

EFFECTS OF THE AGE-COMPOSITION OF SPAWNING SOCKEYE SALMON ON
FUTURE RETURNS OF SOCKEYE SALMON TO BRISTOL BAY, ALASKA


By

Janelle Mueller

RECOMMENDED:




Dr. Gordon Kruse



Dr. Milo Adkison



Dr. Franz Mueter, Advisory Committee Chair



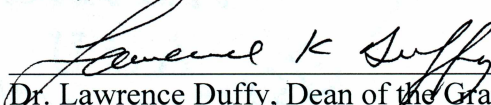
Dr. Milo Adkison,
Chair, Graduate Program in Fisheries Division

APPROVED:



Dr. Michael Castellini

Dean, School of Fisheries and Ocean Sciences



Dr. Lawrence Duffy, Dean of the Graduate School

Dec 6, 2011

Date

EFFECTS OF THE AGE-COMPOSITION OF SPAWNING SOCKEYE SALMON ON
FUTURE RETURNS OF SOCKEYE SALMON TO BRISTOL BAY, ALASKA

A

THESIS

Presented to the Faculty

of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements

for the Degree of

MASTER OF SCIENCE

By

Janelle C. Mueller, B.S.

Fairbanks, Alaska

December 2011

Abstract

The age structure of sockeye salmon on spawning grounds is highly variable, yet little is known about the influence of spawner age composition on subsequent abundance and age composition of recruits. Management of Bristol Bay sockeye salmon relies on estimated spawner abundance to determine escapement goals, without regard to age or size composition. This may not accurately reflect reproductive potential as a basis for setting escapement goals. Parental age structure and environmental conditions were included as independent variables in statistical models to evaluate their effects on the age structure of their progeny. In addition, relationships between spawner age composition and recruit abundance were examined. I found a significant relationship between the age composition of spawners and that of their progeny, as well as environmental effects on age composition. A higher proportion of spawners that spent three years in the ocean were associated with a higher proportion of recruits with this life history pattern, suggesting direct genetic and/or environmental influences. However, redefining spawner-recruit models based on spawner age composition did not significantly improve predictions of the overall number of recruits originating in a given brood year. Nevertheless, the ability to predict the age and hence size composition of returns (with uncertainty), implies that improved predictions of the total biomass of returns in a given year is possible.

Table of contents

	Page
Signature page	i
Title page	ii
Abstract	iii
Table of contents	iv
List of figures	vi
List of tables	vii
List of appendices	ix
Acknowledgements	x
Introduction	1
Effects of the age composition of spawning sockeye salmon on future returns of sockeye salmon to Bristol Bay, Alaska	5
Abstract	5
Introduction	6
Methods	7
Data	7
Multinomial analysis	10
Binomial analysis	14
Ricker stock-recruit analysis	14
Results	16
Trends in spawner age composition	16
Variability in age composition: multinomial logit models	18
Variability in age composition: logistic regression models	19
Ricker model results	20
Discussio	20
Parental effects on age composition	21
Environmental effects on age composition	22
Effects of age composition on recruitment	24
Further insights and caveats	25

Implications for management and general conclusions.....	27
References.....	28
Conclusions.....	45
Literature cited.....	47

List of figures

	Page
Figure 1. Map of Bristol Bay Alaska.....	36
Figure 2. Proportions and absolute numbers of spawners by age-class in the Ugashik River, Bristol Bay, Alaska.....	37
Figure 3. Proportions and absolute numbers of returns by age-class in the Ugashik River, Bristol Bay, Alaska.....	38
Figure 4. (a) Proportions of Ugashik river 3-ocean spawners, (b) Pacific Decadal Oscillation index, (c) Winter average air temperatures at the King Salmon, Alaska, airport, and (d) Ugashik river spawner abundances from 1966 to 2005	39
Figure 5. Estimated against observed proportions of major sockeye salmon age classes returning to the Ugashik River system from 1966 to 2005 based on full model.....	40
Figure 6. Scatterplots of the proportions of four major age classes of sockeye salmon returns to Bristol Bay (1966 – 2005).....	41
Figure A2-1. Age composition data summary for entire Bristol Bay region	53
Figure A2-2. Age composition data summary for Ugashik River system.....	54
Figure A2-3. Age composition data summary for Egegik River system.....	55
Figure A2-4. Age composition data summary for Naknek River system.....	56
Figure A2-5. Age composition data summary for Kvichak River system	57
Figure A2-6. Age composition data summary for Alagnak River system	58
Figure A2-7. Age composition data summary for Wood River system	59
Figure A2-8. Age composition data summary for Igushik River system	60
Figure A2-9. Age composition data summary for Nushagak River system	61
Figure A2-10. Age composition data summary for Togiak River system.....	62

