	1.0	68	1.6	1.6	75.9	81.5			8.3	16.4	0.0		10.0	
	73	0.2	67	2.2	9.8	33.6	36.4			8.4	14.2	23.3	13.7		26.1
	77	1.3	87	3.0	2.2	67.2	10.6	29.1	209.5	6	10.7	25.6	7.6	9.3	2.7
	78	4.1	89	4.8	1.2	60.4	42.9	51.6	337.5	5.9	10.2	15.0	2.3	1.5	6.4
	82	1.1	72	1.6	1.4	58.7	40.0	47.4	326.3	6.8	9.2	3.7	3.0	1.8	32.1
	83	3.6	95	13.0	3.7	73.0	12.8	21.6	190.0	5.3	10.4	68.8	16.9	47.3	3.2
	87	6.1	96	11.4	1.9	72.8	43.6	31.0	204.1	5.5	10.5	21.8	6.1	4.4	12.1
	88	4.1	56	9.4	2.3	68.7	48.9	20.0	150.0	5.8	9.9	42.0	11.6	10.2	13.4
	92	4.7	77	1.3	0.3	72.3	51.3	12.5	86.4	5.7	9.8	16.9	2.1	1.1	3.8
	93	4.1	69	2.4	0.6	55.5	33.0	9.9	74.6	6.2	11.3	27.2	6.1	5.5	7.7
	97	1.5	79	0.6	0.4	68.3	58.6	5.6	49.0	5.8	9.5	39.4	6.7	13.6	4.9
	mean	2.4	75	3.9	2.2	69.2	52.3	33.4	236.3	6.2	11.5	28.6	8.7	6.2	13.7
	median	2.6	74.5	2.2	1.9	68.7	48.9	30.0	206.8	6.0	11.0	23.3	7.6	6.8	12.1

Table 7. Calculation of the Kamchatka pink salmon index. The index is the three year running mean of Kamchatka pink salmon run (return year and previous two years) weighted by age-1 and age-2 Kvichak smolt abundances for each brood year. Weighting by age-specific smolt abundance was necessary because smolts from a brood year migrate during multiple years and therefore experience different interactions with pink salmon, which tend to be abundant in odd-numbered years. Age-2 smolts discounted by 0.58x to account for reduced effect on pink salmon on age-2 versus age-1 smolts (Ruggerone et al. 2003). Pink salmon runs adjusted to align with sockeye's second year in ocean, e.g., age-1 smolts from brood year 1974 interacted with pink salmon from 1977 (avg. 1975-1977). Pink salmon data provided by K. Myers, University of Washington, and Sinakov (1998).

Pink salmon return year	Kamchatka pink salmon run (millions)	Sockeye brood year	Age 1 smolts (millions)	Age 2 smolts (millions)	Pink salmon index (millions)
1975	53.6				
1976	24.7				
1977	90.5	1974	108	114	52.2
1978	21.3	1975	78	213	61.3
1979	102.1	1976	32	26	64.0
1980	22.0	1977	29	10	52.1
1981	87.7	1978	182	32	68.8
1982	43.5	1979	220	89	60.2
1983	167.1	1980	150	76	100.0
1984	95.8	1981	7	38	98.5
1985	29.0	1982	52	2	96.4
1986	38.2	1983	24	53	48.2
1987	62.9	1984	84	330	45.1
1988	36.4	1985	11	87	54.7
1989	70.5	1986	13	7	56.1
1990	56.2	1987	147	41	57.3
1991	100.6	1988	47	34	71.5
1992	26.8	1989	87	61	62.0
1993	64.4	1990	18	204	70.2
1994	122.4	1991	22	30	78.9
1995	78.9	1992	42	17	90.5
1996	94.3	1993	30	10	96.9
1997	92.2	1994	100	15	90.0
1998	136.3	1995	60	27	107.3
1999	90.4	1996	66	0	106.3
2000	84.4	1997	2	7	82.8
2001	45.9	1998	6	12	66.5
2002	49.6	1999	78	108	56.5
2003	61.1				

Table 8. Escapement goals of Bristol Bay salmon stocks in terms of spawners per 1,000 km^2 of lake surface area. Escapement goals provided by Baker et al. (2006).

Stock	Lake area (km^2)	Escapement goal mid-point (millions)	Density (1000/km^2)	Upper escapement goal (milions)	Density (1000/km^2)
Kvichak (peak, pre-)	2889	8.00	2.77	10.00	3.5
Kvichak (off)	2889	6.00	2.08	10.00	3.5
Naknek	791	1.50	1.90	2.00	2.5
Egegik	1132	1.40	1.24	2.00	1.8
Ugashik	385	1.15	2.99	1.80	4.7
Wood R	425	1.10	2.59	1.50	3.5
Nush/Nuy	279	0.55	1.97	0.76	2.7
Igushik	74	0.33	4.39	0.45	6.1
Togiak	49	0.20	3.98	0.27	5.5
Avg. excl. Igushik & Togiak			2.17		3.11

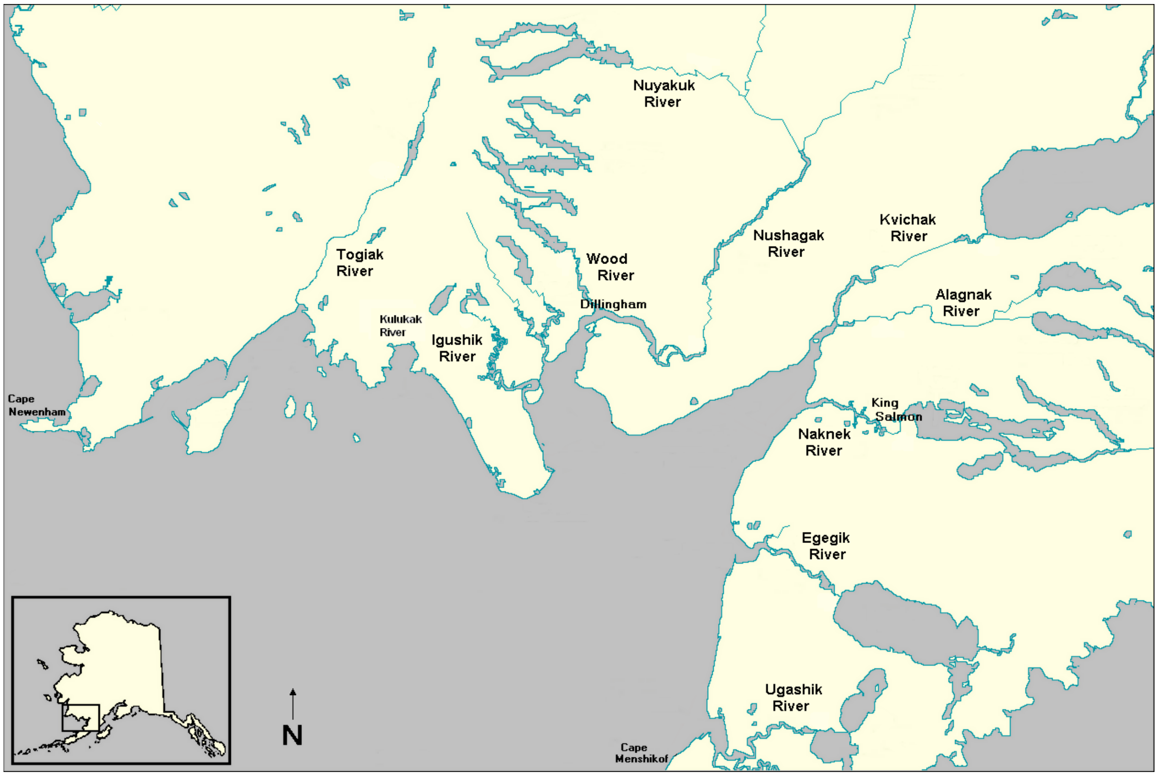

Fig. 1. Map of the Bristol Bay region showing the major salmon watersheds. Source: Fair et al. 2004.

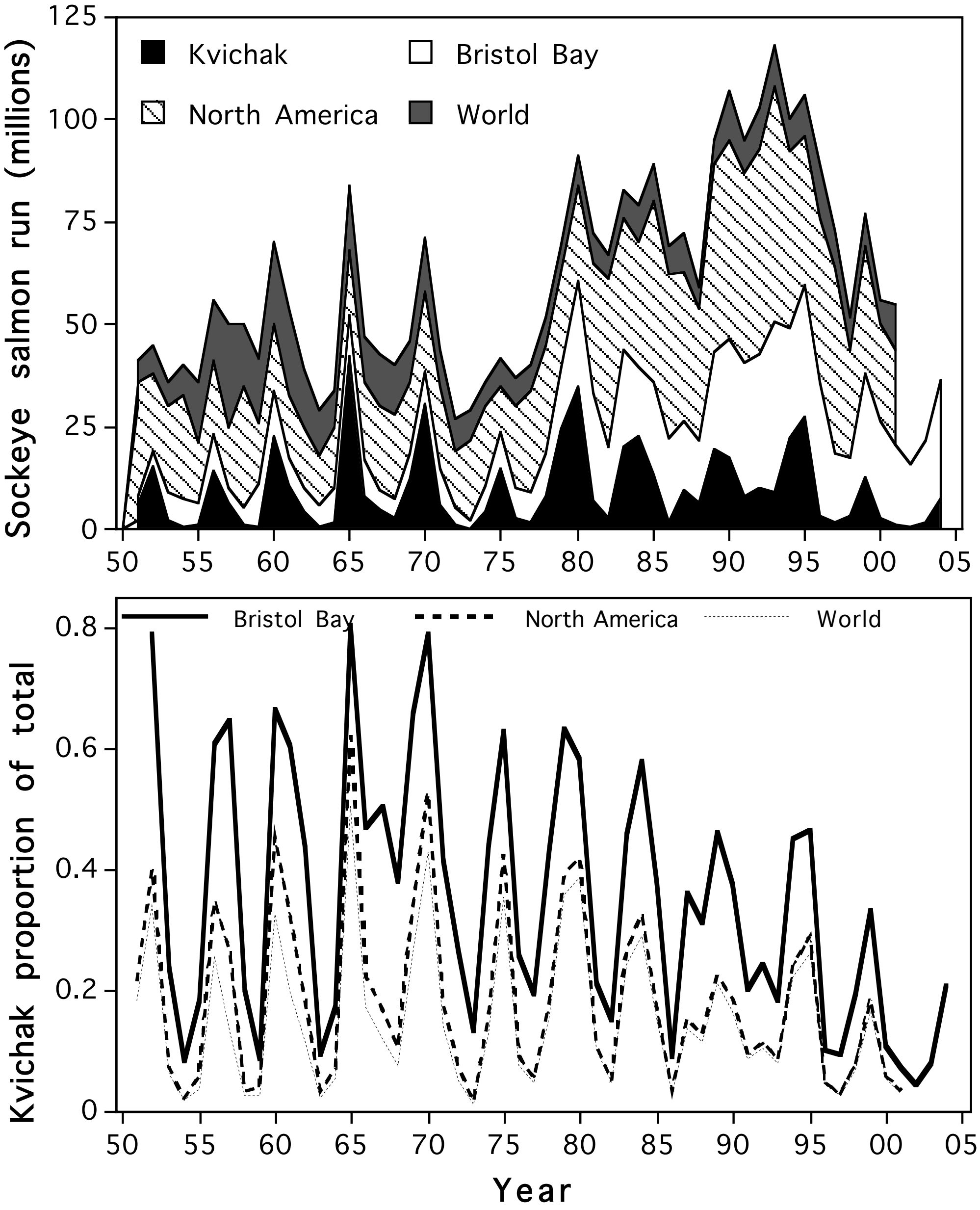

Fig. 2. Sockeye salmon runs returning to the Kvichak River, total Bristol Bay, North America, and the world (upper graph), and the corresponding proportion of total runs in each area represented by Kvichak salmon, 1952-2004 (some recent years missing). Values in upper graph are inclusive of runs from the smaller regions. Kvichak contributions to high seas fisheries (primarily prior to mid-1970s) were attributed to world catches, but not to Kvichak runs. Data sources: Rogers (2001) and ADFG statistics.

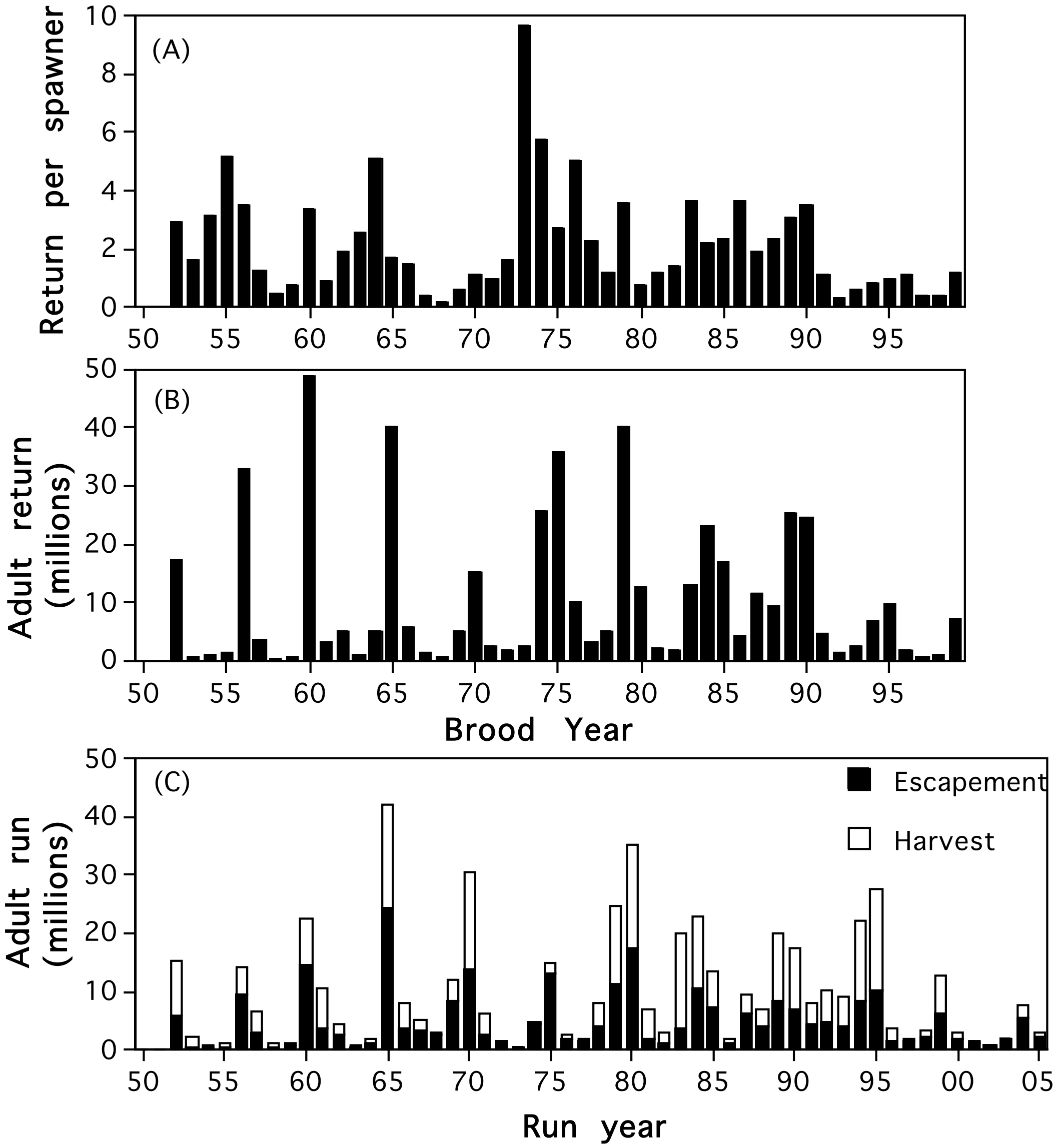

Fig. 3. Return per spawner (A), total return (B), and run size of Kvichak sockeye salmon (C), 1952-2005. Upper graphs arranged by parent spawning year (brood year), 1952-1999.

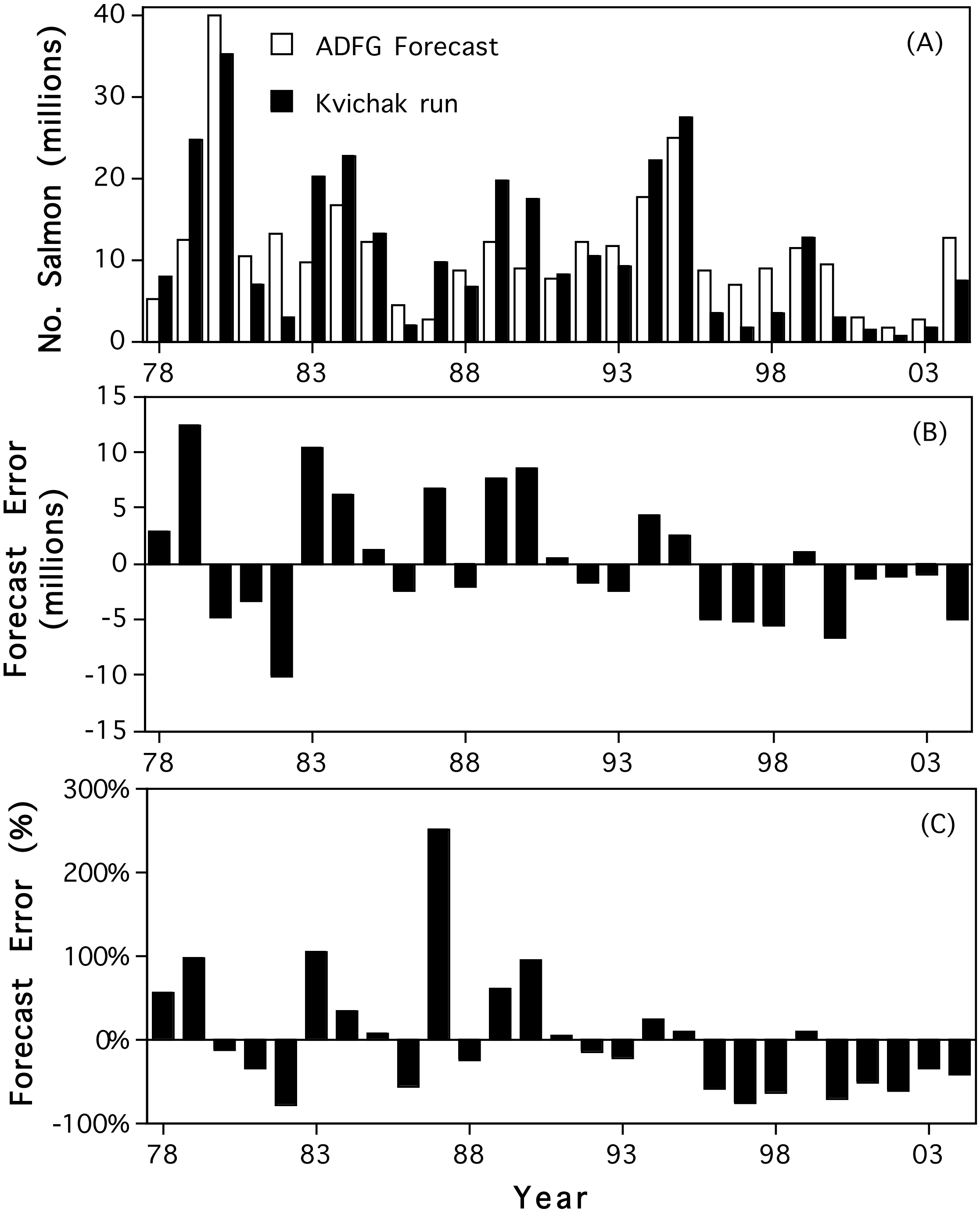

Fig. 4. Observed and predicted sockeye salmon runs to the Kvichak River (A) and associated forecast error (B, C), 1978-2004. Values based on inshore ADFG records.

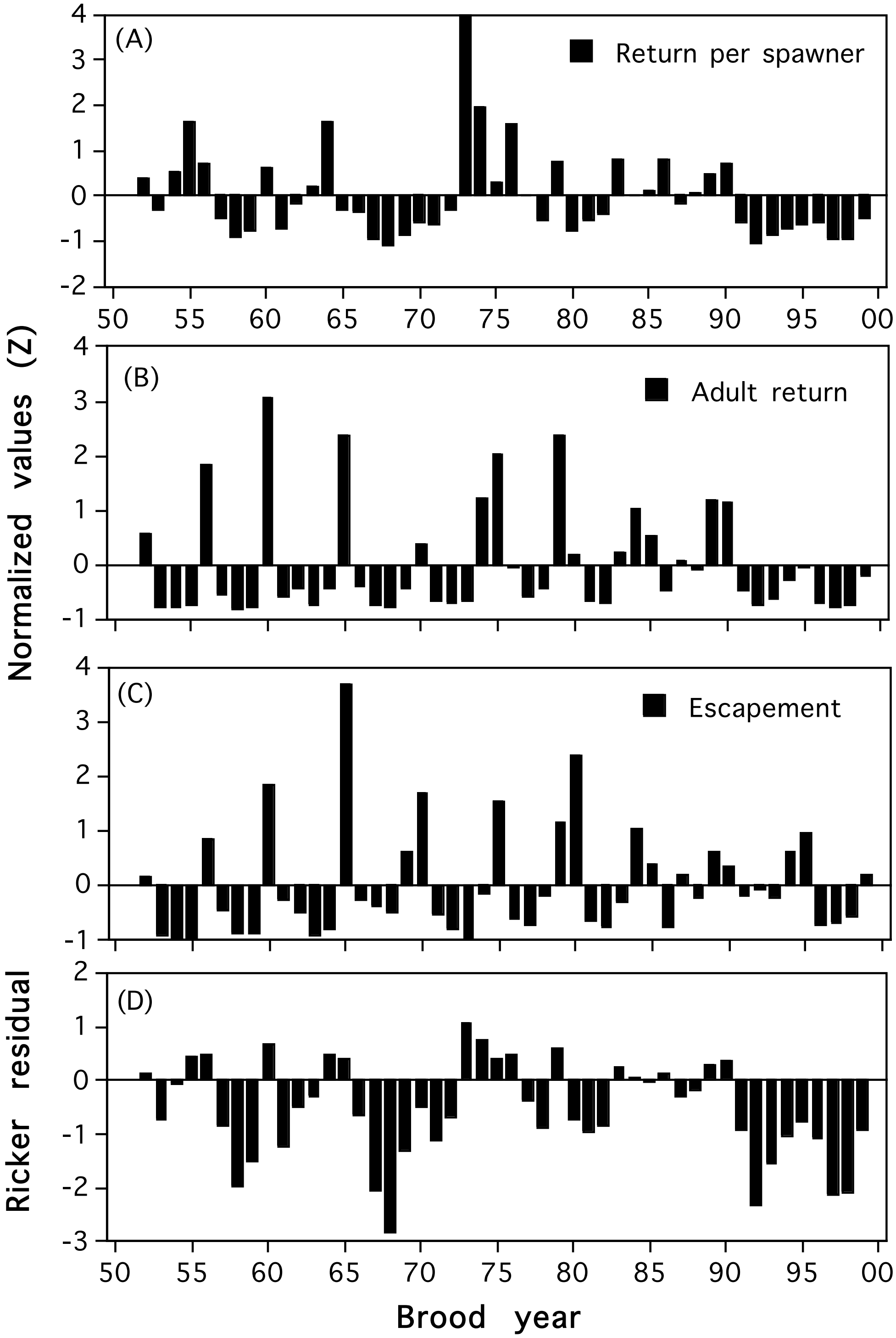

Fig. 5. Normalized values of Kvichak sockeye salmon return per spawner (A), adult return (B), and spawning escapement (C) during brood years 1952-1999, and the residual (Ln R/S) from the Ricker recruitment curve generated during brood years 1973-1990, a period of high production in Bristol Bay.