List of tables

	Page
Table 1. Matrix of pairwise Pearson's product moment correlations for predictor variables: 3-ocean Spawners (M), air temperature (AT) from November to March, Pacific decadal oscillation (PDO) from November to March, and spawner abundance (S)	42
Table 2. Comparison of multinomial models to predict the age composition of sockeye salmon returns to the Ugashik River and to all of Bristol Bay (Baywide) using different combinations of environmental predictors	43
Table 3. Signs of coefficients from best Ugashik River multinomial model	44
Table 4. Comparison of binomial models of age-1.3 and age 2.2 sockeye salmon returns to the Ugashik River, Bristol Bay, Alaska.....	44
Table 5. Comparisons of Ugashik River Ricker models and Bristol Bay generalized Ricker models with different predictor variables.....	44
Table A2-1. Bristol Baywide spawner age composition (1956-2007)	63
Table A2-2. Bristol Baywide return age composition (1956-2004).....	65
Table A2-3. Ugashik River spawner age composition (1956-2007)	67
Table A2-4. Ugashik River return age composition (1956-2004).....	69
Table A2-5. Egegik River spawner age composition (1956-2007)	71
Table A2-6. Egegik River return age composition (1956-2004).....	73
Table A2-7. Naknek River spawner age composition (1956-2007).....	75
Table A2-8. Naknek River return age composition (1956-2004).....	77
Table A2-9. Kvichak River spawner age composition (1956-2007).....	79
Table A2-10. Kvichak River return age composition (1956-2004).....	81
Table A2-11. Alagnak River spawner age composition (1956-2007).....	83
Table A2-12. Alagnak River return age composition (1956-2004).....	85
Table A2-13. Wood River spawner age composition (1956-2007).....	87
Table A2-14. Wood River return age composition (1956-2004)	89
Table A2-15. Igushik River spawner age composition (1956-2007)	91
Table A2-16. Igushik River return age composition (1956-2004)	93

Table A2-17. Nushagak River spawner age composition (1973-2007)	95
Table A2-18. Nushagak River return age composition (1980-2003)	96
Table A2-19. Togiak River spawner age composition (1956-2007)	97
Table A2-20. Togiak River return age composition (1956-2004)	99
Table A3-1. King Salmon airport temperature (1955-2008)	101
Table A3-2. Pacific Decadal Oscillation (1900-2009)	103

List of appendices

	Page
Appendix I: multinomial sample size correction factor derivation	51
Appendix II: age data summary for Bristol Bay	53
Appendix III: environmental data summary	101

Acknowledgements

I would like to thank my adviser, Dr. Franz Mueter, for his ongoing support and encouragement throughout the program. I thank my committee members Dr. Milo Adkison and Dr. Gordon Kruse for their thorough revisions and investment in the success of my project. Thanks also to Tim Baker who supplied me with the original age composition data and was the main reason I was funded and accepted into the program to begin with. Thanks to all of the Fish and Game folks that have helped me grow during my time in Bristol Bay and to my Lena Point peers for their input and interest. Also, thanks to the office ladies Gabbi, Louisa and Debi for their ability to navigate through my paperwork. Finally, thanks to my family for giving me examples that have pushed me to follow my heart and live my dreams.

Introduction

Bristol Bay, Alaska, supports one of the largest sockeye salmon (*Oncorhynchus nerka*) runs in the world (Berkeley et al. 2004b; Holt and Peterman 2004; Baker 2006; Morgan et al. 2007; Dann et al. 2009). Annual returns from this sockeye salmon fishery have ranged from less than one million to more than 66 million fish since 1956 (Flynn et al. 2006) with an ex-vessel value of up to \$200 million (Morstad et al. 2009). Bristol Bay sockeye salmon are widely considered to be an example of successful management, which involves meeting harvest and escapement goals while attempting to conserve genetic diversity of the runs (Hyun et al. 2005). All Alaska salmon stocks were certified as sustainable by the Marine Stewardship Council in 2000 and were re-certified in 2007.

Sockeye salmon are anadromous and spawn in the summer in or near freshwater lakes in the Bristol Bay region. After fry emerge the following spring, they rear in fresh water for 1-2 winters before migrating to the ocean as smolts. After outmigration, sockeye salmon follow a westward migration path towards the Kamchatka Peninsula, Russia, then migrate south into the Gulf of Alaska (Straty and Jaenicke 1980). They spend 1-4 years in the ocean where they undergo seasonal feeding migrations between the Gulf of Alaska and the Bering Sea. Upon reaching maturity they return to their natal river system (Burgner 1980; Groot and Margolis 1991), where they are either intercepted in the fishery (catch) or swim upriver to spawn (escapement). Bristol Bay sockeye salmon return to spawning streams at different ages, primarily as 4, 5, and 6 yr-old fish, which complicates the escapement goal-based management strategy of the commercial fishery.

To determine how many fish from a given brood year return to spawn, age compositions of catches and escapements are estimated each year. These estimates are used to construct brood tables for each system, which summarize the number of salmon returning to the system by age class. Age classes are denoted by two numbers, the first representing how many winters the fish spent in freshwater and the second representing how many winters

they spent in the marine environment. For example, if a sockeye salmon spent one winter in freshwater after emergence and three years in the ocean, their age would be denoted as 1.3.

In accordance with statewide salmon management policies, escapement goals for salmon consist of a fixed target range specifying the number of salmon that are intended to escape the fishery to return to the spawning grounds. Fishery biologists in Bristol Bay set separate escapement goals for each of the major river systems in the region as determined by spawner-recruit analysis (Minard and Meacham 1987). At the beginning of the commercial fishing season, the Alaska Department of Fish and Game (ADF&G) uses the Port Moller test fishery on the north side of the Alaska Peninsula to forecast the abundance of returns. The age composition of salmon that are caught in both test and commercial fisheries are used to project return timing (early/late) and the size of the return. Escapement is monitored continuously throughout the season and the commercial fishery is regulated through short-term openings within each of five fishing districts to meet escapement goals. Management of fisheries for Bristol Bay stocks poses unique challenges due to the short duration of the run (Burgner 1980). Approximately 65% of the total run passes through the fishing districts within a period of about two weeks in July. Peak abundances occur around July 4th and run timing is reasonably consistent among years (Minard and Meacham 1987).

In-season management requires quantifying catches and escapement, as well as obtaining biological samples throughout the fishing season to estimate length, weight, and age compositions of the commercial catch, in test fisheries and at escapement towers. More recently, fin clip samples have been taken to collect genetic information that assists in completing genetic stock identification. For age determinations, a scale is removed from each sampled sockeye salmon, and is sent to the King Salmon ADF&G scale ageing laboratory. Age data are used to help with in-season management. Biologists compare what has been forecast with what actually returns. Each river is associated with a certain

age composition, therefore when sockeye return to the fishery biologists can gauge the abundance of returns to each river.

The age composition of returning salmon is frequently used to forecast returns one year ahead using sibling age-class models. These models relate the returns of adult sockeye salmon at age a to the abundance of the same cohort of fish returning in the preceding year at age $a-1$. Holt and Peterman (2004) found substantial evidence for long-term trends in parameters of sibling models for sockeye salmon stocks in British Columbia and Alaska. Most trends showed increasing age-at-maturity. The parameters of these models were positively correlated among the different stocks, suggesting that large-scale factors may potentially drive long-term changes in age-at-maturity and hence in the age composition of returning sockeye salmon.

Spawner age composition may have important effects on fecundity, size, and viability of eggs and may contribute to variations in recruitment. For example, Berkeley et al. (2004a) showed that larger female black rockfishes (*Sebastes melanops*) produce larvae that are more robust to starvation and grow at faster rates than those of younger, smaller females. Scott et al. (2006) simulated stock-recruitment scenarios for Atlantic cod (*Gadus morhua*) with different age/size parameters to examine the impact of fishing on population structure. They compared stocks with similar spawning biomass and found that stocks with higher fishing mortality and lower mean age had much lower reproductive potential. Results from a meta-analysis in the Northeast Atlantic showed that spawner age structure may be important to the productivity of some fish stocks (Brunel 2010). Brunel analyzed 39 marine fish stocks as a group and individually and showed that recruitment and sensitivity of recruitment to temperature was related to spawner age composition across several groups of demersal and pelagic species. These examples illustrate the potential importance of spawner age or size structure to fecundity and recruitment of some marine species.

Observed changes in age at maturity of sockeye salmon may affect their reproductive potential. Potential effects of age composition of spawners on future production of sockeye salmon have not been studied. Current Bristol Bay management focuses on the total number of spawners only and does not consider spawner age-composition when setting and implementing escapement goals. We hypothesize that age composition, in addition to the total number of spawners, affects future recruitment and age structure.

The main goal of this study was to better understand the influence of spawner age composition in Bristol Bay on subsequent returns. Specifically, I first quantified the changes over time (1960-2002) in the age composition of sockeye salmon escapement for the Ugashik River, as well as for other river systems in Bristol Bay, Alaska. Second, I quantified the influence of spawner age composition on the age composition of future sockeye salmon returns in Bristol Bay. Third, I examined potential effects of spawner age composition on recruitment.

Effects of the age composition of spawning sockeye salmon on future returns of sockeye salmon to Bristol Bay, Alaska¹

Abstract

The age structure of sockeye salmon on the spawning grounds is highly variable, yet little is known about the influence of spawner age composition on subsequent abundance and age composition of recruits. Management of Bristol Bay sockeye salmon relies on estimated spawner abundance to determine escapement goals, without regard to age or size composition. This may not accurately reflect reproductive potential. Parental age structure and environmental conditions were included as independent variables in statistical models to evaluate their effect on age structure of their progeny. In addition, relationships between spawner age composition and the abundance of recruits were examined. We found a significant relationship between the age composition of spawners and that of their progeny, as well as environmental effects on the age composition of returns. A higher proportion of spawners that spent three years in the ocean were associated with a higher proportion of recruits with a similar life history pattern, suggesting direct genetic and/or environmental influences. However, redefining spawner-recruit models based on spawner age composition did not significantly improve predictions of the overall number of recruits originating in a given brood year. Nevertheless, the ability to predict the age and hence size composition of returns (with uncertainty), implies that improved predictions of the total biomass of returns in a given year is possible.