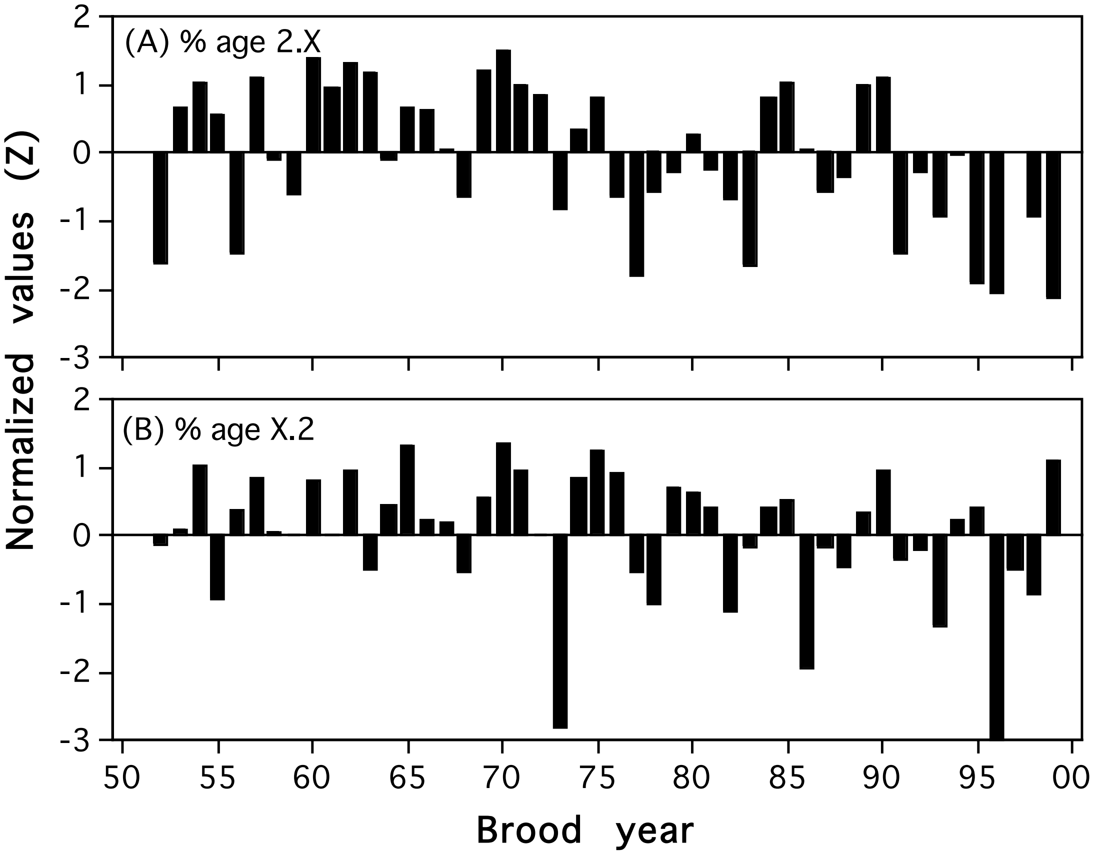

Fig. 6. Normalized values of Kvichak freshwater age composition (A) and ocean age composition (B) in the adult returns, 1952-1999.

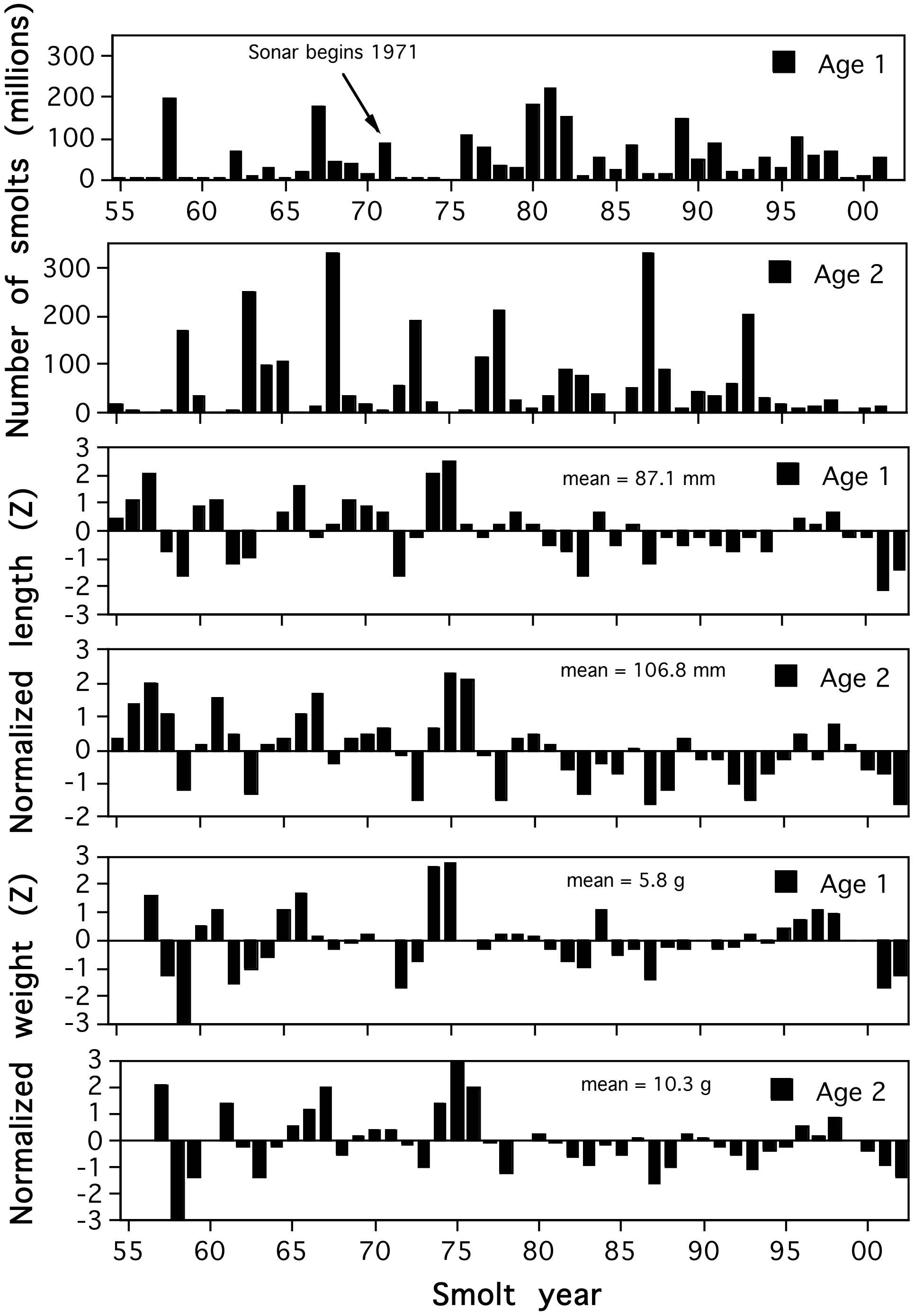

Fig. 7. Number of age-1 and age-2 Kvichak smolts, normalized values of age-1 and age-2 smolt length and normalized values of age-1 and age-2 smolt weight, 1955-2002. Values based on expanded fyke net catches until sonar deployed in 1971 (D. Rogers, University of Washington, pers. comm.; see Rogers and Poe 1984). Smolt abundance after 1994 based on Egegik smolt model.

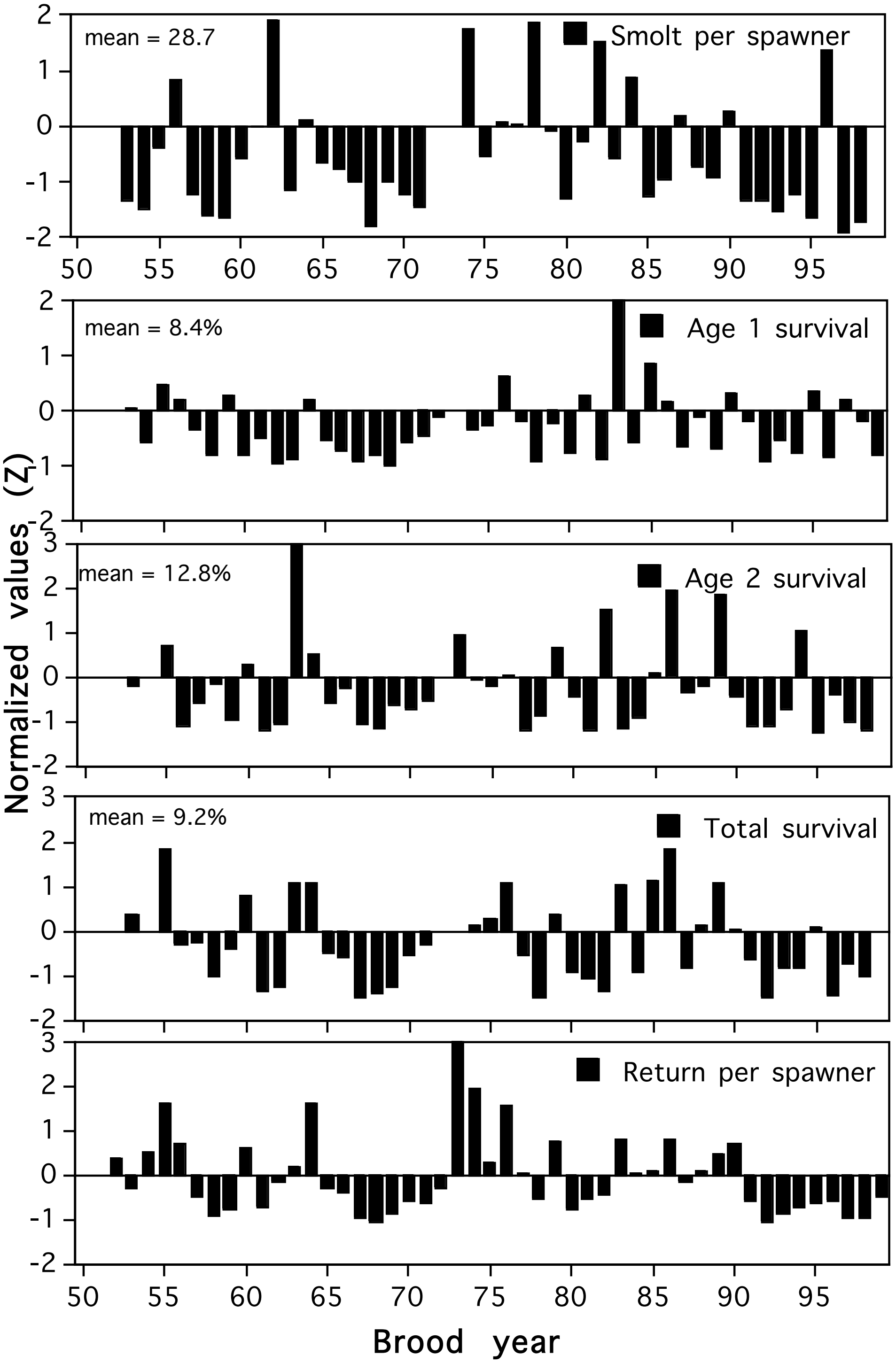

Fig. 8. Normalized values of smolts per spawner, age-1 smolt survival, age-2 smolt survival, total smolt survival, and adult return per spawner, brood years 1953-1999. Values are relative to observations during 1973-1990 (means are shown), a period of relatively high productivity. Smolt survival after 1994 smolt year based on smolts predicted from Egegik smolt model (see text).

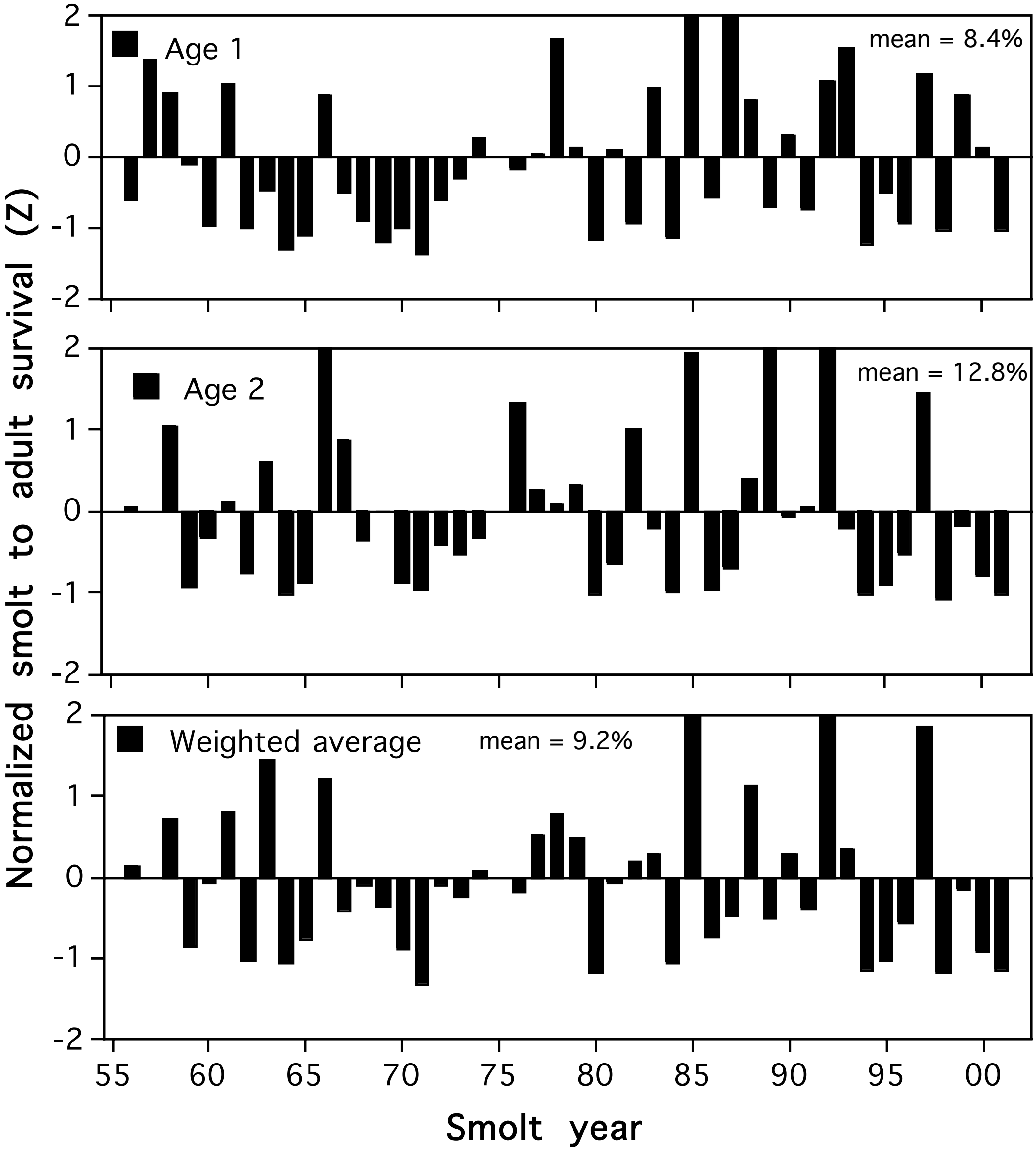

Fig. 9. Normalized values of smolt-to-adult survival of Kvichak sockeye salmon, 1955-2001. Values prior to 1971 were based on fyke net counts rather than sonar counts of smolts. All values are relative to mean values during 1971-1994 (means are shown). Values from 1995-2001 were based on smolts predicted from Egegik smolt model.

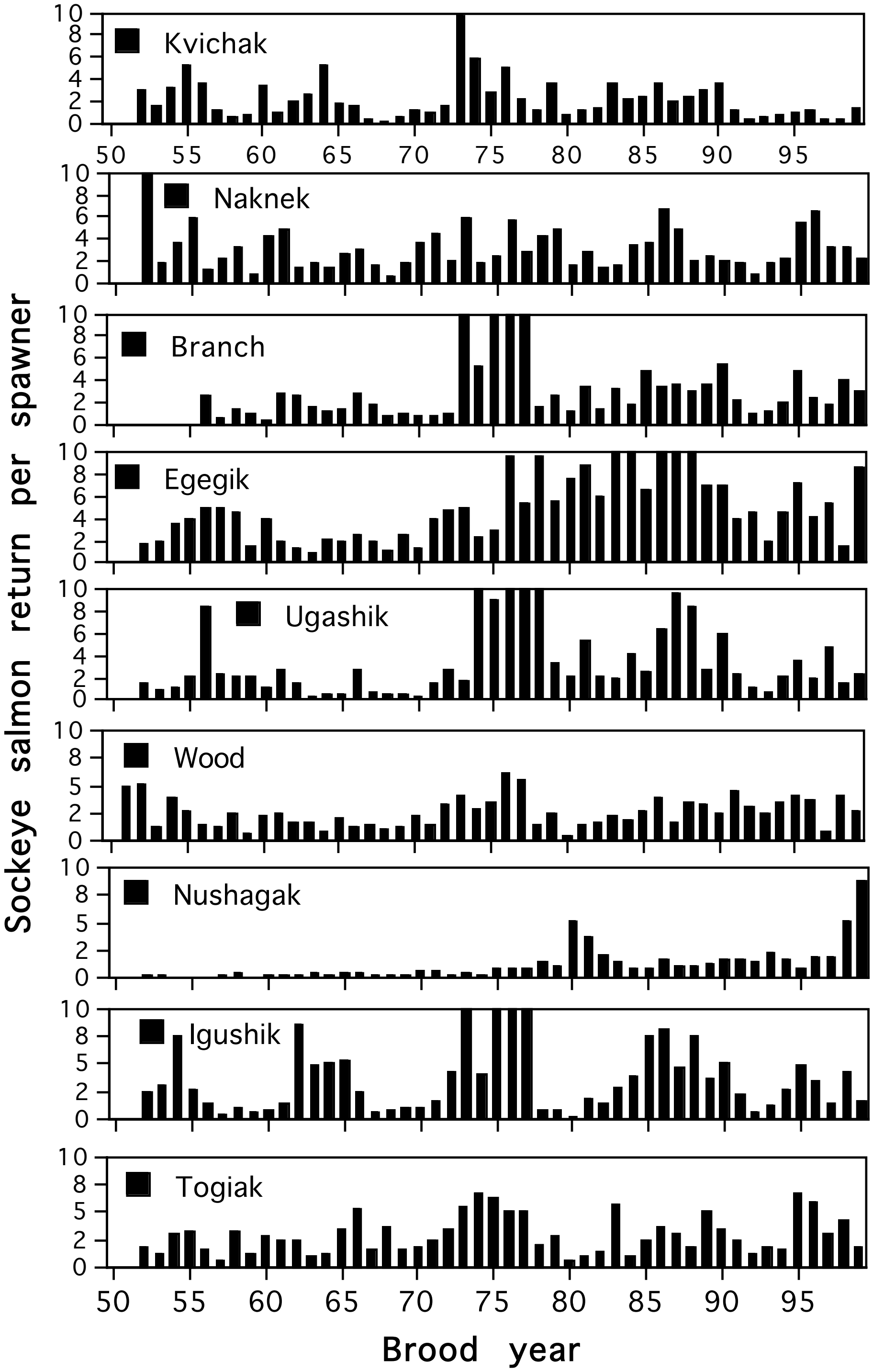

Fig. 10. Adult sockeye salmon return per spawner for each watershed in Bristol Bay, brood years 1952-1999.

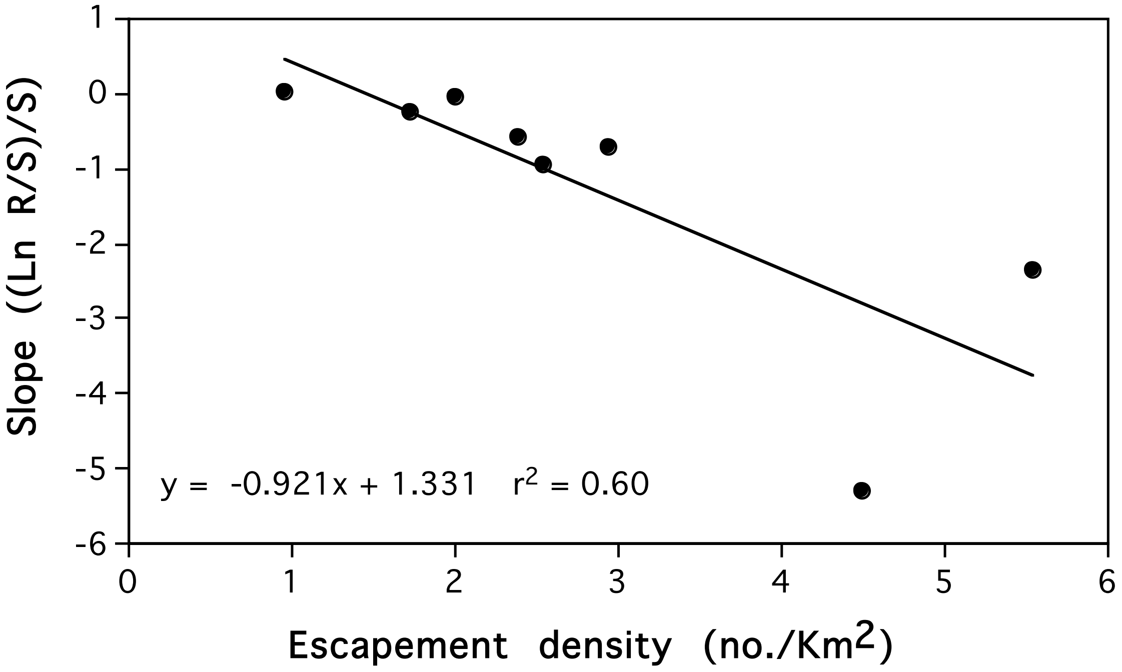

Fig. 11. Slope of linear form of Ricker recruitment curve regressed on mean spawning escapement density of eight Bristol Bay watersheds, 1973-1990. Relationship suggests density dependence increases with spawning density.

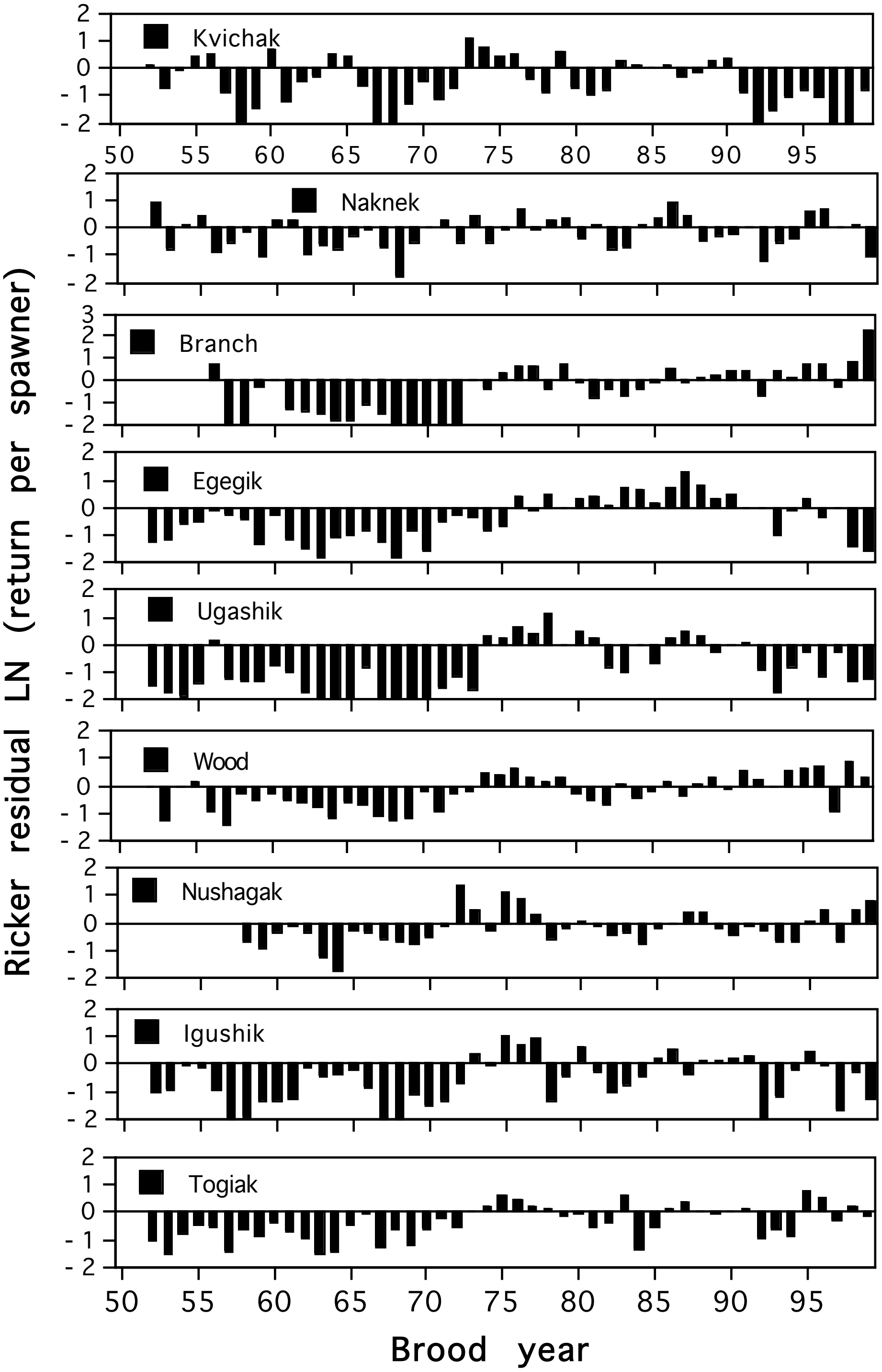

Fig. 12. Residuals from the Ricker recruitment curve of each Bristol Bay stock, 1952-1999. Recruitment curve based on data from 1973-1990, a highly productive period.