¹ Mueller, J.C., F.J. Mueter, T.T. Baker, Canadian Journal of Fisheries and Aquatic Sciences, Effects of the age composition of spawning sockeye salmon on future returns of sockeye salmon to Bristol Bay, Alaska (in prep)

Introduction

Bristol Bay, Alaska (Fig. 1) supports one of the largest sockeye salmon (*Oncorhynchus nerka*) runs in the world (Holt and Peterman 2004; Baker 2006; Scott et al. 2006; Morgan et al. 2007). Annual returns from this sockeye salmon fishery have ranged from less than one million to more than 66 million fish since 1956 (Flynn et al. 2006) with an ex-vessel value of up to \$200 million (Morstad et al. 2009). Bristol Bay sockeye salmon are widely considered to be an example of a successfully managed stock, which involves meeting harvest and escapement goals while attempting to conserve genetic diversity of the runs (Hyun et al. 2005). All Alaska salmon fisheries were certified as sustainable by the Marine Stewardship Council in 2000 and were re-certified in 2007.

To determine how many fish from a given brood year return to their natal river systems, age compositions of salmon intercepted in the fishery (catches) and of salmon escaping upriver to spawn are estimated each year. These estimates are used to construct brood tables for each system, which summarize the number of salmon returning to the system by age class.

In accordance with statewide salmon management policies, escapement goals for salmon consist of a fixed target range specifying the number of salmon that are intended to escape the fishery to return to the spawning grounds. Fishery managers in Bristol Bay set separate escapement goals for each of the major river systems in the region as determined by spawner-recruit analysis (Minard and Meacham 1987). Escapement is monitored continuously throughout the season and the commercial fishery is regulated through short-term openings within each of five fishing districts to meet escapement goals.

Spawner age composition may have important effects on fecundity, size, and viability of eggs and may contribute to variations in recruitment. For example, Berkeley et al. (2004) showed that larger female black rockfishes (*Sebastes melanops*) produce larvae that are more robust to starvation and grow at faster rates than those of younger, smaller females. Scott et al. (2006) simulated stock-recruitment scenarios for Atlantic cod (*Gadus morhua*) with different age/size parameters to examine the impact of fishing on population structure. They compared stocks with similar spawning biomasses and found that stocks with higher fishing mortality and lower mean age had much lower reproductive potential. Results from a meta-analysis in the Northeast Atlantic showed that spawner age structure may be important to the productivity of some fish stocks (Brunel 2010). These examples illustrate the potential importance of spawner age or size structure to fecundity and recruitment of a number of marine species.

Current Bristol Bay management focuses on the total number of spawners only and does not consider spawner age-composition when setting and implementing escapement goals. We hypothesize that age composition, in addition to the total number of spawners, affects subsequent abundance and age structure of recruits. Therefore, the main goal of this study was to understand the importance of spawner age composition in Bristol Bay on future returns. We quantified the changes over time (1960-2002) in the age composition of sockeye salmon escapement, quantified the influence of spawner age composition on the age composition of future sockeye salmon returns and examined the effect of spawner age composition on recruitment in Bristol Bay.

Methods

Data

We used historical data on the age composition of escapements and total runs over 1956-2008 for nine Bristol Bay river systems. Harvest, escapement, and age composition estimates from individual rivers were collected by the Alaska Department of Fish and Game (ADF&G), to estimate total annual run size (numbers of fish) for each of the major

river systems in Bristol Bay. Commercial harvests, in numbers of salmon by district, were taken from summaries of final fish tickets (sales receipts of delivered landings). Sockeye salmon, harvested in the commercial fisheries in each district, were allocated to their river of origin using the following methods. In districts with only one major river system (e.g. Ugashik, Egegik, and Togiak), all the sockeye salmon commercially harvested in that district were assumed to have originated from that river. In districts with more than one major river system (e.g. Naknek-Kvichak, Nushagak), commercially harvested salmon were allocated to each river using the “Pooled” method of Bernard (1983) that separates the harvest by age-class based on the proportion of each age-class observed in the escapement of each river. One of the assumptions of this method is that sockeye salmon from each of the rivers was proportionally represented in the commercial fisheries. Sockeye salmon escapement was estimated using visual counting towers in the Ugashik, Egegik, Naknek, Alagnak, Kvichak, Wood, Igushik, and Togiak rivers (Anderson 2000). Hydroacoustics were used to estimate sockeye salmon in the Nushagak River (Brazil 2008).

Age compositions of sockeye salmon in the harvest and escapement were estimated each year. ADF&G uses stratified sampling to randomly sample sockeye salmon from the commercial harvest and from escapements in Bristol Bay. Sockeye salmon were sexed, measured for length (to the nearest 1 cm) and weight (to the nearest gram), and a scale was taken to determine age. Scales were taken from the left side of the fish approximately two rows above the lateral line in the area crossed by a diagonal from the posterior insertion of the dorsal fin to the anterior insertion of the anal fin. Salmon ages were determined by examining patterns of growth on the scales. Age and growth can be differentiated between freshwater and saltwater life stages. Ages were denoted by two numbers following European notation (Koo 1962): the first number representing how many winters the fish spent in freshwater and the second number representing how many winters they spent in the marine environment. For example, if a sockeye salmon spent one year in freshwater after emergence and three years in the ocean, its age would be

denoted as age-1.3. Total age of the fish from the time of deposition equals the sum of these two digits plus one.

Total run estimates by age class were used to create brood-year (brood) tables that show the number of sockeye salmon that spawned in that year (escapement) and the number of sockeye salmon by age-class that were produced and returned in subsequent years. The brood tables from the nine major river systems in Bristol Bay were combined to create a brood table for all sockeye salmon in Bristol Bay.

For this study, we focused on the four major age classes of sockeye salmon: ages 1.2, 1.3, 2.2, and 2.3, which, in most years, comprise over 98% of the total returns (Murphy et al. 2007). For the initial analysis, we focused on the Ugashik River data set for 1966-2005 because this data set had few catch allocation problems; that is, the majority (77-90% in 2006-2008) of the sockeye salmon harvested in the Ugashik District originated from the Ugashik River (Dann et al. 2009). Sockeye salmon from the Ugashik River were also harvested in smaller numbers in other districts (primarily Egegik District) in Bristol Bay. To examine whether our results may be applicable to other systems, we repeated the analysis using data from all Bristol Bay stocks combined.

In addition to the effects of parental age composition on the age composition and number of returns, we also examined the possible effects of total spawner abundance and environmental conditions. To account for potential density dependence, we included spawner abundance (S) as an index of egg production, where S was defined as the total number of spawners in a given brood year (Baker 2006). To represent environmental conditions during freshwater residence, air temperature (AT) was calculated as the average winter air temperature (November-March) during the second winter following a spawning event (Table A3-1). Temperatures during the second winter determine spring conditions experienced by the first smolts of a given brood stock that outmigrate to the ocean. Air temperature during the winter months may affect ice formation and thickness,

as well as the timing of spring breakup, which could affect the timing and magnitude of forage production in the lake. As an alternative to winter air temperatures, we considered mean spring (May-July) air temperature (ATS), also during the second year after spawning, because it may better reflect when break-up occurs. To account for large-scale temperature variability in the marine environment, we included a winter (November-March) average of the Pacific Decadal Oscillation (PDO) (Mantua 1997) (Table A3-2).

Parental age composition was quantified as the proportion of 3-ocean spawners (M), defined as the number of fish that spent three years in the ocean (age-1.3 + age-2.3 spawners) divided by the total number of spawners. Our rationale for this measure was that it reflects the size-composition of spawners because salmon that spend more time in the ocean are generally larger (Hislop 1988; Kjesbu et al. 1996). To distinguish potential effects of freshwater residence from effects of ocean residence, we used the proportion of 2-freshwater spawners, defined as the number of spawners that spent two winters in freshwater (age-2.2 + age-2.3 spawners divided by total), as an alternative proxy for parental age composition (M2).

Multinomial analysis

We examined the effects of spawner age composition and environmental variability on their offspring by constructing empirical models of the age composition of the total returns in a given year. Representative samples from both the catches and from the escapement are taken each year and the number of sampled fish in each of the major age classes 1.2, 2.2, 2.3, or 1.3 may be assumed to follow a multinomial distribution with underlying probabilities π_i that a fish belongs to age class i . Therefore, we used a multinomial logit model to estimate the proportion by age of the four major age classes returning in a given year as a function of measures of spawner age composition (M), spawner abundance (S), winter air temperature (AT) during the freshwater phase and average winter PDO during the marine stage:

$$(1) \quad \log\left(\frac{\hat{p}_{i,t}}{\hat{p}_{ref,t}}\right) = \hat{\beta}_{0,i} + \hat{\beta}_{1,i}M_{t^*} + \hat{\beta}_{2,i}S_{t^*} + \hat{\beta}_{3,i}AT_{t^*} + \hat{\beta}_{4,i}PDO_{t^*}$$

$$\hat{p}_{ref,t} = 1 - \sum_{i=1}^{z-1} \hat{p}_{i,t}$$

where \log is the natural log, $\hat{p}_{i,t}$ is the predicted proportion of returns in return year t that are in age class i , t^* is explained below, $\hat{\beta}_{0,i}$ through $\hat{\beta}_{4,i}$ are regression parameters, $z = 4$ is the number of age classes, and $\hat{p}_{ref,t}$ is the predicted proportion of returns in the reference age class, which was arbitrarily chosen to be age-2.3. In the multinomial model, the probability that n_i out of N fish sampled in a given year are in age class i is given by:

$$\Pr(\mathbf{n} = \{n_1, \dots, n_z\}) = \binom{N}{n_1 \dots n_z} \pi_1^{n_1} \pi_2^{n_2} \dots \pi_z^{n_z}$$

where N is the total (effective) number of fish sampled and aged during return year t and π_i is the probability of a fish belonging to age class i . The ratio $\hat{p}_{i,t} / \hat{p}_{ref,t}$ in eq. 1 is also referred to as the odds ratio and the multinomial logit model predicts the log-odds ratio as a linear function of a set of predictor variables. Models were fitted using the 'vglm' function in the VGAM library (Yee 2010) for R (R Development Core Team 2010).

Parental age composition and spawner abundance were lagged to correspond to the time period when parental fish would have been spawning. In any given return year, returns are primarily composed of offspring from fish that spawned four (age classes 1.2), five (1.3, 2.2), and six (2.3) years earlier. Therefore, to model returns in year t , we averaged spawner age composition as follows:

$$M_{t^*} = (M_{t-6} + M_{t-5} + M_{t-4})/3$$

Spawner abundances were averaged over the same three years to obtain S_{t^*} . Similarly, the PDO index and the air temperature index were averaged over those winters when the major age classes of the fish returning in year t would have been present in the marine or freshwater environment, respectively:

$$PDO_{t^*} = (PDO_{t-3} + PDO_{t-2} + PDO_{t-1})/3$$

$$AT_{t^*} = (AT_{t-5} + AT_{t-4} + AT_{t-3})/3$$

In addition to the model in eq. 1, we considered all possible subsets of the selected explanatory variables, as well as models with two-way interactions included. The best model for drawing inferences about variability in age composition was selected based on the small sample corrected Akaike Information Criterion (Burnham and Anderson 1998) and residuals from the best models were examined for non-normality, heteroscedasticity, autocorrelation, and other patterns that may violate regression assumptions.

The models predict the proportion of age-1.2, 1.3 and 2.2 returns relative to the proportion of age-2.3 returns. Predicted values will be referred to as \hat{p}_{12} , \hat{p}_{13} , \hat{p}_{22} and \hat{p}_{23} , where $\hat{p}_{23} = 1 - \hat{p}_{12} - \hat{p}_{13} - \hat{p}_{22}$. Although a large number of fish are sampled each year (approximately 4,400), the effective sample size for such samples is generally much smaller than the actual number of fish measured. Using the square root of the sample size has frequently been used for analysis of similar age or length samples (Thompson 1995); hence we started with a sample size of 67 ($\cong \sqrt{4400}$) each year. However, preliminary analyses revealed that the resulting distribution was still overdispersed relative to a multinomial distribution; hence we used a correction factor to estimate an effective

sample size for use in the analysis. The initial sample size was multiplied by a correction factor, f :

$$f = \left(\text{var} \left(r_{it} \cdot \sqrt{\frac{N_{\text{int},t}}{\hat{p}_{it} \cdot (1 - \hat{p}_{it})}} \right) \right)^{-1} \quad (\text{See Appendix I for full derivation})$$

where p_{it} is the observed proportion in age class a and year t , \hat{p}_{it} is the expected proportion in age class a and year t , $N_{\text{int},t}$ is the initial (assumed) sample size in year t and r_{it} is equal to $p_{it} - \hat{p}_{it}$ (McAllister and Ianelli 1997; Maunder 2010). The effective sample size was assumed to be constant over time. Starting with $N=67$, N was updated iteratively until it converged to an estimated effective sample size of 37 for each sampling year, for a total sample size of 1480 observations across the 40 year time series. Using the same approach, baywide models had an effective sample size of 44. The observed proportions in each age class and year were multiplied by the total effective sample size and rounded to the nearest integer to obtain effective sample sizes by age class.

To evaluate the model fit, we also computed pseudo- R^2 values to quantify the proportion of variability in age composition for each age class as:

$$SSE_i = \sum_{t=1}^T (p_{it} - \hat{p}_{it})^2$$

$$SST_i = \sum_{t=1}^T \left(p_{it} - \frac{\sum p_{it}}{T} \right)^2$$

$$R^2_i = 1 - \left(\frac{SSE_i}{SST_i} \right)$$

where the p_{it} and \hat{p}_{it} are the observed and predicted proportions of returns of age class i in year t , respectively and T represents total sample years.

Binomial analysis

To gain further insight into the variability in individual age classes, we modeled proportions of fish in all four age classes individually using a logistic regression with the same explanatory variables that were identified as most important in the best multinomial model:

$$\log\left(\frac{\hat{\rho}_i}{(1-\hat{\rho}_i)}\right) = \hat{\alpha} + \sum \hat{\beta}_j X_{jt}$$

where the response $\hat{\rho}_i$ is the predicted proportion of age class i in the returns in year t , X_j is the j^{th} explanatory variable, t^* defines lagged terms as explained above, $\hat{\alpha}$ and $\hat{\beta}_j$ are linear regression coefficients.