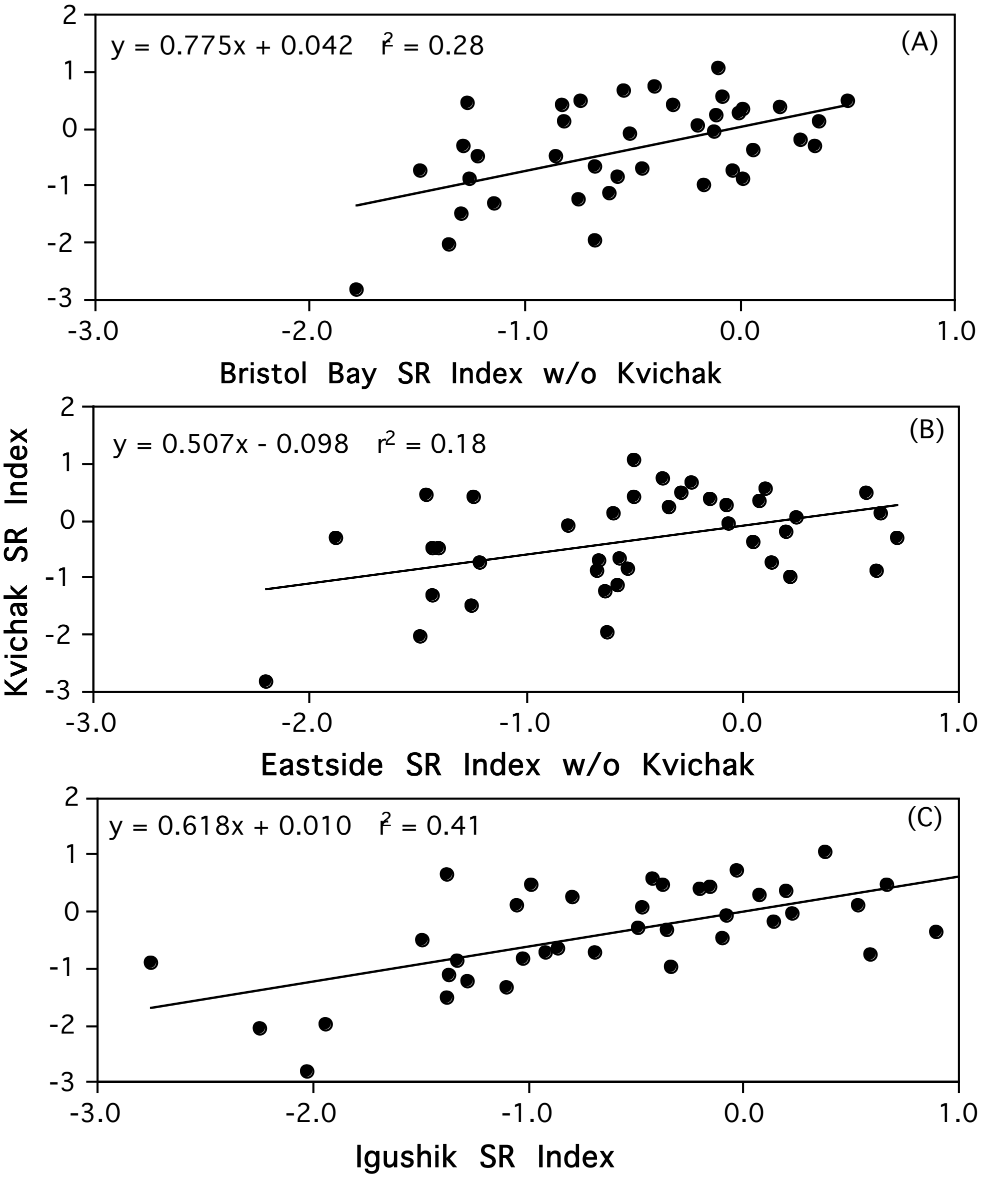

Fig. 13. Regression of Kvichak spawner-recruit index on (A) Bristol Bay SR index, (B) Eastside SR index, and (C) Igushik SR index, brood years 1952-1990. Area-wide SR indices did not include Kvichak salmon.

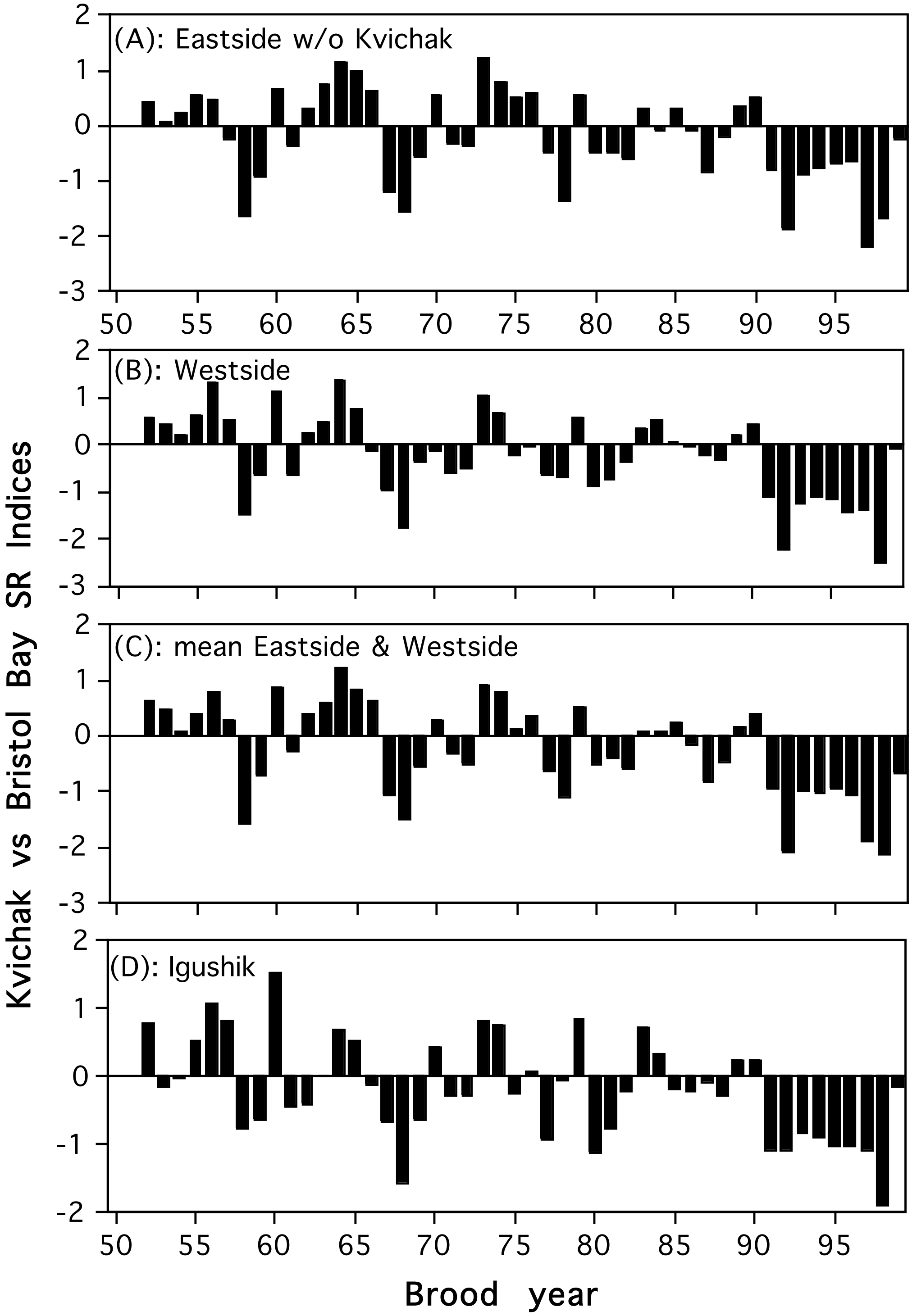

Fig. 14. Residuals of Kvichak spawner-recruit index regressed on spawner-recruit index of (A) Eastside stocks without Kvichak, (B) Westside stocks, (C) mean of Eastside and Westside stocks, and Igushik stock, 1952-1999. Regressions used to create residuals are shown in previous graph and were based on years 1952-1990.

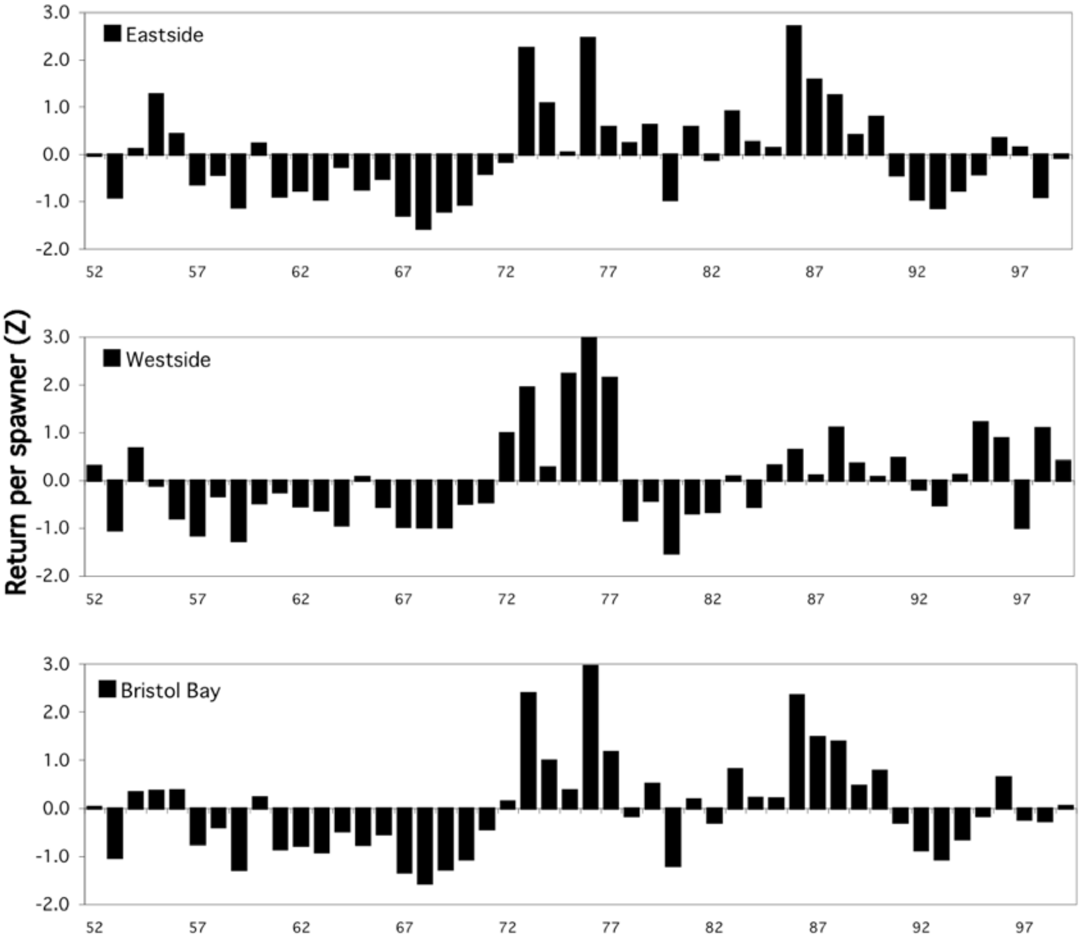

Fig. 15. Normalized return per spawner of sockeye salmon originating from Eastside, Westside, and all districts of Bristol Bay, brood years 1952-1999. Values were weighted by returns to individual districts.

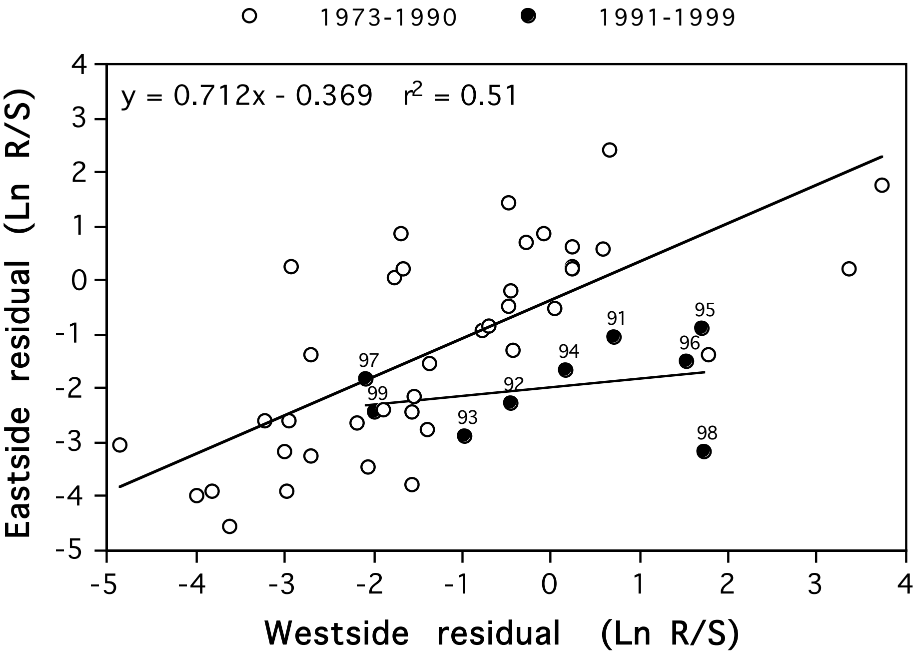

Fig. 16. Correlation of SR Index (Ricker recruitment residuals) for Eastside and Westside Bristol Bay sockeye salmon, brood years 1952-1990 vs. 1991-1999. Brood years are shown for the recent period. Similar relationship was observed when correlating adult return per spawner.

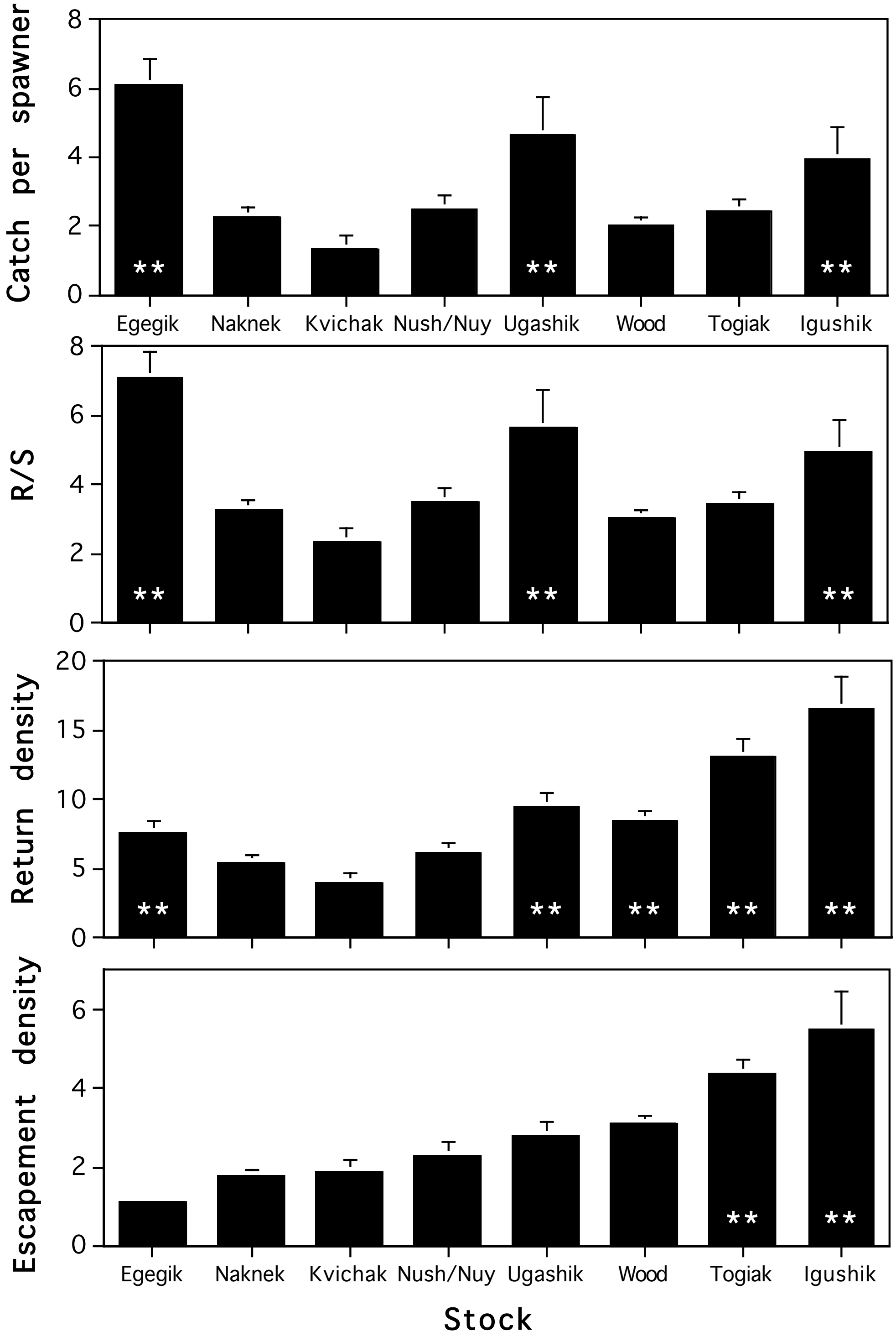

Fig. 17. Spawner density, adult return density, return per spawner, and catch per spawner of Bristol Bay sockeye salmon stocks, 1973-1999. Density is 1,000s of fish per km^2 of lake surface area. Values are mean ± 1 SE. Asterisk identify stocks that were statistically greater than Kvichak (ANOVA multiple range test, $P < 0.001$).

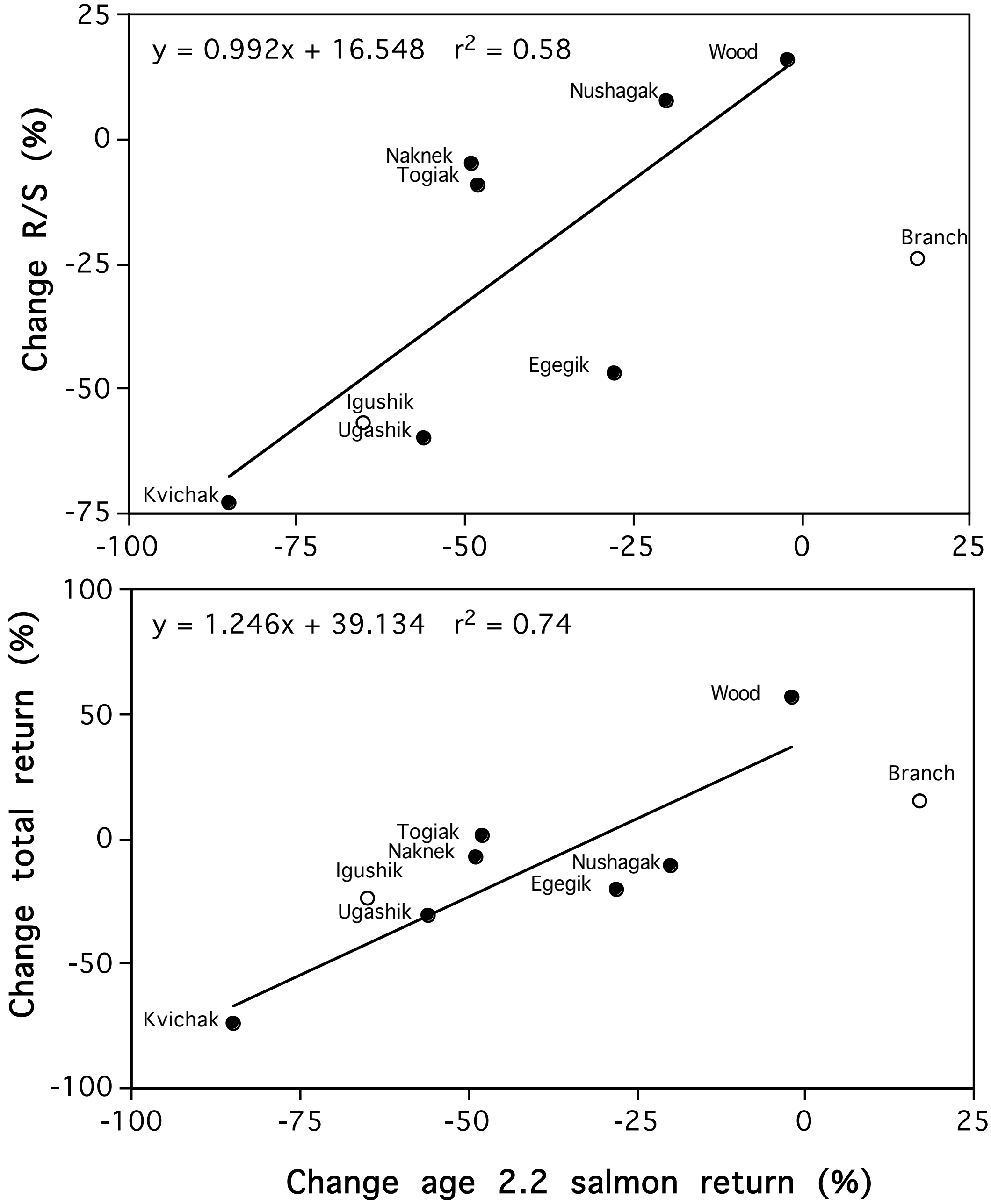

Fig. 18. Change in R/S and total adult return of sockeye salmon stocks from brood years 1973-1990 to 1991-1999 in relation to decline in numbers of age-2.2 salmon in the adult return. Annual R/S values excluded when parent spawning escapement was less than 30% of mean escapement because relatively low escapements tend to produce high R/S. Igushik and Branch stocks excluded from regression because values have higher uncertainty due to mixed stock fishery. Stocks are identified.

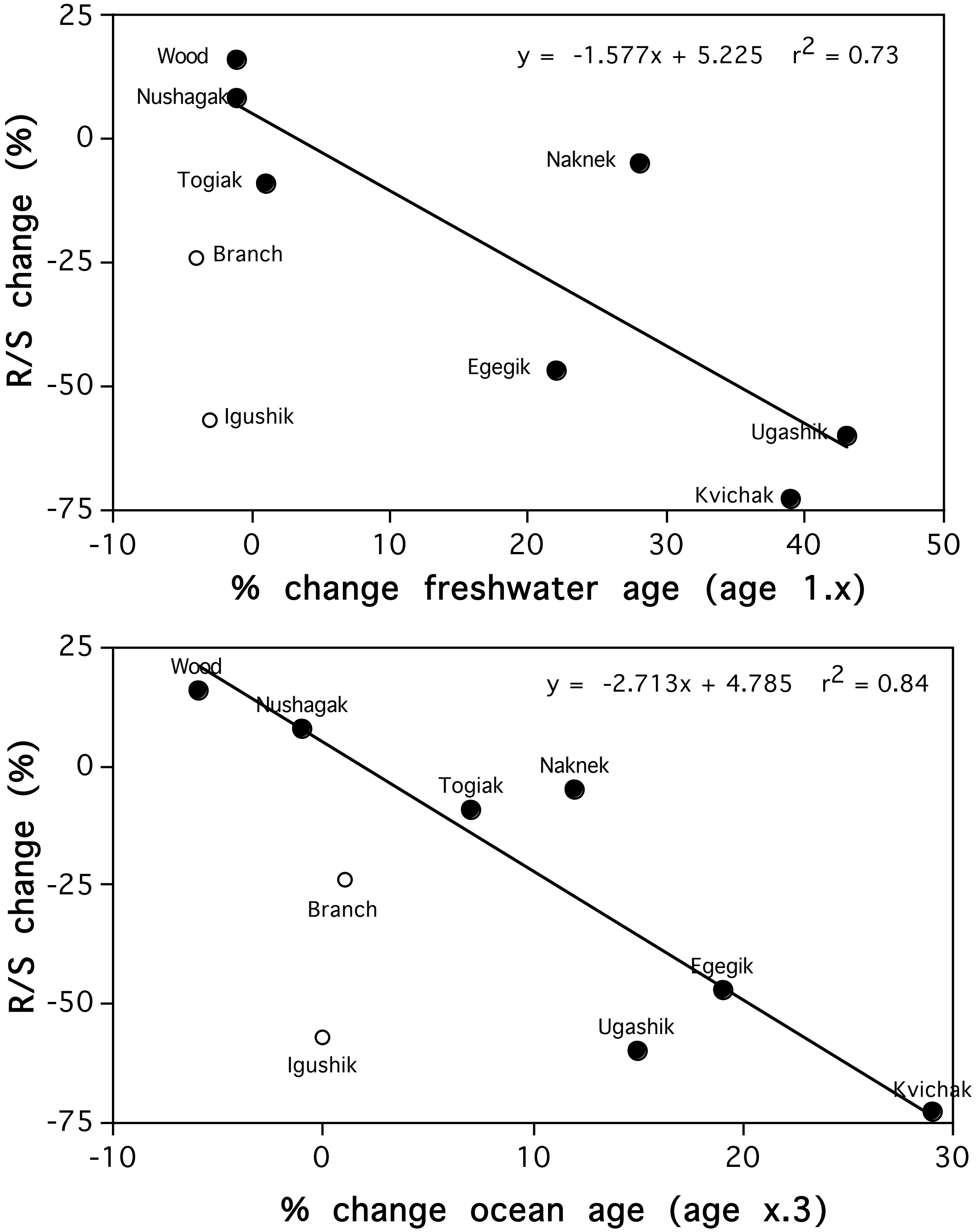

Fig. 19. Change in return per spawner (R/S) from 1973-1990 to 1991-1999 in relation to the change in age-1.x (freshwater age) and age-x.3 (ocean age) in adult returns of each major stock in Bristol Bay. Annual R/S values excluded when parent spawning escapement was less than 30% of mean escapement because relatively low escapements tend to produce high R/S. Igushik and Branch stocks excluded from regression because values have higher uncertainty due to mixed stock fishery.

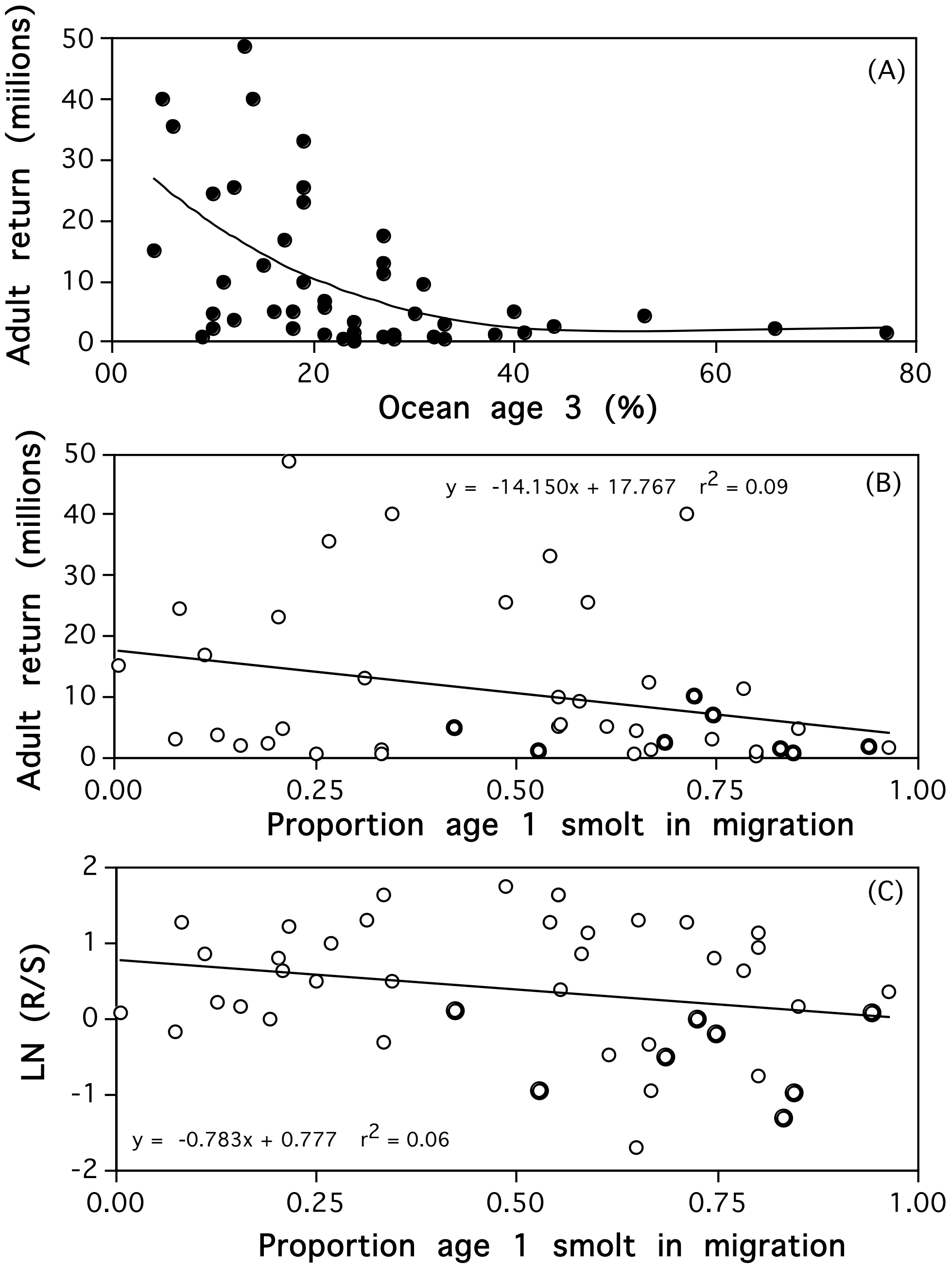

Fig. 20. Relationship between Kvichak adult salmon returns and (A) the percentage of ocean age-3 salmon in the return, (B) the percentage of age-1 smolts in the migration, and (C) productivity of Kvichak salmon (Ln R/S) in relation to percentage of age-1 smolts that produced the return, brood years 1952-1998. Brood years 1991-1998 are highlighted.

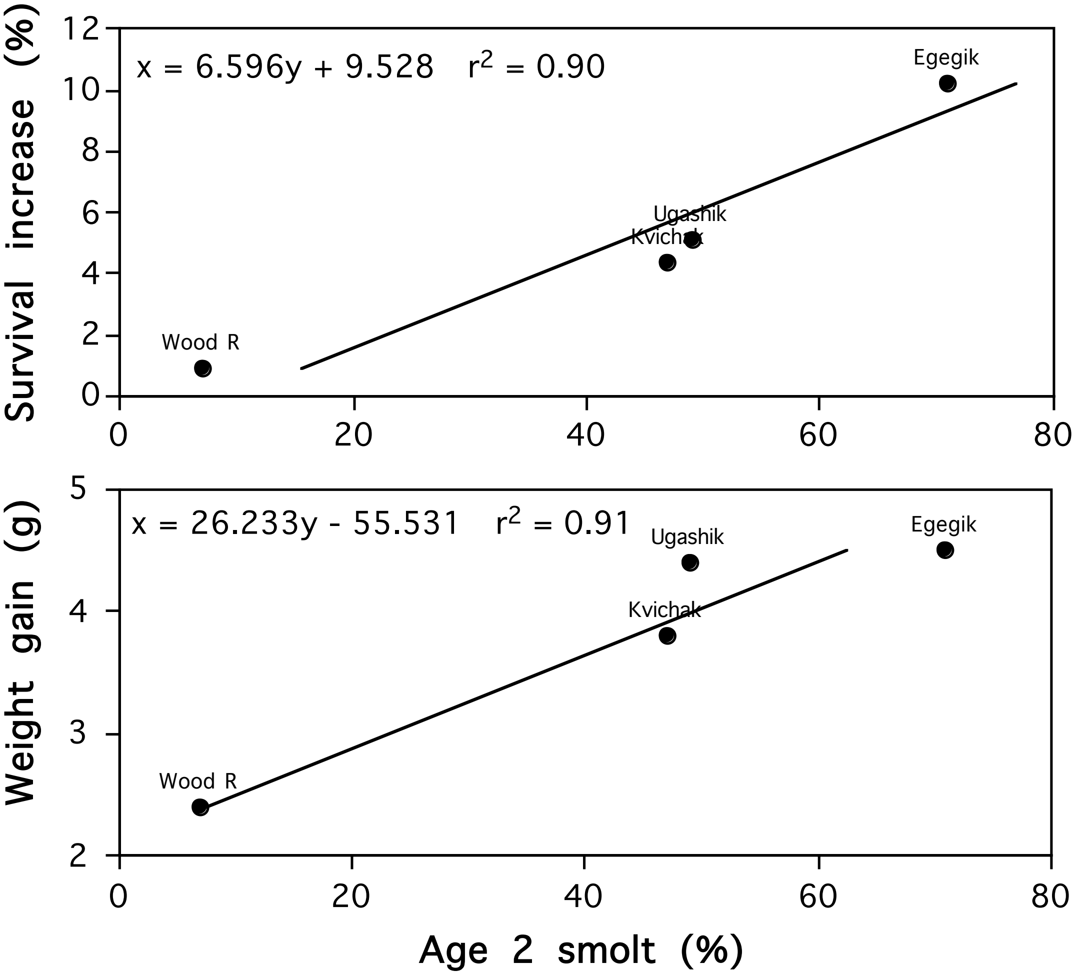

Fig. 21. Mean weight gain and geometric mean marine survival benefit of staying in freshwater for additional year in relation to the mean percentage of age-2 smolts in the migration. Stocks are identified. See Table 3 for data.

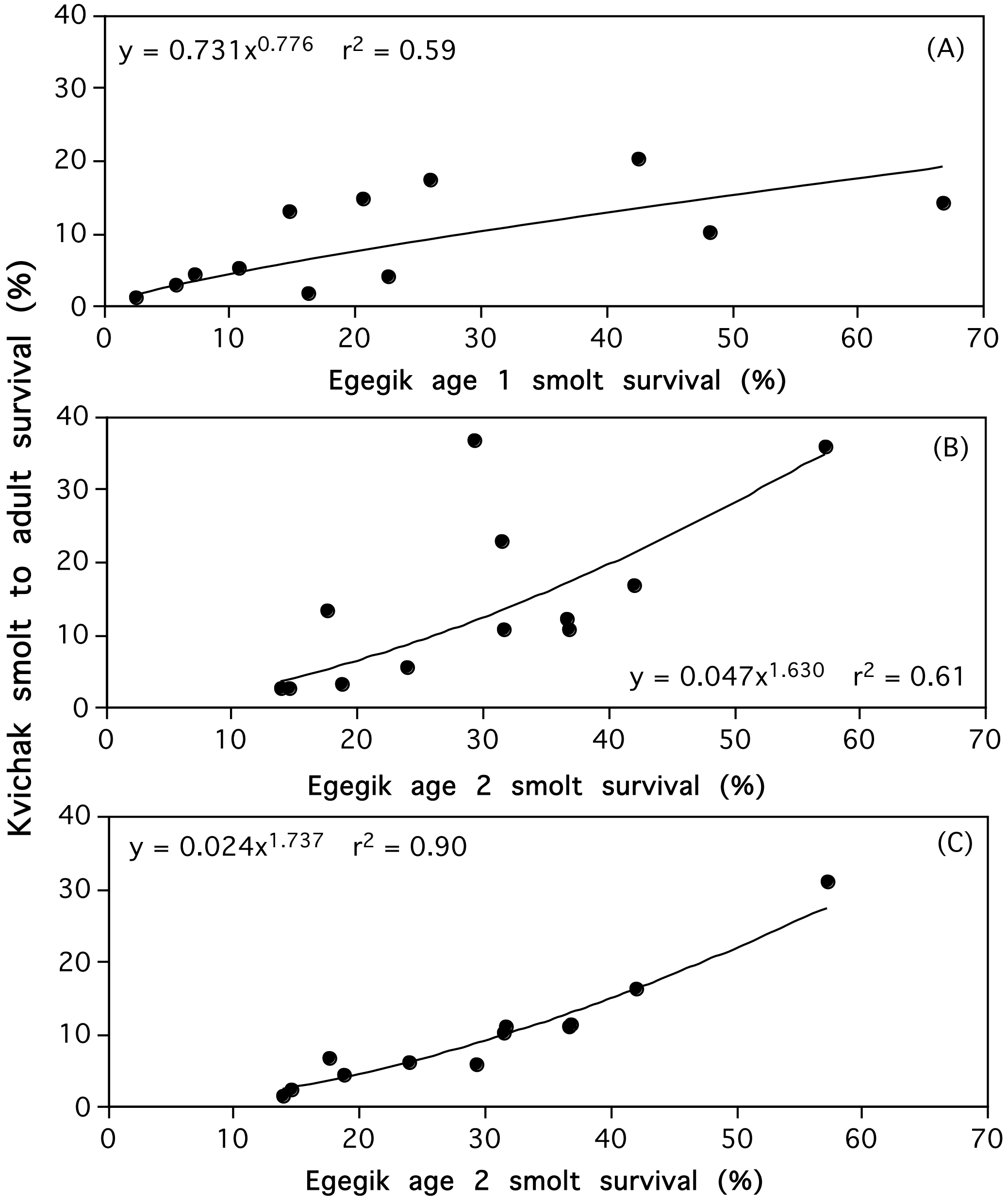

Fig. 22. Survival of age-1 smolts (A), age-2 smolts (B), and total Kvichak salmon smolts (C) in relation to survival of Egegik salmon smolts during the same year of migration, 1982-1994. Data after 1994 excluded because Kvichak smolt counter was in error. The 1985 smolt year was excluded because it was obvious outlier (Kvichak smolt survival: age-1: 47%, age-2: 32%).

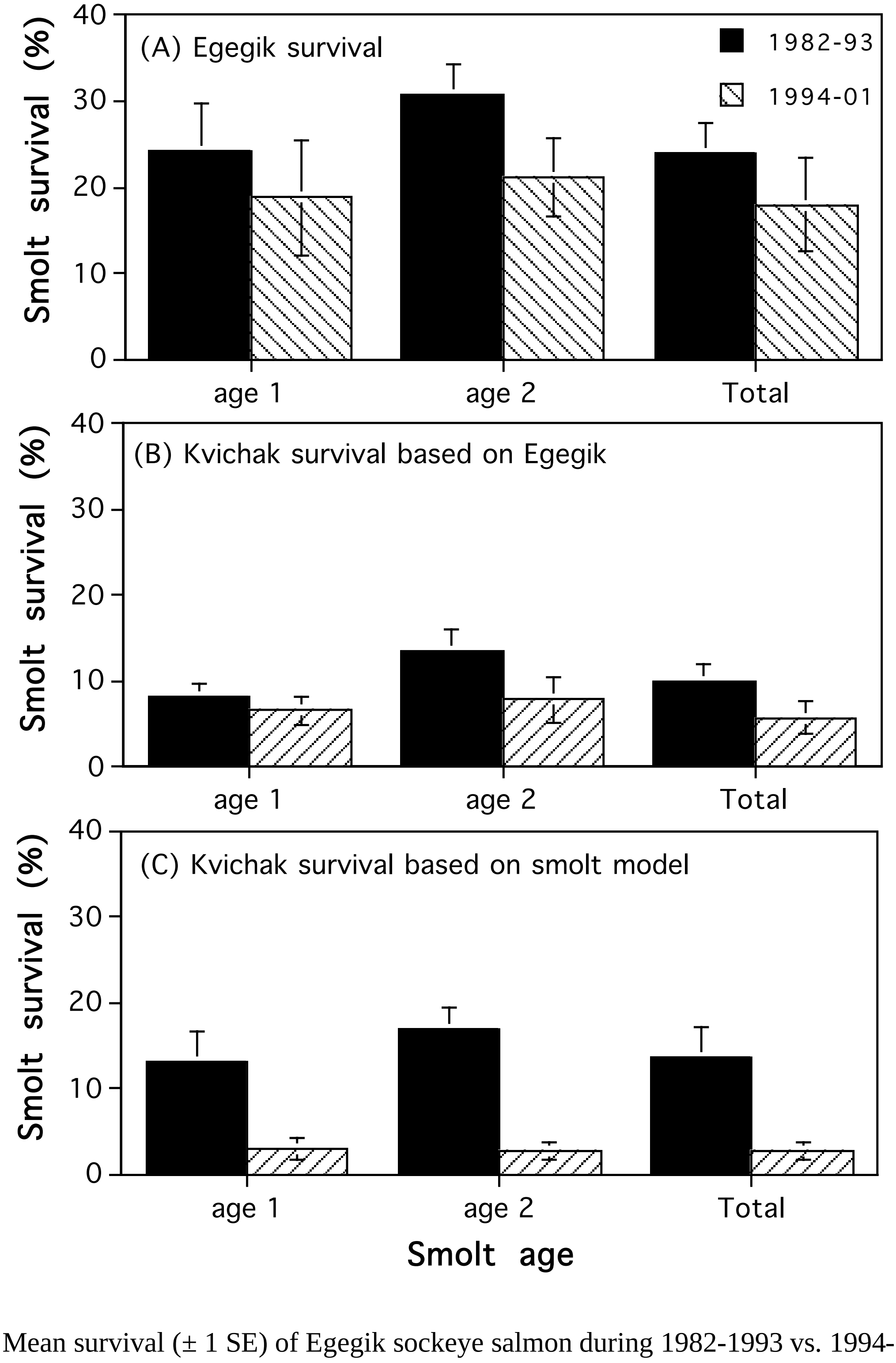

Fig. 23. Mean survival (± 1 SE) of Egegik sockeye salmon during 1982-1993 vs. 1994-2001 smolt years (A), and estimates of Kvichak smolt survival based on (B) regression of Kvichak survival on Egegik survival (see previous graphs), and (C) Kvichak smolt survival based on predicted smolt estimates and observed adult returns. Reported Kvichak survival shown for smolt years prior to 1995.

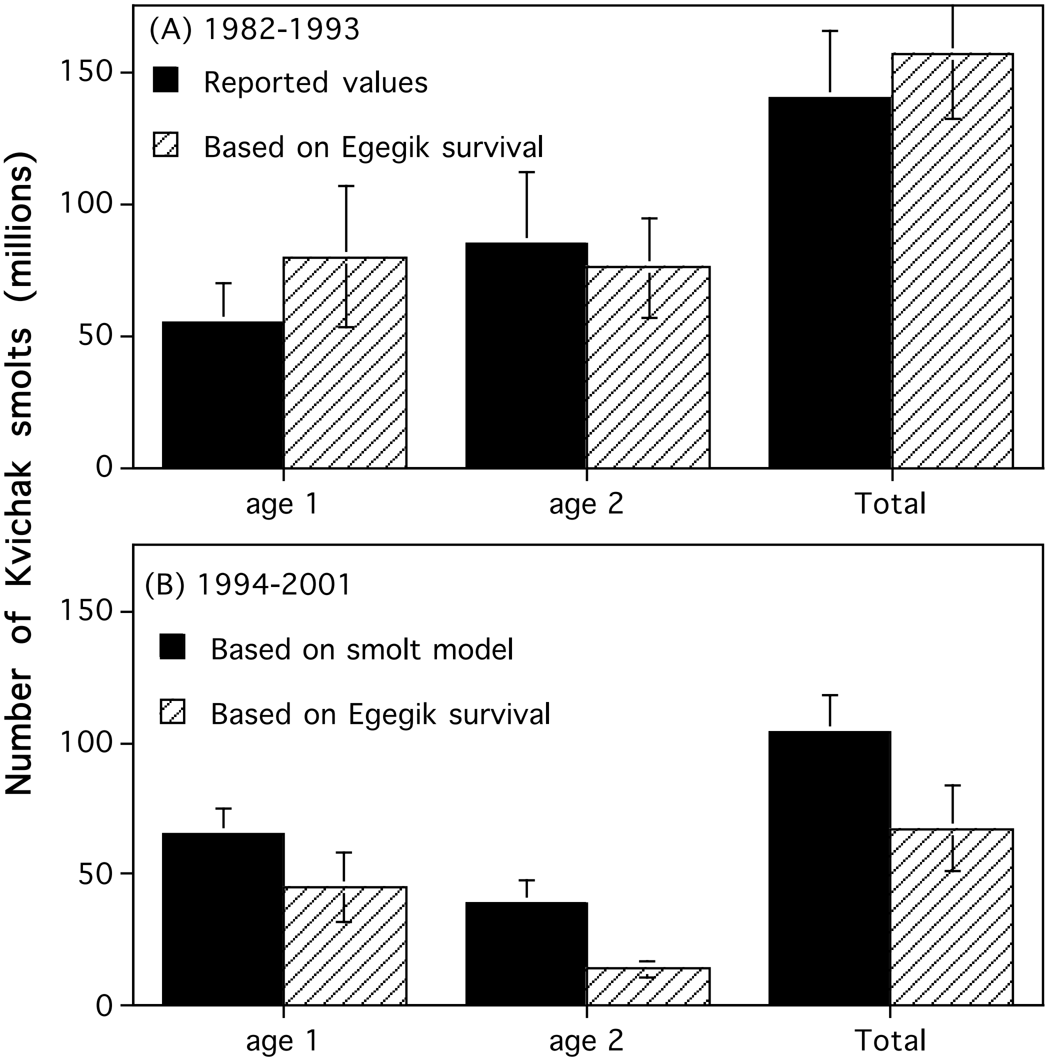

Fig. 24. Mean numbers of Kvichak sockeye salmon smolts (± 1 SE) during 1982-1993 (A) and 1994-2001 smolt years (B). Values based on reported (1982-1993) or smolt model counts (1994-2001) (black bar) and back-calculation from predicted Kvichak smolt survival and observed age-specific adult returns (white bar).

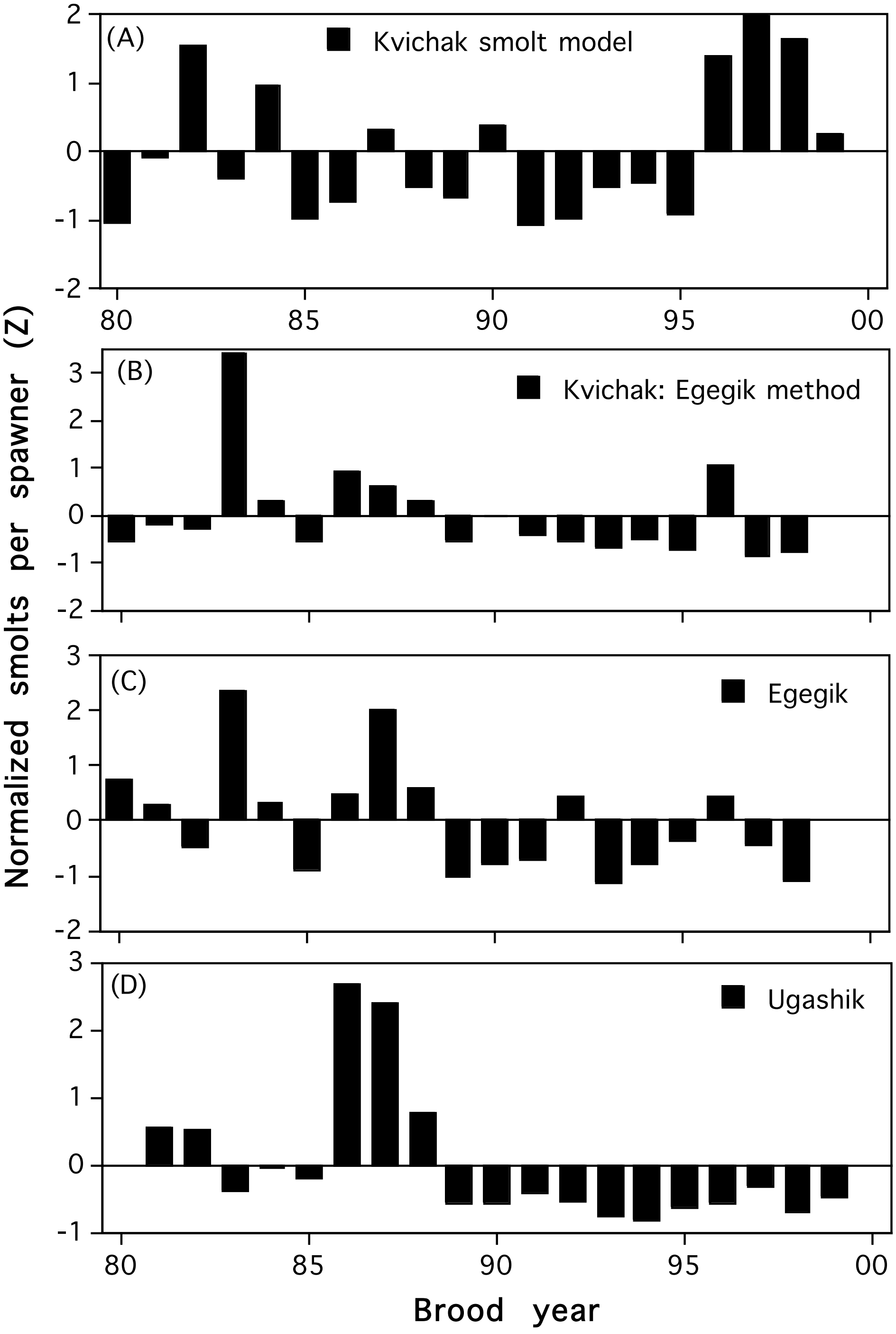

Fig. 25. Normalized smolts per spawner of Kvichak smolts based on the smolt model and reported smolt counts (A), Kvichak smolts based on back calculations from Egegik ocean survival (B), Egegik salmon (C), and Ugashik salmon (D), 1980-1999. No values for Egegik in 1999 because the Egegik smolt project was terminated in 2001.