Model results were used to assess the significance of the predictors at the 95% level ($p < 0.05$) and to illustrate the effect of spawner age composition and environmental variables on the proportions of the two major age classes (1.3 and 2.2) in the returns.

Ricker stock-recruit analysis

To address the potential impacts of spawner age composition on recruitment, we incorporated measures of age composition into models of recruitment. We used a generalized Ricker Model with spawner abundances redefined in one of several ways to represent both the number of spawners and their age composition. For these models, we considered both full (1960-2002) and restricted time series (1976-2002), due to a known environmental regime shift in 1976/77 that affected the productivity of sockeye salmon (Peterman et al. 1998) and due to changes in management strategy that occurred in the late 1970s. The general Ricker model has the form:

$$R_t = \alpha S_t e^{-\beta S_t + \sum \gamma_j X_{tj}} = \alpha S_t e^{-\beta S_t} e^{\sum \gamma_j X_{tj}}$$

where R_t is the number of recruits from brood year t , S_t is the number of spawners in year t , α is the productivity parameter, β is the density dependent parameter, $\sum \gamma_j X_{tj}$ represents a multiplicative effect of one or more other variables X_j on recruitment, which may be lagged by one or more years, and γ_j are the coefficients capturing effects of X_j on recruitment. The model can be linearized as follows:

$$\log(R_t / S_t) = \log(\alpha) - \beta S_t + \sum \gamma_j X_{tj}$$

thus observed variability in log(recruits-per-spawner) among years can be modeled in the form of a multiple linear regression with intercept $a = \log(\alpha)$ and regression coefficients $b = -\beta$ and γ_j :

$$(2) \log(R_t / S_t) = a + bS_t + \sum \gamma_j X_{tj} + \varepsilon_t$$

The residuals, ε_t , were assumed to be independent and normally distributed but were examined for possible autocorrelation.

We fitted several alternative models that use different approaches to quantifying reproductive potential. First, we modeled $\log(R_t/S_t)$ as a function of both spawner abundance and spawner age composition:

$$\log(R_t / S_t) = a + bS_t + \gamma M_t + \varepsilon_t$$

where, as before, S_t is the number of spawners in a given brood year and M_t is the proportion of those spawners that spent three years in the marine environment. Including M_t allowed us to directly quantify the additional proportion of the overall variability in $\log(R_t/S_t)$ that could be explained by spawner age composition and to test whether the effect is significant.

In a second approach, we separately estimated potential effects of smaller, 2-ocean fish, and larger, 3-ocean fish on recruitment by modeling $\log(R_t/S_t)$ as a function of the abundance of 2-ocean and 3-ocean spawners:

$$\log(R_t / S_t) = a + b_1 * S2_t + b_2 * S3_t + \varepsilon_t$$

where $S2_t$ and $S3_t$ are the abundances of spawners that spent two and three years in the marine environment, respectively.

As a third measure of reproductive potential, we estimated egg production based on the number of years spent in the ocean and the average fecundity of 2-ocean and 3-ocean spawners, respectively, in Bristol Bay (Brandon Chasco pers. comm.). We modeled $\log(R_t/S_t)$ as a function of the estimated number of eggs as follows:

$$\log(R_t / S_t) = a + b * E_t + \varepsilon_t$$

where the number of eggs spawned in a given year was estimated as:

$$E = w2 * E2 + w3 * E3$$

where $w2$ and $w3$ are the proportions of 2-ocean and 3-ocean spawners, respectively, and $E2 = 3,196$ and $E3 = 4,350$ are the average number of eggs of 2-ocean and 3-ocean spawners. Generalized Ricker models were compared using AICc values to select the best overall models for predicting log-survival. However, models that did not have biologically reasonable parameter estimates were rejected.

Results

Trends in spawner age composition

In the Ugashik system, proportions of the four major spawner age classes fluctuated considerably through time (Fig. 2), but did not show a significant long-term trend over 1966-2005 based on linear regressions of the observed age-class proportions on year ($p = 0.254, 0.182, 0.054,$ and 0.199 for ages 1.2, 1.3, 2.2, and 2.3, respectively). The proportions of 3-ocean fish varied from 11% to 69% of the spawners in a given year. Age-1.3 spawners showed the greatest variability, ranging from 0.2% to 86% of the

spawning population. The absolute number of spawners drastically increased in the late 1970s due to changes in ocean productivity and management (Fig. 2). The mean numbers of spawners during 1966-1978 and 1979-2005 were approximately 281,000 and 1,200,000, respectively.

The age composition of all sockeye salmon (catches + escapement) returning to the Ugashik system showed similar variability (Fig. 3) and no significant linear trend over time for any of the age classes ($p = 0.725, 0.210, 0.094, 0.800$ for ages 1.2, 1.3, 2.2 and 2.3, respectively). The proportion of 3-ocean returns varied from 2% to 92% of the returns in a given year. The absolute number of returns to the Ugashik River (Fig. 3b) shows a similar trend to the Ugashik River spawners (Fig. 2b).