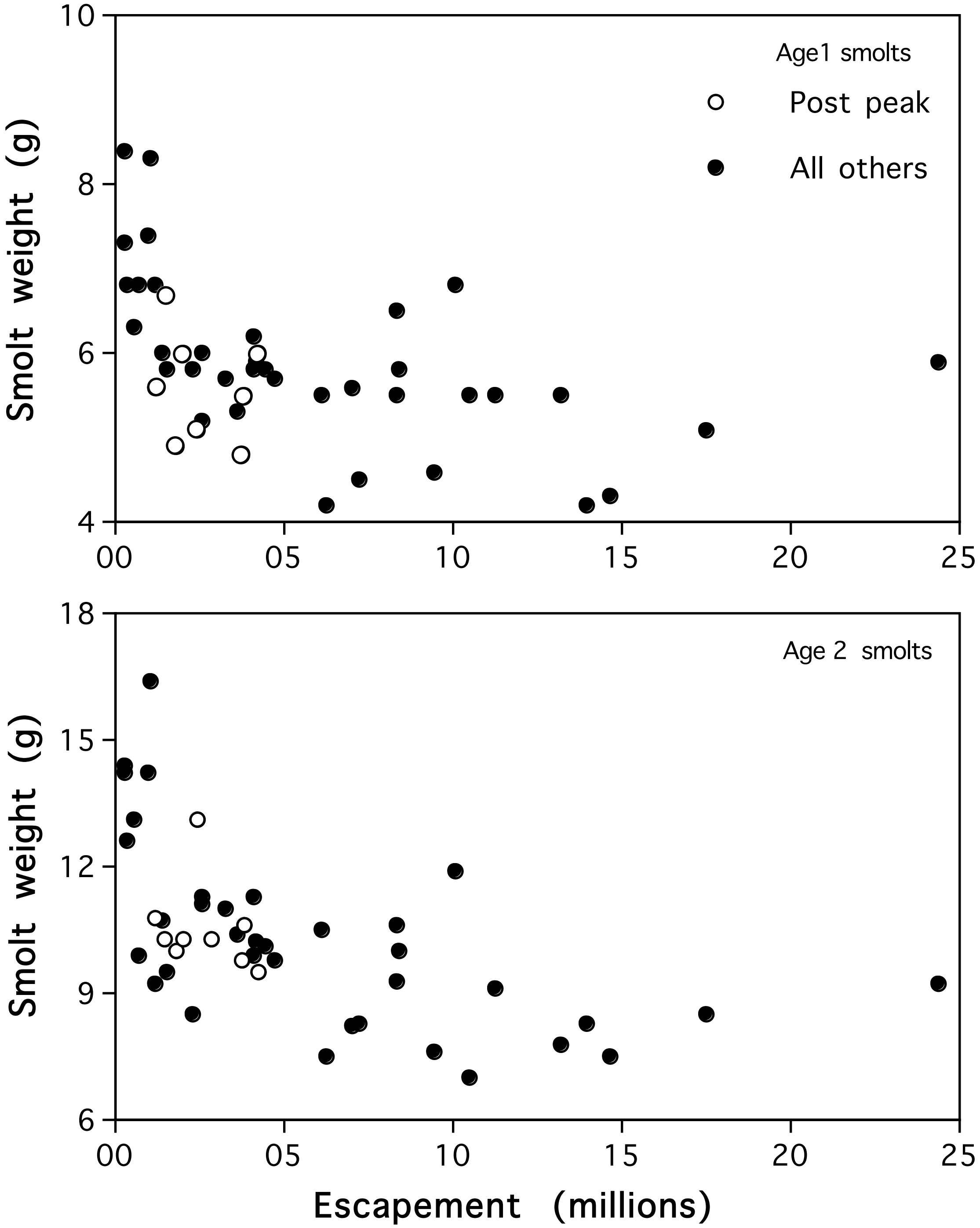

Fig. 26. Relationship between age-1 and age-2 smolt weight and numbers of Kvichak parent spawners, brood years 1954-1999.

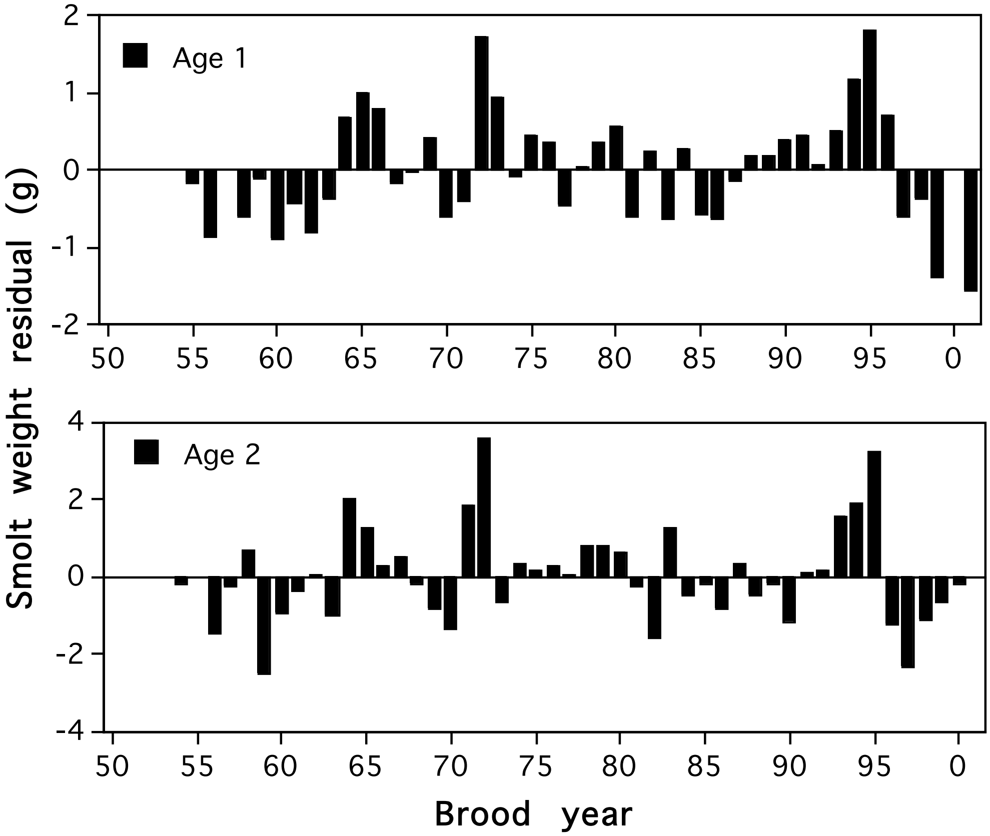

Fig. 27. Time series of Kvichak smolt weight residuals from statistical models based on brood years 1954-1990. Models are shown below. Air temperature is deviation during second winter through summer.

Age-1 wt (g) = 6.71 - .554 (Ln parent spawners) - .052 (previous-year spawners), $R^2 = 0.63$.

Age-2 wt (g) = 11.678 - 1.153 (Ln parent escapement) -.464 (air temperature), $R^2 = 0.72$

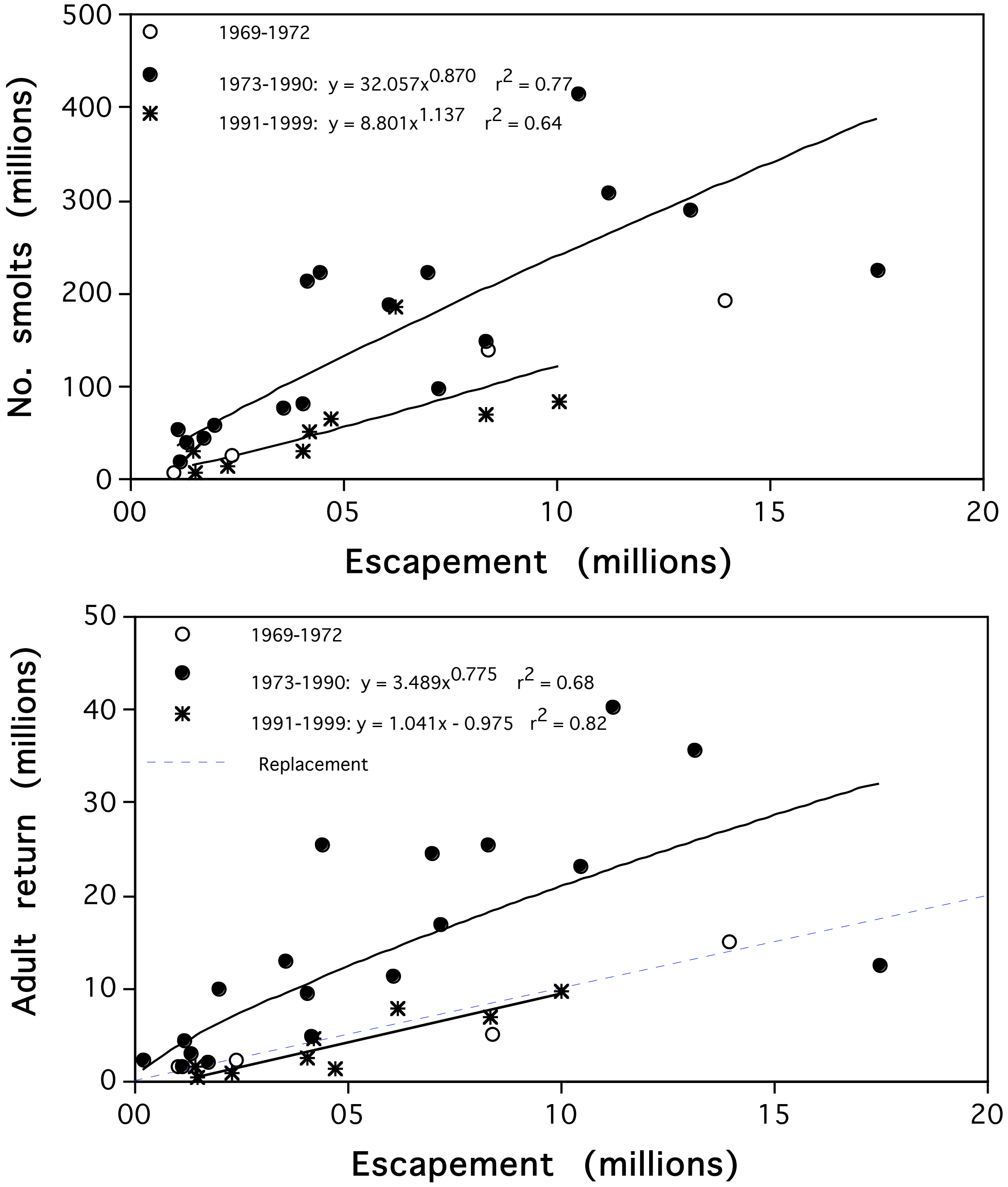

Fig. 28. Number of smolts and adult returns of Kvichak sockeye salmon produced by parent spawners during brood years 1969-1999. Regression curves are shown for 1973-1990 and 1991-1999 time periods. The line in which adult returns replace parent escapement is shown.

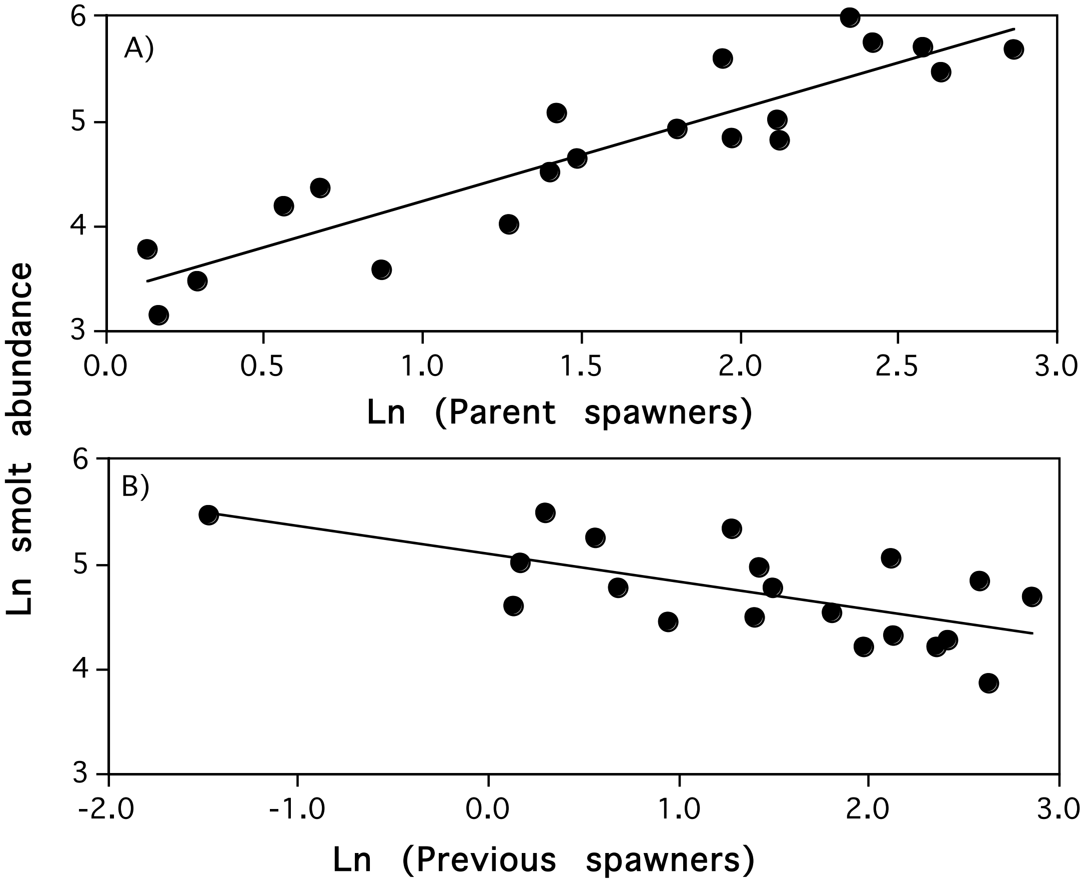

Fig. 29. The effect of parent spawners (A) and previous-year spawners (B) on total smolt abundance, brood years 1969-1990, i.e., years when smolts were estimated by sonar. Smolt abundance values are partial residuals (Larsen and McCleary 1972) produced from the following multivariate equation:

Ln Smolts (millions) = 3.725 + .879 (Ln parent spawners) – .263 (Ln previous-year spawners),

n = 20, $R^2 = 0.82$, overall $P < 0.001$, P (parent spawners) < 0.001, P (previous-year spawners) = 0.004), serial autocorrelation = -0.13 ($P > 0.05$).

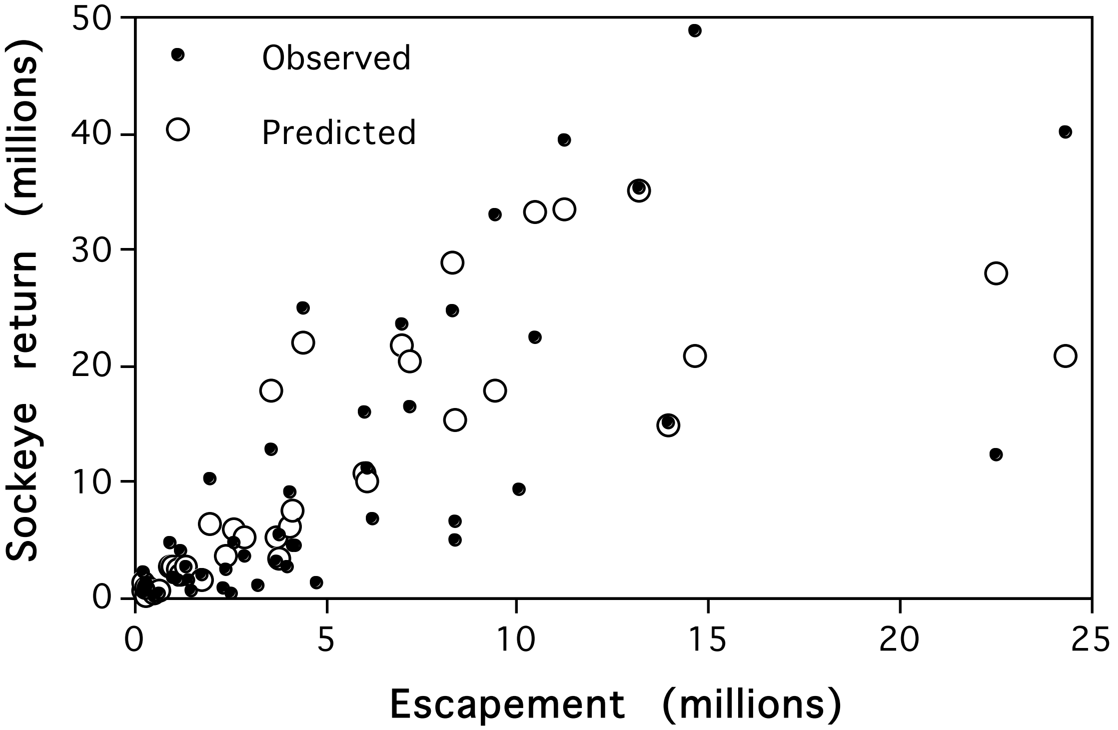

Fig. 30. Plot of observed and predicted adult sockeye recruits to Kvichak River, 1952-1990. Predicted values based on the following multivariate model:
$R_i = S_i \exp\left(1.139 - .0000514 S_i - .0000415 S_{i-1} - .964 I + .703 P + \varepsilon\right)$

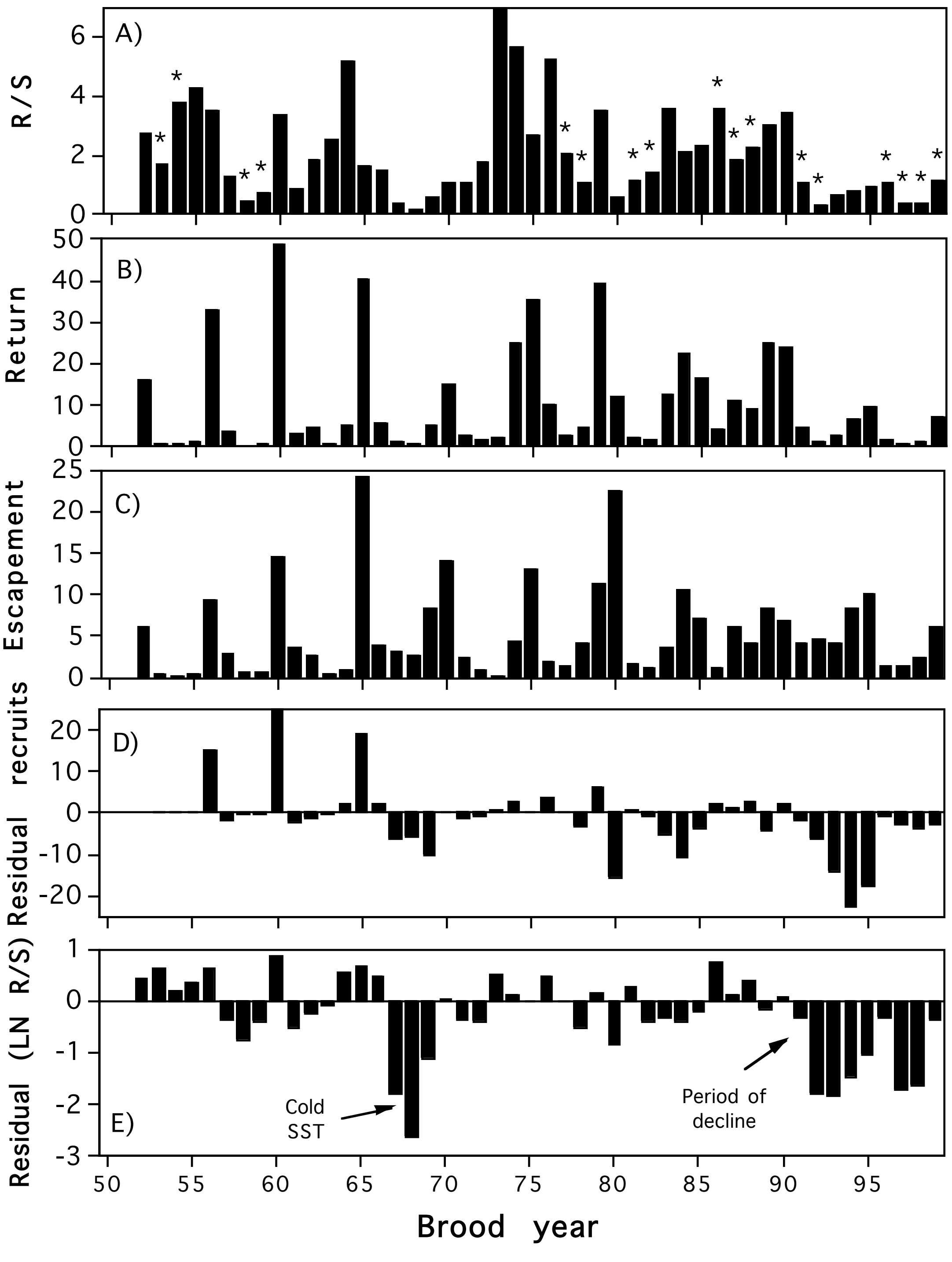

Fig. 31. Comparison of observed Kvichak R/S (A), adult return (B), parent escapement (C), recruitment residuals of the multivariate recruitment model (D): $R_i = S_i \exp\left(1.139 - .0000514S_i - .0000415S_{i-1} - .964I + .703P + \varepsilon\right)$, and productivity residuals (LN R/S) of the multivariate model. Asterisks indicate years in which Egegik and Ugashik returns were more than twice that of Kvichak salmon. All values are in millions of sockeye salmon except for R/S values.

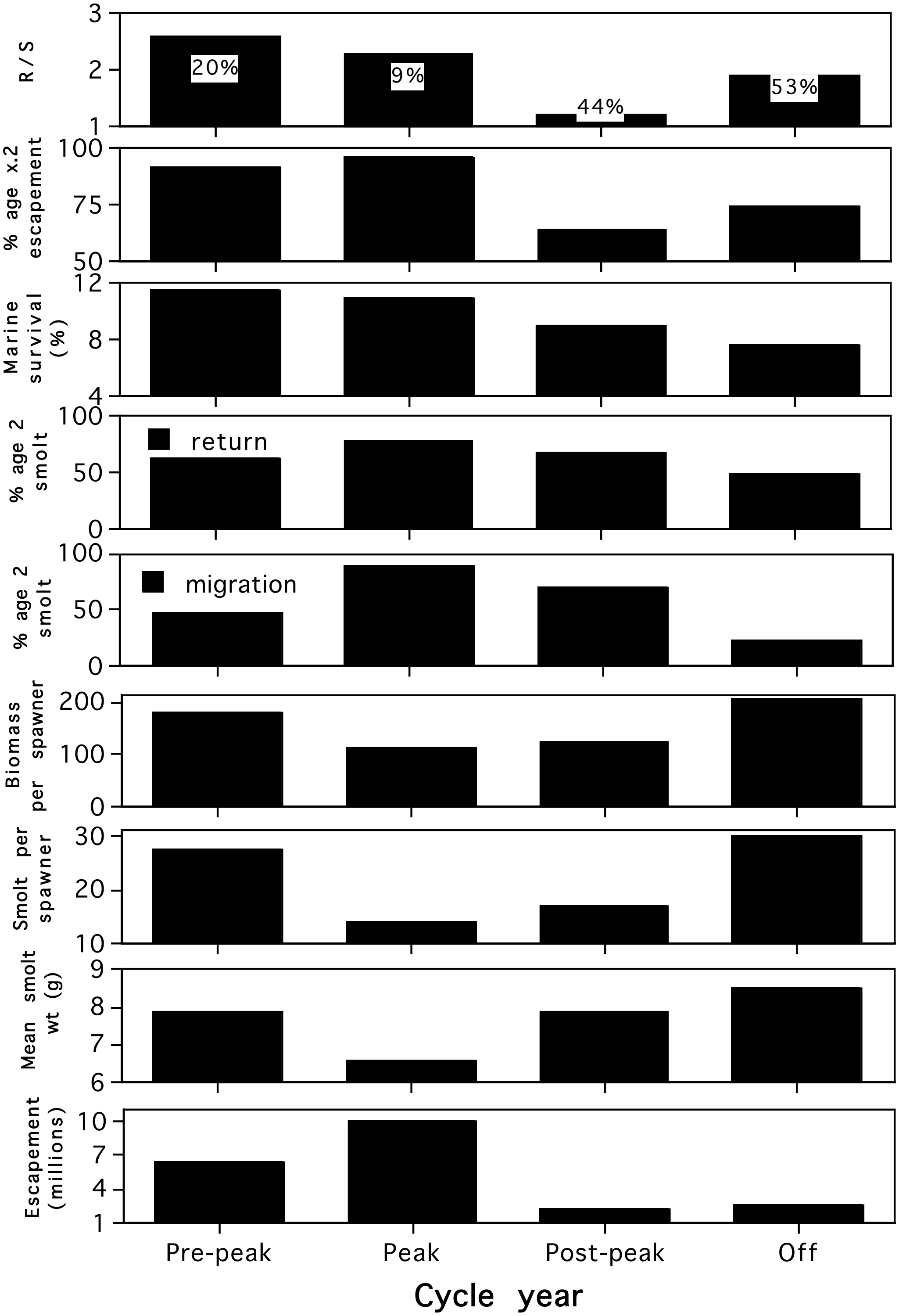

Fig. 32. Median population and productivity characteristics of Kvichak cycle years, 1952-1999. Values involving smolt abundances exclude brood years 1992-1999 and years prior to sonar smolt counts. Percentage of years when Egegik and Ugashik return exceeded 2x Kvichak return are show in top graph.

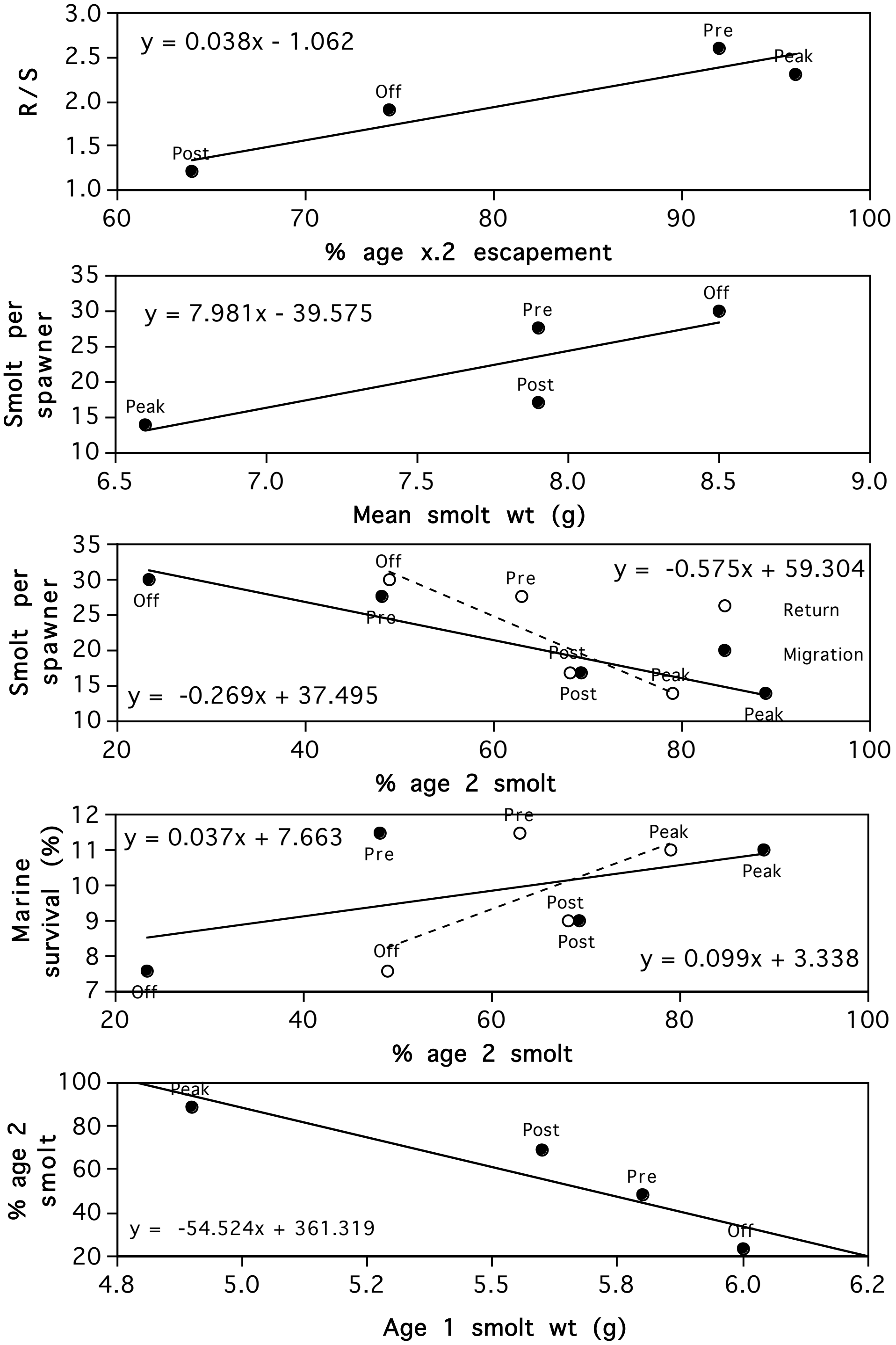

Fig. 33. Relationships between median cycle year productivity estimates (pre-peak, peak, post-peak, and off-cycle years) and smolt or escapement characteristics of the cycle.

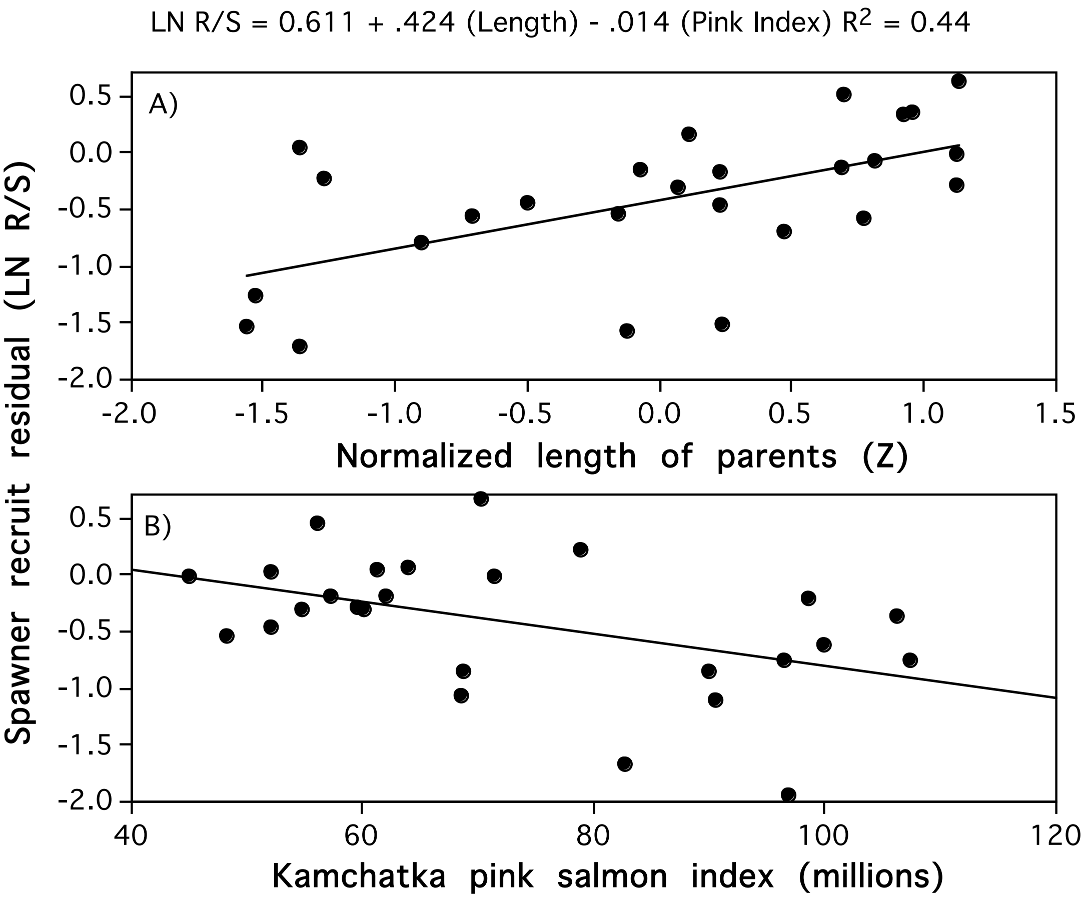

Fig. 34. Multivariate analysis of residuals from the Kvichak spawner-recruit brood interaction model (equation 6) regressed on (A) mean parent length at age, and (B) an index of adult Kamchatka pink salmon abundance aligned to sockeye's second year at sea, brood years 1974-1999. Spawner recruit values shown in graph are partial residuals of the multivariate model (see Larsen and McCleary 1972).

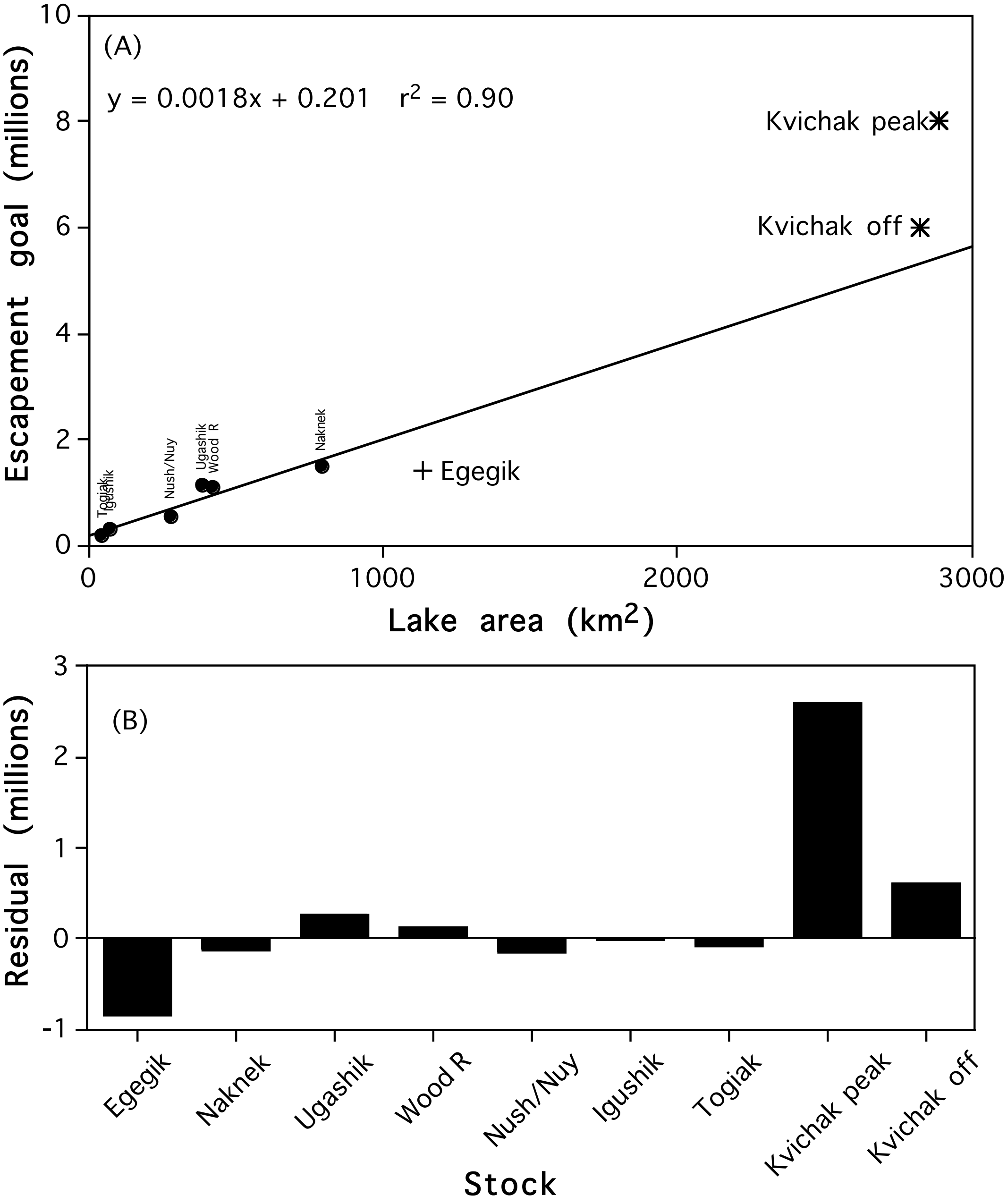

Fig. 35. Relationship between mid-point escapement goals of sockeye salmon and lake surface areas of Bristol Bay watersheds (A) and regression residuals (observed - predicted) of all Bristol Bay stocks (B). Escapement goals are from Baker et al. (2006). Regression excluded Egegik because its goal appeared to be an outlier (to low) compared with other Bristol Bay stocks (possibly due to limited spawning habitat). Kvichak also excluded from regression.

APPENDIX

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Kvichak smolt sonar error and revised estimates of smolt abundances

July 6, 2004

Memorandum

To: Michael Link, Dave Gaudet, BBSRI

From: Greg Ruggerone

INTRODUCTION

Concern about the accuracy of the Kvichak smolt counters began in the 1990s when ADFG estimated large numbers of smolts (primarily age-1) leaving the Kvichak watershed, but few adult salmon returned from the migrations. Several approaches were used in this report to identify 1) whether biological correlates with smolt abundance indicate large smolt abundance error, 2) the year in which significant error in smolt abundance may have begun, 3) whether the error was consistent or intermittent among all recent years, and 4) whether smolt age composition was in error. This analysis was based on several statistical models that predicted smolt abundance and age composition from biological variables such as spawning escapement and juvenile growth in the lakes. Error in adult salmon forecasts provided an initial indication of smolt counter error.

This memo was initially sent to Bristol Bay Science and Research Institute during July 2004. The memo was updated in May 2005 to include smolt estimates based on back calculations from smolt-to-adult survival and adult returns of Kvichak salmon. The report on the decline of Kvichak salmon provides additional details on the Egegik-based methodology that was used to estimate survival at sea of Kvichak salmon.

ADULT FORECAST ERROR

Comparison of ADFG preseason forecasts of Kvichak sockeye salmon runs in relation to the observed inshore runs, 1978-2003, shows that Kvichak forecasts closely mimic the cyclic trends in Kvichak sockeye abundance (Fig. 1). In a given year, forecast error can be large (12 million fish), especially when the run is large. Typically, the observed run is within 100% of the preseason forecast and it is frequently within 50%.

Ideally, a trend should not be present in a time series of forecast error, rather forecast error should vary randomly over time if forecast methods adequately capture factors influencing run size. However, as shown in Fig. 1, the time series of Kvichak forecast error shows a prolonged period where run size was typically smaller (avg. 50% error) than the preseason forecast. The period of relatively small run size began with the 1996 run and continued through the 2003 run. Within this period, run size exceeded the forecast only in 1999, but by a small margin. The return in 1999 was the peak in the five-year Kvichak cycle, thus the 1999 run was anticipated to be relatively large. In comparison to previous peak-year runs, the 1999 run was relatively small, fueling concerns that something was seriously wrong with the Kvichak stock (see report above).

Preseason forecasts by ADFG and Fisheries Research Institute, University of Washington (FRI) are based on the sum of individual forecasts for each dominant age group of sockeye salmon. Typically, forecasts of age-2.2 sockeye salmon, which is the dominant age group in the Kvichak run, are made from estimates of age-2 smolt abundance two years earlier and age-2.1 jack returns during the previous year (multivariate analysis). The adult return of age-1.2 sockeye salmon, which may be abundant when growth in the lakes leads to significant migration of age-1 smolts, is typically forecasted from age-1.1 jacks and sometimes age-1 smolts. Age-1.3 sockeye returns are forecasted from age-1.2 sockeye returns during the previous year. Age-2.3 sockeye salmon are typically forecasted from the return of age-2.2 salmon during the previous year.

Residuals (observed – predicted returns) in the Kvichak forecast model predictions and hindcasts show that the age-2.2 forecast model consistently over-estimated the observed return of age-2.2 sockeye salmon from 1996 through 2003 (Fig. 2)[14]. During this eight year period, the age-2.2 forecast model, which is influenced by smolt abundance, overestimated the return of age-2.2 sockeye salmon by 4.1 million fish per year. The age-1.2 forecast model, based on age-1 smolt abundance, also consistently over-estimated the observed return of age-1.2 sockeye salmon beginning in 1996 (avg. 6 million fish per year). In contrast, residuals from the age-1.2 model that relied on age-1.1 jack returns were only slightly negative over a long time period (avg. 1.4 million fish). The 1.1 jack model is currently relied upon to forecast age-1.2 returns even though the relationship is largely influenced by one datum. Age-1.3 sockeye salmon tend to be less abundant than other age groups and the age-1.3 forecast model did not exhibit consistent bias in its forecasts.

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[14] The forecast models used to develop these residuals was restricted to years prior to potential smolt counter error so that deviations from past relationships could be detected. These forecast models are basically the same as those used by ADFG and FRI, but years of data included in the forecast model differs. Typically, the preseason forecast models are continually updated and utilize data up to the forecast year. Sometimes some earlier data may be dropped from the model, e.g. the age-1.3 model.

The age-specific forecast models that rely upon smolt abundance data suggest that either smolt abundance estimates that produced the 1996-2003 adult runs were too high, fish survival at sea was exceptionally low, or both. The 1996 adult return of ocean age-2 salmon, the dominant ocean age of Kvichak salmon, was produced by age-1 and age-2 smolts that migrated in 1994. These smolts originated from the 1991 (age-2.2) and 1992 (age-1.2) parent spawning years (brood years).

Although these data show that significant forecast error began in 1996 (Figs. 1 and 2), it is possible that smolt enumeration error, if present, began after the 1994 smolt year and that poor survival contributed to adult forecast error in 1996 or other years. Therefore, the analyses shown below were conducted in order to further evaluate years when smolt enumeration may have faltered.

ALTERNATIVE SMOLT ABUNDANCE ESTIMATES

Estimates of age-1 and age-2 smolt abundances during migration years 1994 to 2003 were developed from multivariate statistical models that incorporated variables likely to influence smolt abundance. The models were based on smolt abundance data associated with smolt migration years 1955-1993 (data provided by D. Rogers, University of Washington). A few years within this period were missing data and therefore could not be incorporated into the analysis. Sampling gear used to estimate smolt abundance in the Kvichak River changed from a fyke net to Bendix sonar in 1971. Fyke net catches were expanded by D. Rogers to be consistent with sonar counts (see Rogers and Poe 1984). The relationship between smolt abundance and explanatory variables did not significantly change in relation to sampling gear ($P > 0.05$), therefore all available years were included in the analysis. Smolt migration years after 1993 were excluded from the models in order to evaluate whether recent sonar-based smolt estimates were different from values predicted by the statistical smolt models.

Age-1 smolt abundance was estimated from parent spawning escapement, escapement during the previous year, and air temperature during the first year in the lake (April to October). These variables were chosen for consideration in the model because they make biological sense. Greater parent escapement should, on average, produce more smolt. Spawning escapement during the previous year may reduce prey availability and lead to reduced growth and fewer age-1 smolt (Eggers and Rogers 1987, Ruggerone and Rogers 2003). Higher temperature during spring and summer when fry reared in the lake should lead to greater growth and more age-1 smolt. A multivariate model that explains age-1 smolt abundance is:

$$\text{Age-1 smolt} = -134.1 + 7.24\,(\text{parent spawners}) - 2.80\,(\text{prev. spawners}) + 23.5\,(\text{temp.}),$$

where $n = 38$; overall $P < 0.001$; P (escapement) <0.001; P (previous escapement) < 0.04, P (temperature) < 0.005; serial autocorrelation = -0.02; $R^2 = 0.56$.

Residuals (observed-predicted) of the age-1 smolt abundance model shows that sonar counts of age-1 smolts were unusually high from 1995 through 2001 (Fig. 3). On average, sonar smolt counts were 135 million fish higher than that predicted from the age-1 smolt model.

Importantly, the unusually large deviation between sonar smolt counts and the model predictions began in 1995, rather than 1994 as suggested by the error in adult return forecasts (see above).

In 2002, operation of sonar in the Kvichak River was hampered by ice in the river and the gear was removed early. No sonar-based smolt estimates are were available in 2002. In 2003, ADFG used new sonar gear to estimate smolt abundance (BioSonics side-looking echo sounder). Preliminary age-1 smolt estimates in 2003 provided by ADFG (L. Fair, pers. comm..) indicated that approximately 36 million age-1 smolts migrated during the period of sampling from May 17-June 10. An additional 5 million age-1 smolt may have migrated during non-sampled periods, indicating approximately 41 million age-1 smolts. The estimate of smolt abundance in 2003 is approximately 33 million less than that predicted by the smolt model, suggesting that the ADFG smolt estimate in 2003 was not biased high as in previous years.

Age-2 smolt are typically much more abundant than age-1 smolt in the Kvichak River. Age-2 smolt abundance was estimated from parent spawning escapement, air temperature during spring when fry emerged from gravel (April to May), and weight of age-2 smolt. These variables make biological sense because age-2 smolt abundance should be positively correlated with parent escapement, negatively correlated with temperature that enhanced juvenile growth and produced more age-1 smolt, and negatively correlated with smolt weight because numerous yearlings in the lake will reduce growth. A multivariate model that explained age-2 smolt abundance is:

$$\text{Age-2 smolt} = 221.2 + 9.62\ (\text{parent spawners}) - 14.4\ (\text{temperature}) - 15.8\ (\text{smolt wt.}),$$

where $n = 35$; overall $P < 0.001$; P (escapement) <0.001; P (temperature) < 0.002, P (smolt wt.) < 0.01; serial autocorrelation = 0.095; $R^2 = 0.77$.

The age-2 smolt abundance model explained more of the variability in smolt abundance (77%) than did the age-1 smolt model (56%). Residuals of the age-2 smolt abundance model shows that sonar counts of age-2 smolts were slightly high during 1996-1998, but not unreasonably high compared with residuals during 1957-1994 (Fig. 3). Sonar estimates of age-2 smolt abundance were consistent with the model predictions during 1994, 1995, and 1999-2001. Overall, the age-2 model suggests that sonar counts of age-2 smolts during 1994-2001 were within the range expected from the smolt abundance model, although sonar estimates tended to be slightly greater than those estimated by the statistical model.

In 2003, ADFG estimated approximately 9.5 million age-2 smolts during May 17 to June 10 (preliminary estimate), based on deployment of new sonar equipment. It is possible that some age-2 smolts migrated prior to sampling because age-2 smolts typically migrate earlier than age-1 smolts. In contrast, the age-2 smolt model predicted 39 million smolts in 2003, or approximately 29.5 million more smolt than indicated by the ADFG smolt counts. Thus, the statistical smolt models estimated a total smolt migration in 2003 (age-1 & 2) that was 63.5 million fish greater than the new sonar gear (Table 1).

Total abundance of smolts produced by the parent spawning years was predicted from three variables that are biologically reasonable (see above):

$$\text{Total smolt} = 271.2 + 15.5\ (\text{parent spawners}) - 4.4\ (\text{previous-year spawners}) - 19.6\ (\text{age-2 smolt wt}),$$

where n = 34; overall $P < 0.001$; P (escapement) <0.001; P (previous-year escapement) < 0.03, P (smolt wt.) < 0.02; serial autocorrelation = -0.093; $R^2 = 0.80$.

The total smolt model predicts smolts produced by spawning parents, thus age-1 and age-2 smolts originated from adjacent years of migration. Residuals of the total smolt abundance model shows that sonar counts of smolt abundance were unusually high from brood year 1993 through 1996, corresponding to migration years 1995-1997/1998 (Fig. 4). Sonar smolt estimates corresponding to brood years 1997 and 1998 were above average, but not unusually high. These brood years correspond with migrations in 1999 and 2000/2001. The residual pattern for total smolt production is consistent with those shown previously for age-1 and age-2 smolts.

Total annual smolt counts based on sonar and fyke net methods were compared with the combined smolt counts from the age-specific smolt abundance models developed from data collected during 1957-1994 (Table 1). Comparisons of total reported smolt counts (sonar) were also made with predictions of smolt abundance during 1995-2001, and 2003 (no data available for 2002).

During 1957-1994, the two age-specific smolt models explained 46% of the variability in the sonar/fyke net counts (Fig. 5). During 1995-2001, sonar smolt counts were consistently greater than the modeled annual counts, although two years (1999, 2000) were within the range of past years. Importantly, sonar counts during 1995-2001 remained correlated with the modeled smolt counts ($R^2 = 0.88$, Fig. 5), indicating smolt error was not random. On average, sonar smolt counts were 2.55 times greater than the modeled smolt counts. The ratio of sonar/model counts was not significantly correlated with modeled smolt counts ($R^2 = 0.20$, $P = 0.32$), indicating the ratio remained fairly constant in relation to increasing modeled smolt counts (Fig. 6).

The above analyses indicate sonar counts of age-1 smolts were unusually high and likely in error during 1995-2001. Importantly, the potential error was not random but correlated with smolt abundance based on smolt models ($R^2 = 0.88$). This suggests the error was systematic and related to smolt abundance rather than with factors unrelated to smolt abundance. On average, total annual sonar counts were 2.55 times greater than modeled counts. Sonar counts of age-2 smolts appeared to be more reasonable, but may have been somewhat high during 1996-1998. New sonar gear was deployed in 2003. The statistical models suggest the sonar counts may have been somewhat low in 2003, possibly because some fish may have migrated before and after the sampling period.

Predictions of smolt abundances in 2002 to 2005 are shown in Table 1, except for age-2 smolt in 2004 and 2005 (smolt weight is needed for model). Adult forecasts from 2002 predicted smolt migrations (108 million age-2 smolt, 33 million age-1 smolt) indicated approximately 11 million age-2.2 adults in 2004, a forecast that was quite similar to the preseason forecasts by ADFG (12 million adults) that was largely based on age-2.1 jacks that returned in 2003. However, the actual return of age-2.2 adults (5.54 million) was much less than predicted indicating smolt abundance estimates were too high or survival at sea was below average.

<u>Updated Smolt Abundance Estimates</u>

Analyses in the report on the decline of Kvichak sockeye production demonstrated that Kvichak and Egegik smolt-to-adult survival estimates were correlated during 1982-1994. Egegik smolt survival explained from 59% (age-1 smolt) to 61% (age-2) to 90% (total smolt) of Kvichak smolt survival. Therefore, Kvichak smolt abundance estimates were reconstructed from predicted estimates of smolt-to-adult survival and age-specific adult returns to the Kvichak watershed. The predicted smolt abundance estimates based on Egegik smolt survival are shown in Table 1. The report on the decline of Kvichak salmon abundance should be consulted for more details on the Egegik and Kvichak analyses.

This analysis indicated that sonar error was greater than indicated by the smolt models that utilized spawning escapement and temperature. The relationship between sonar smolt estimates and revised smolt estimates based on smolt-to-adult survival are shown in Fig. 7. The revised smolt estimates were correlated with sonar counts during the period of sonar error. The sonar-based counts were 5.9 times greater than the Egegik-based estimates, on average (Fig. 8).

The Egegik-based estimates of smolt survival is likely more accurate than estimates based on spawner abundances because the Egegik-based estimates reflect year-to-year changes in survival at sea and presumably in spawner to smolt abundances.

ACCURACY OF SMOLT AGE COMPOSITION

Previous research by Rogers et al. (1991) determined that smolt age composition in a cohort produced from a spawning season could be estimated from the length of age-0 cohorts sampled in Iliamna Lake during September before the age-1 migration[15]. This relationship has been used to determine whether the peak-cycle year shifts from the typical five-year cycle to a four year cycle in response to rapid growth and early smolt migration. We used the relationship between fry length and smolt age composition during brood years 1961-1990 to evaluate potential error in age composition beginning in the mid-1990s. Fry length data were provided by Rogers et al. (2002).

The percentage of age-1 smolts increased linearly in response to greater growth of fry during spring through September of the previous year (Fig. 9). Percentage age-1 smolts in the cohort was explained by the following relationship, which incorporated the arcsine-square root transformation to normalize percentage data:

$$\text{AS \% age-1} = -1.376 + 0.038\,(\text{September fry length}),$$

where $n = 28$, $P < 0.002$, serial autocorrelation = -0.121, $R^2 = 0.54$.

Residuals in the relationship show large deviations in some years (e.g., brood years 1961, 1963, 1983, 1990) (Fig. 10). However, beginning in brood year 1992 (smolt migrations 1994 and

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[15] % age-1 smolts = (# age-1 smolts migrating in BY+2)/(# age-1 smolts migrating in BY+2 + # age-2 smolts migrating in BY+3)

1995) the percentage of age-1 smolts estimated by ADFG tended to be higher than expected from the fry length model. This finding is consistent with the previous finding that the number of age-1 smolts estimated by sonar was unusually high during the 1995-2001 smolt migrations. This model predicted 8% age-1 smolts in the 1999 brood year and 54% age-1 smolts in the 2000 brood year. Thus, the majority of the 1999 peak cycle cohort should return in 2004 (age-2.2) rather than 2003 (age-1.2), whereas progeny from post-peak cycle 2000 brood should be evenly split between 2004 (age-1.2) and 2005 (age-2.2).

The age composition model was improved by incorporating April-May air temperature during the year of age-1 smolt migration. This revised model is shown in the following equation, which incorporates brood years 1964-1990:

$$\text{AS \% age-1} = -1.022 + 0.040\,(\text{September fry length}) + 0.048\,(\text{temperature}),$$

where $n = 25$, overall $P < 0.001$, P (fry length) < 0.001, P (temperature) $= 0.016$, serial autocorrelation = -0.304, $R^2 = 0.70$.

Inclusion of spring air temperature during the year of migration improved the model fit, but sonar based estimates of age composition still led to relatively high percentages of age-1 smolts during brood years 1992-1994, and 1998 (Fig. 10). This model predicted 9% age-1 smolts in the 1999 brood year and 61% age-1 smolts in the 2000 brood year.

Annual estimates of smolt age composition in the migration were developed from the two smolt abundance models (see Table 1) and averaged fro comparison with age composition measured in the river by ADFG. During 1957-1994, the percentage of age-1 smolts calculated by models and filed estimates were correlated ($R^2 = 0.64$). No apparent bias in one of the methods was observed, i.e., the slope was near 1 (Fig. 11). However, during 1995-2001, sonar-based estimates of age-1 smolts were higher than expected, except for 1996 and 1999.

CONCLUSIONS

Adult return forecasts and statistical models that predict smolt abundance and age composition were examined in an effort to evaluate whether the sonar in the Kvichak River overestimated smolt abundance since the early 1990s. Evidence from these analyses indicated sonar-based estimates of age-1 smolts were too high during 1995 through 2001. During this period, age-1 smolts were the dominant age group in four of the six years and it was nearly equal to age-2 abundance in the other two years.

Importantly, the potential overestimation of smolt abundance by sonar during 1995-2001 was not random. Instead, potential error was correlated with independent estimates of smolt abundance. Smolt prediction models based on escapement and temperature indicated sonar overestimated smolt abundance by a factor of approximately 2.55 during 1995-2001. Smolt prediction models based on Egegik smolt-to-adult survival and Kvichak adult returns indicated sonar overestimated smolt abundance by a factor of approximately 5.9 during 1995-2001. The Egegik-based smolt estimates are believed to be more accurate than the estimates based on spawning escapement.

The sonar counting system has undergone a series of changes beginning in 1989 (L. Fair 2002). In 1993, smolt sampling was moved to a new site and the sonar equipment was changed to the 1982 Bendix sonar model with extended cables. The system was unchanged from 1993-1995. During 1996-1998, the sonar was moved to another new site. These changes in sonar sites and gear overlap but do not precisely match estimates of sonar error suggested by the statistical models. In 2003, new sonar gear was deployed and the apparent over-counting of smolts was not apparent. Instead, the new gear produced a smolt estimate that was somewhat lower than expected based on past data.

It is important to note that although the statistical smolt abundance models appear to provide reasonable estimates of smolt abundance, they should not be considered as a substitute for field estimates of smolt abundance. The statistical models are based on past relationships involving relatively few variables. Thus, while statistical models might be helpful in years when logistical difficulties prevent fielded sampling of smolt abundance, the models will not capture unique events that impact smolt abundance. Furthermore, the age-2 smolt model, based on escapement, requires field sampling of smolt weight and the age composition model requires sampling of fry length in September. The Egegik-based model requires sonar in Egegik River, but sonar operations were discontinued in 2001. The analyses presented here indicates the high value of Egegik smolt estimates for evaluating both Egegik and Kvichak sockeye smolt populations.

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Table 1. Estimates of Kvichak River smolt abundances (millions of fish) based on sonar/fyke net counts and two statistical models, 1955-2005. Smolt counts prior to 1971 were based on expanded fyke net counts (Rogers and Poe 1984). Smolt models developed from data prior to 1994, i.e. the first obvious outlier. Sonar estimates during 1994-2001 that were likely too high are shown in bold. Negative smolt abundances predicted by the escapement model indicates low smolt abundance. The Egegik model is based on predicted Kvichak smolt survival and observed adult returns (see text).

Smolt	Observed Smolt Counts (millions)				Escapement Model Smolt Counts (millions)				Egegik Model Smolt Counts (millions)			
year	Age 1	Age 2	Total	% Age 1	Age 1	Age 2	Total	% Age 1	Age 1	Age 2	Total	% Age 1
1955	1	15	16	6%	29	NA	NA	NA	NA	NA	NA	NA
1956	2	3	5	40%	3	NA	NA	NA	NA	NA	NA	NA
1957	2	0.5	2.5	80%	-1	-16	-17	NA	NA	NA	NA	NA
1958	199	4	203	98%	146	NA	NA	NA	NA	NA	NA	NA
1959	5	169	174	3%	28	120	148	19%	NA	NA	NA	NA
1960	4	34	38	11%	27	30	56	47%	NA	NA	NA	NA
1961	2	1	3	67%	35	-22	13	*100%*	NA	NA	NA	NA
1962	69	4	73	95%	124	52	177	70%	NA	NA	NA	NA
1963	8	250	258	3%	33	197	229	14%	NA	NA	NA	NA
1964	28	98	126	22%	30	61	91	33%	NA	NA	NA	NA
1965	4	106	110	4%	16	41	57	28%	NA	NA	NA	NA
1966	16	1	17	94%	7	21	29	26%	NA	NA	NA	NA
1967	175	13	188	93%	177	-9	168	*100%*	NA	NA	NA	NA
1968	41	332	373	11%	7	294	301	2%	NA	NA	NA	NA
1969	36	33	69	52%	33	30	63	52%	NA	NA	NA	NA
1970	11	18	29	38%	58	39	97	60%	NA	NA	NA	NA
1971	86	6	92	93%	69	16	85	81%	NA	NA	NA	NA
1972	1	54	55	2%	87	103	190	46%	NA	NA	NA	NA
1973	5	192	197	3%	-15	231	216	*0%*	NA	NA	NA	NA
1974	3	21	24	13%	36	45	81	45%	NA	NA	NA	NA
1975	No data	No data	No data	No data	*57*	*-75*	-18	*100%*	NA	NA	NA	NA
1976	108	3	111	97%	44	-64	-20	*100%*	NA	NA	NA	NA
1977	78	114	192	41%	102	103	205	50%	NA	NA	NA	NA
1978	32	213	245	13%	5	206	211	2%	NA	NA	NA	NA
1979	29	26	55	53%	52	71	123	43%	NA	NA	NA	NA
1980	182	10	192	95%	101	-1	100	*100%*	NA	NA	NA	NA
1981	220	32	252	87%	107	21	129	83%	NA	NA	NA	NA
1982	150	89	239	63%	144	129	273	53%	152	156	309	49%
1983	7	76	83	8%	-43	178	135	*0%*	*5*	*63*	68	8%
1984	52	38	90	58%	44	80	124	36%	15	29	44	34%
1985	24	2	26	92%	48	20	67	71%	NA	NA	NA	NA
1986	83	53	136	61%	50	65	115	43%	94	30	123	76%
1987	11	331	342	3%	47	236	282	17%	17	224	241	7%
1988	13	87	100	13%	29	137	166	18%	29	70	99	29%
1989	147	7	154	95%	68	26	94	73%	190	22	213	90%
1990	47	41	88	53%	74	80	153	48%	32	30	62	52%
1991	87	34	121	72%	99	51	150	66%	43	90	133	33%
1992	18	61	79	23%	81	82	163	50%	34	63	98	35%
1993	22	204	226	10%	27	100	127	21%	42	130	172	24%
1994	54	30	84	64%	102	78	180	57%	42	24	66	64%
1995	**210**	11	**221**	95%	59	17	75	78%	30	17	47	63%
1996	**277**	**96**	**373**	74%	120	22	142	85%	100	10	111	91%
1997	**269**	**94**	**363**	74%	81	54	136	60%	60	15	74	80%
1998	**192**	**103**	**295**	65%	54	65	119	45%	66	27	93	71%
1999	**131**	12	**143**	92%	48	-10	48	*100%*	*2*	*0*	2	85%
2000	**106**	24	**130**	82%	28	31	60	47%	6	7	13	49%
2001	**231**	95	**326**	71%	78	84	162	48%	53	12	64	82%
2002	NA	NA	NA	NA	33	108	141	23%	NA	NA	NA	NA
2003	41	9.5	50.5	81%	74	39	114	65%	NA	NA	NA	NA
2004	NA	NA	NA	NA	67	NA	NA	NA	NA	NA	NA	NA
2005	NA	NA	NA	NA	12	NA	NA	NA	NA	NA	NA	NA

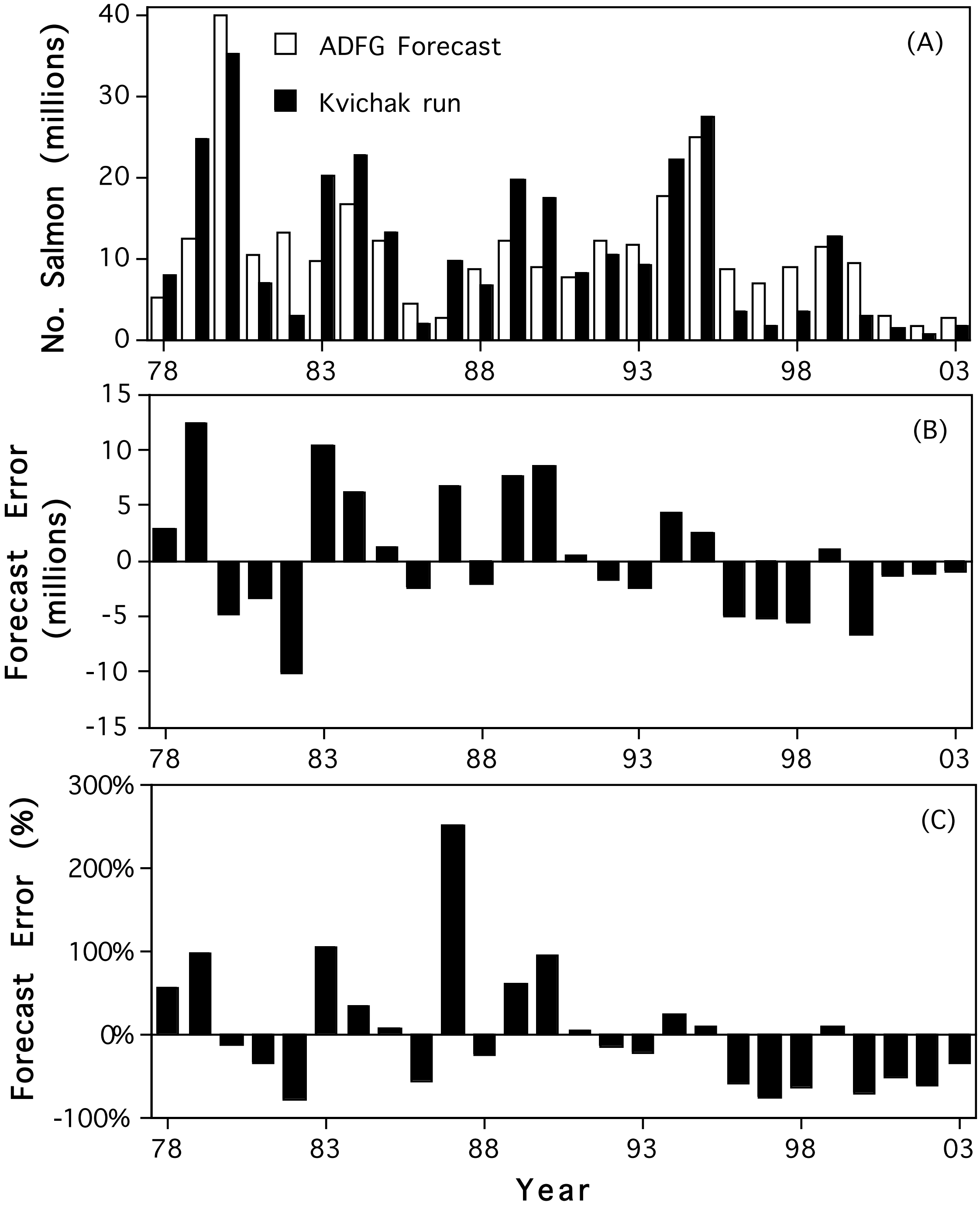

Fig. 1. Observed and predicted sockeye salmon runs to the Kvichak River (A) and associated forecast error (B, C) for Kvichak sockeye salmon, 1978-2003. Values based on inshore ADFG records. Forecast trends by Fisheries Research Institute, University of Washington (FRI) show similar pattern of forecast error.

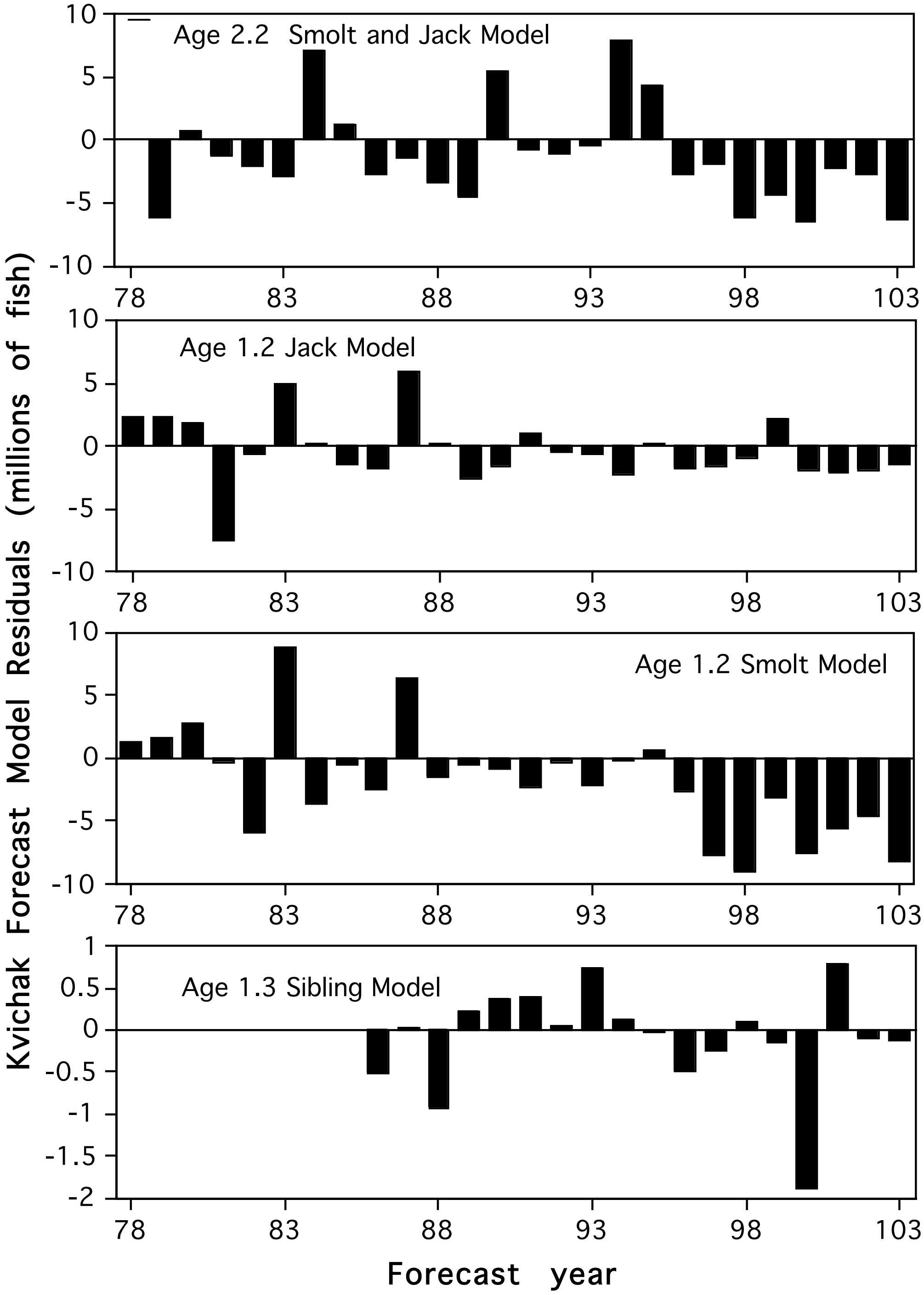

Fig. 2. Residuals (observed – predicted) from Kvichak forecast models. Age-1.2 and 2.2 forecast models based on brood years 1974-1990; age-1.3 model based on brood years 1981-1990. Residuals after 1990 are shown to determine whether relationships shifted during the recent period. Data types used in each forecast is indicated in the graph titles.

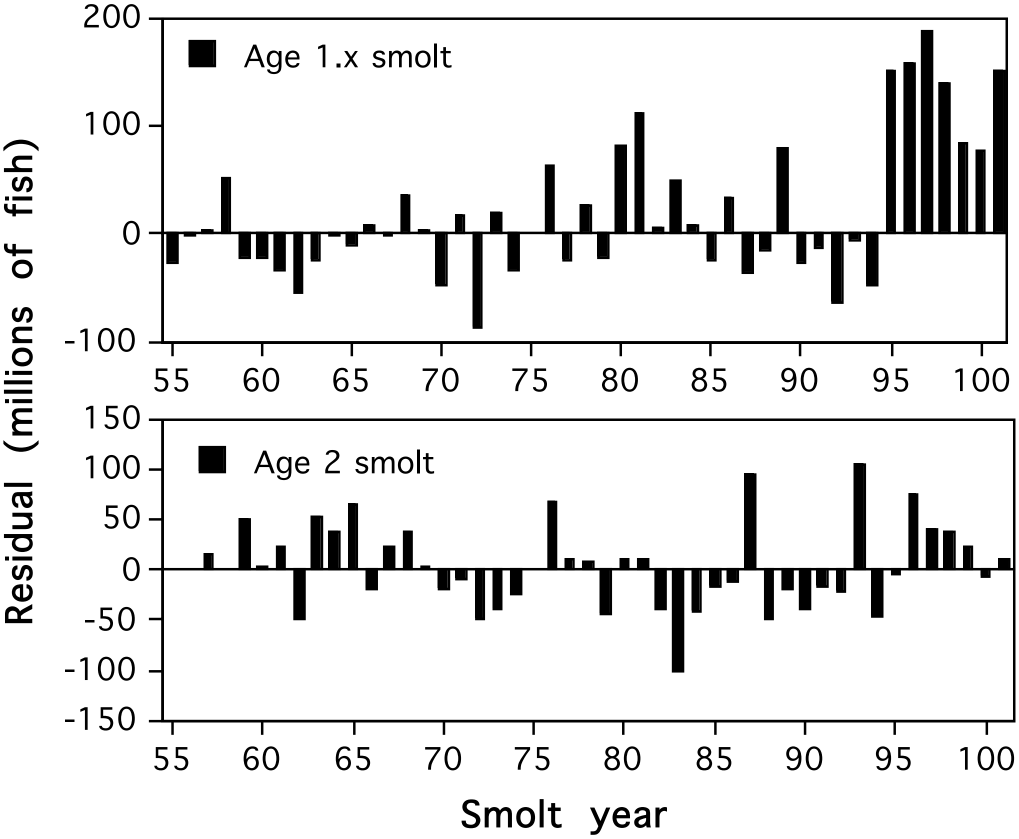

Fig. 3. Observed-predicted (residuals) of a multivariate models that predict age-1 and age-2 smolts migrating each, 1955-2001. Model developed from migration years 1955-1993.

Age-1 smolt = -134.1 + 7.24 (Escapement) - 2.80 (Previous Escapement)
+ 23.54 (Apr-Oct fry air temp.); $R^2 = 0.56$, n = 38.

Age-2 smolt = 221.2 + 9.62 (Escapement) - 14.36 (spring temp. (fry)) - 15.83 (age-2 smolt wt);
$R^2 = 0.77$, n = 35.

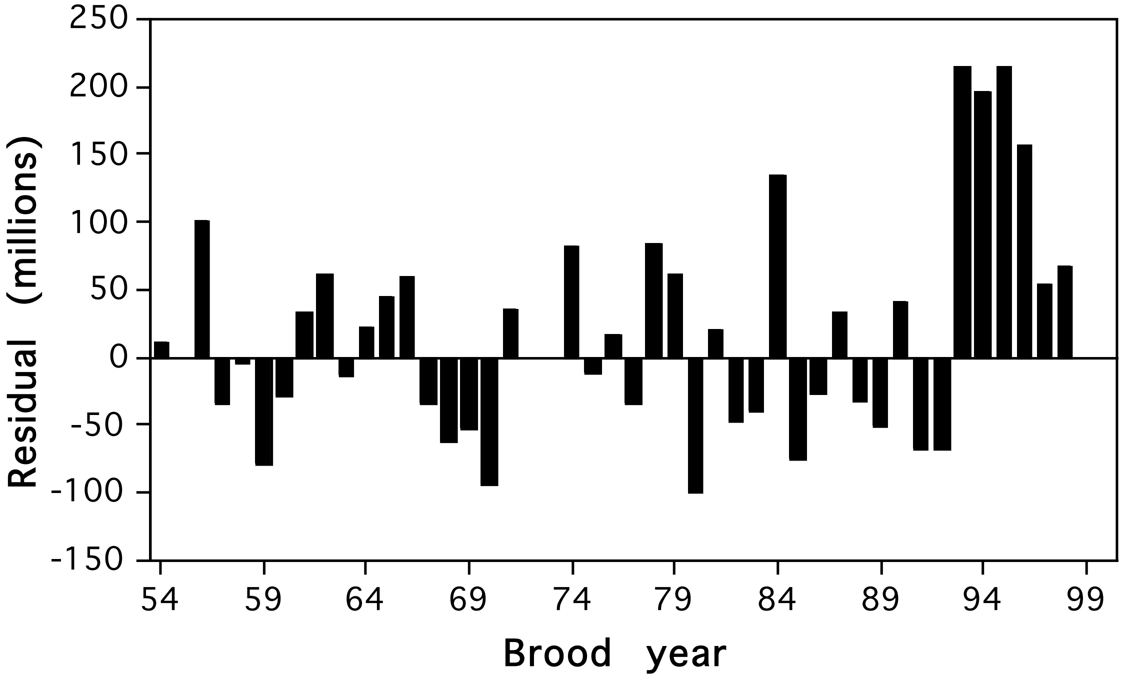

Fig. 4. Observed-predicted (residuals) of a multivariate model to predict total smolts produced by each brood year, 1954-1998. Model developed from brood years 1954-1991.

Total BY smolt = 271.2 + 15.48 (Escapement) - 4.40 (Previous Escapement)
- 19.56 (age-2 smolt wt); $R^2 = 0.80$, n = 34.

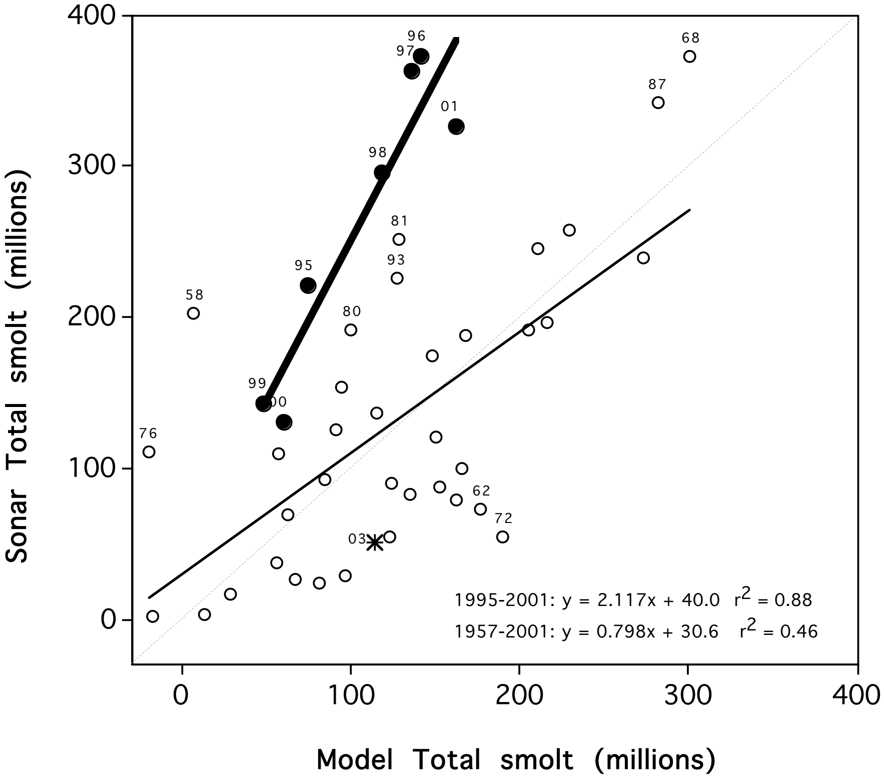

Fig. 5. Comparison of total annual smolt counts based on sonar and fyke net methods versus the combined smolt counts from the two age-specific smolt count models based on parent escapement. Sonar counts during 1995-2001 (solid symbols) were consistently greater than expected based on data from 1957-1994 (open symbols). Sonar counts in 2003 (star symbol) were below average.

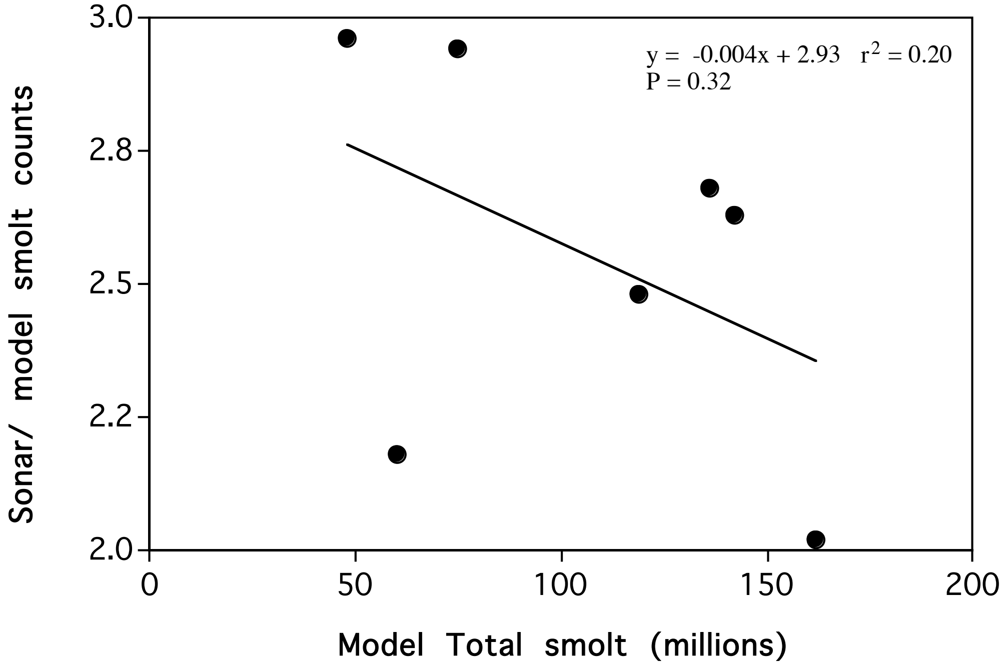

Fig. 6. Comparison of the sonar: model smolt count ratio with modeled smolt counts based on parent escapement during 1995-2001. The relationship was statistically insignificant indicating the high ratio (avg. 2.55) was relatively constant during this period.

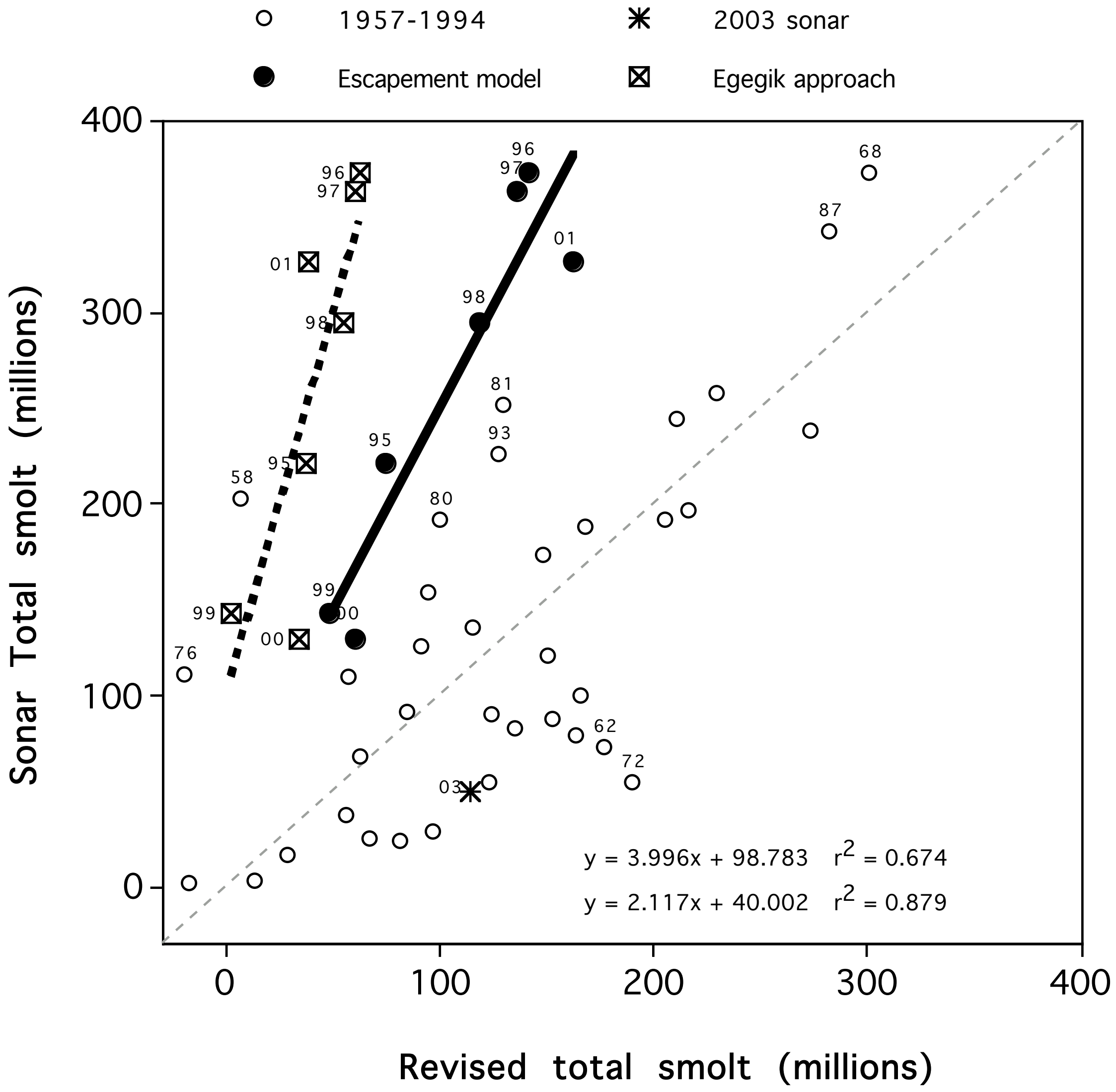

Fig. 7. Relationship between total smolts estimated by sonar and total smolts estimated by the two statistical models during 1995-2001.

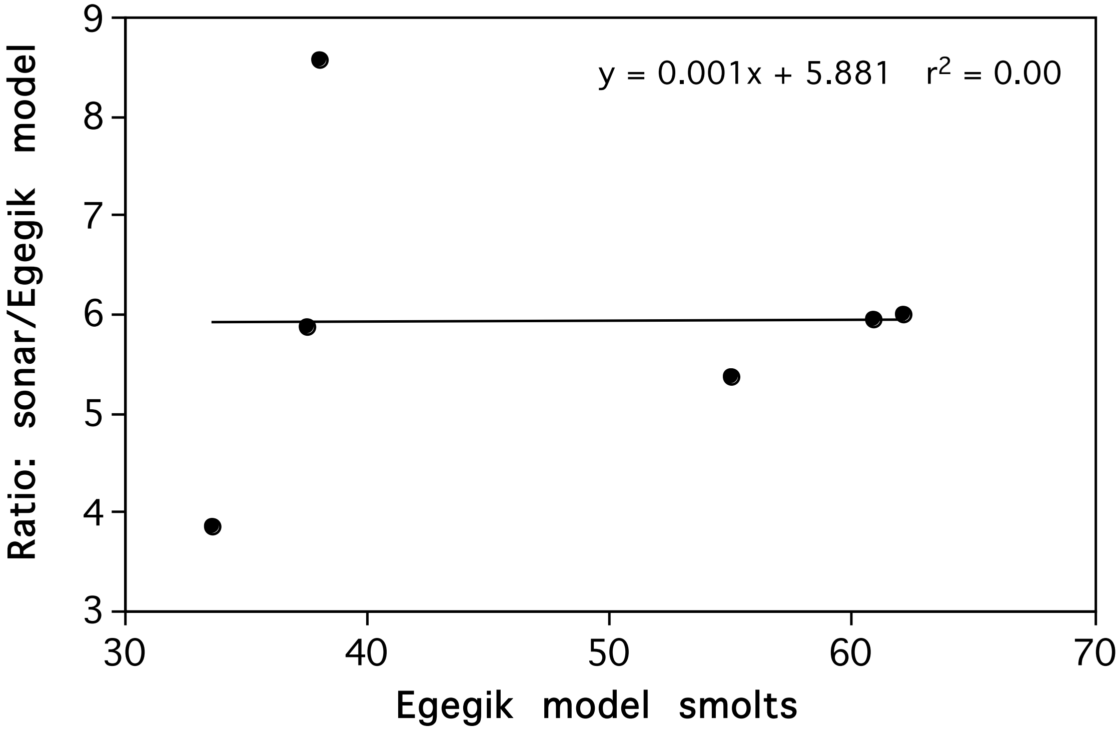

Fig. 8. Ratio of sonar smolt counts to Egegik model counts in relation to modeled counts, 1995-2001. Figure excludes 1999 smolt year where sonar/model ratio was 50 and Egegik model predicted only 3 million smolts (few Kvichak salmon returned when smolts entered the cold ocean in 1999).

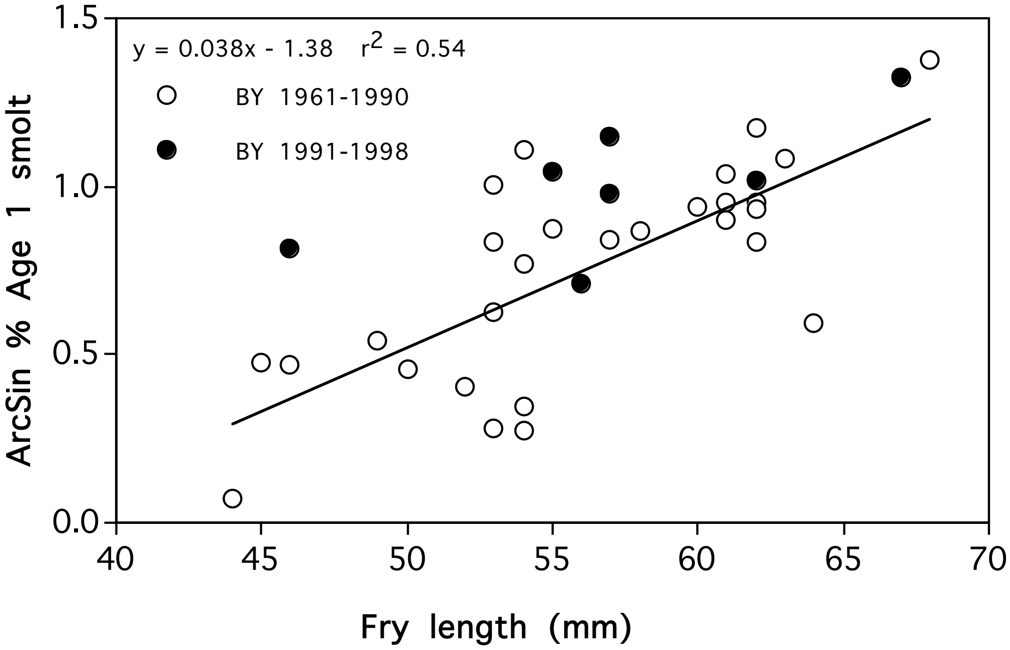

Fig. 9. Relationship between percentage age-1 smolt in a cohort (ArcSin transformed) and fry length in Iliamna Lake during September of the previous year.

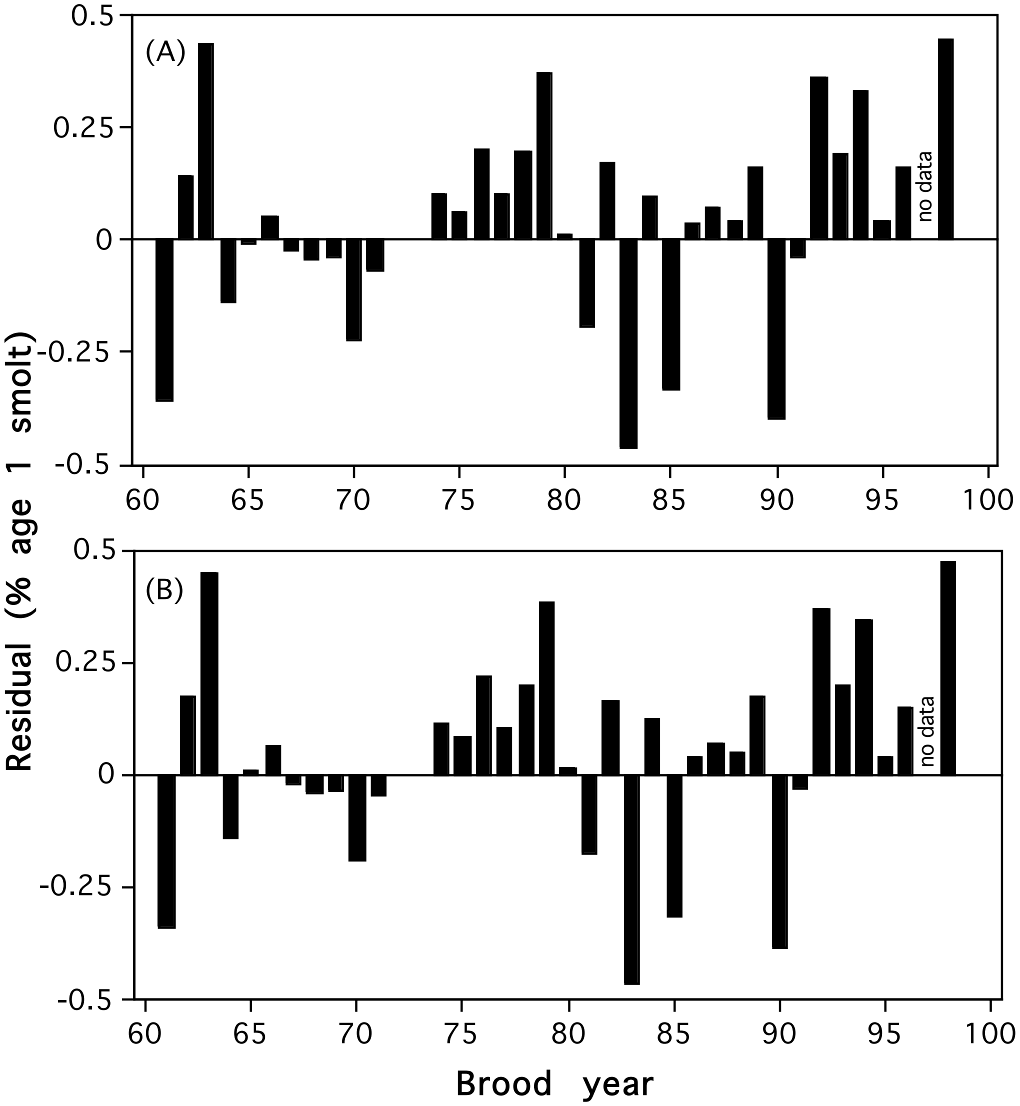

Fig. 10. Residuals (observed-predicted) of models that estimate the percentage of age-1 smolt in a cohort.

(A): AS % age-1 = -1.376 + 0.038 (September fry length)

(B): AS % age-1 = -1.022 + 0.040 (September fry length) + 0.048 (temperature).

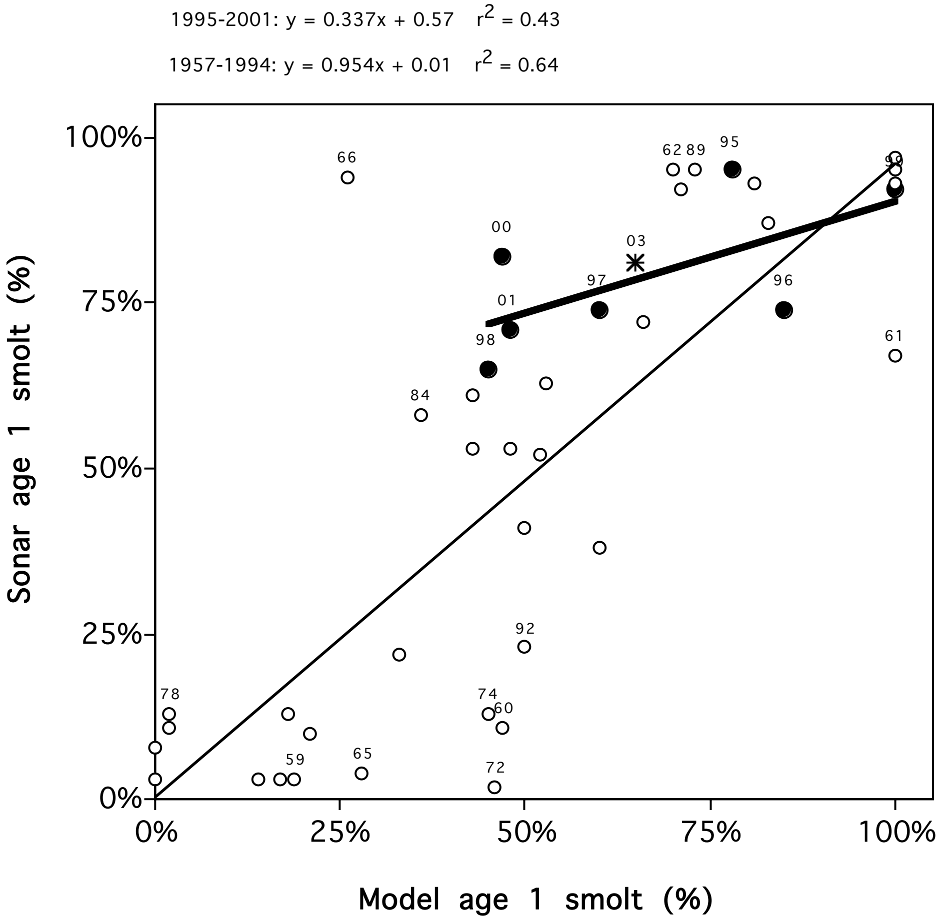

Fig. 11. Comparison of annual smolt age composition based on sonar/fyke net methods and the two age-specific smolt abundance models (see Table 1).