Environmental time series and spawner abundance showed high interannual variability and decadal-scale trends (Fig. 4). We fitted models with both spring and winter air temperatures as independent variables; winter air temperatures generally provided the best fits based on AICc ($\Delta AICc > 10$, in all cases). Winter air temperature and the PDO showed substantial warming associated with a climate regime shift in the late 1970s and two subsequent cool periods in the early 1990s and early 2000s (Fig. 4). Linear regressions of winter air temperature and the PDO showed significant increasing trends over time ($p = 0.0002$ and 0.003 , respectively), primarily due to the warming in the late 1970s. Spawner abundance was relatively low prior to the mid-1980s and increased thereafter with two pronounced peaks in the mid 1980s and mid-1990s (Fig. 4d). The proportion of 3-ocean spawners showed high interannual variability with an increasing trend and decreasing variability over time (Fig. 4a). In particular, the proportion of 3-ocean spawners was generally above 30% after 1990 but was frequently lower in earlier years. In the Ugashik River system, 3-ocean spawners represented less than 11% to over 68% of the spawning population.

The effects of different variables could not always be clearly separated because of confounding among the independent variables (Table 1). For example, spawner abundances were moderately to strongly correlated both with air temperatures and with the PDO and air temperature was strongly correlated with the PDO.

Variability in age composition: multinomial logit models

Multinomial logit models of the age composition of returns provided reasonable fits to the data (Fig. 5). The full model (Eq. 1) using 3-ocean spawners (M), as opposed to 2-freshwater spawners (M2) as a proxy for spawner age composition provided a much better fit (lower AICc, Table 2). Hence, we only discuss results for models that used 3-ocean spawners to represent spawner age composition. The AICc-best multinomial model included spawner age composition, spawner abundance, winter air temperature and the Pacific Decadal Oscillation as explanatory variables (Table 2) and accounted for approximately 29% of the variability in overall age composition. None of the two-way interactions improved the model fit based on AICc.

The proportion of age-1.3 and age-2.2 returns was significantly related to spawner age composition ($p = 0.031$ and 0.023 , respectively). Of the four age classes modeled in the multinomial model, age-1.3 and age-2.2 showed the strongest relationships with spawner age composition and the best model explained 44% and 22%, respectively, of the variability in the proportion of these age classes across years (Fig. 6). Model residuals were approximately normally distributed, did not show obvious heteroscedasticity or time trends, and were not autocorrelated (Durbin-Watson test: $p > 0.05$ in all cases).

The proportion of 3-ocean spawners (M) had an apparent positive effect on the proportion of returns that spent three years at sea (age 1.3 and age-2.3) (Fig. 6). In contrast, the proportion of returns that spent two years at sea (age-1.2 and age-2.2) decreased with M. Positive PDO anomalies during the marine phase were associated with lower proportions of age-1.3 and age-2.2 returns (negative coefficients, Table 3) and a higher proportion of age 1.2 returns. Warm winter air temperatures during the

freshwater phase were significantly associated with higher proportions of age-2.2 returns at the 90% significance level ($p = 0.089$, based on linear regressions) and with lower proportions of age-1.3 returns ($p = 0.064$). Estimated coefficients for S imply that higher spawner abundances are associated with lower proportions of age-1.2 returns and higher levels of both age-1.3 and age-2.2 returns, relative to age-2.3 returns (Table 3).

Baywide multinomial model results were very similar to those for the Ugashik River system. Based on AICc, the best-fit model used spawner age composition, spawner abundance, winter air temperature and PDO as predictors (Table 2) and accounted for approximately 24% of the overall variability in age class proportions (25%, 25%, 24%, and 17% for ages 1.2, 1.3, 2.2, and 2.3, respectively). The estimated effects of environmental variables on baywide proportions of different age classes were very similar to those estimated for the Ugashik River.

Variability in age composition: logistic regression models

Results from the binomial models further supported the results of our multinomial models. Binomial models of age-1.3 and age-2.2 returns provided reasonable fits to the data, while models for age-1.2 and age-2.3 returns were not significant. When modeling age-1.3 returns, using M, S, PDO and AT as predictors produced the best fit (Table 4). When modeling age-2.2 returns, the model using M, PDO and AT had the best fit (Table 3), however a model with only M and AT as predictors had a similar AICc value ($\Delta\text{AICc} < 1$).

Spawner age composition showed strong relationships with the proportion of age-1.3 and age-2.2 returns ($p = 0.0004$ and 0.0043 , respectively). A large proportion of 3-ocean spawners was associated with a subsequent increase in the proportion of age-1.3 returns and a corresponding decrease in age-2.2 returns. For both age classes, other predictor variables that were selected based on AICc did not show significant relationships with the age composition of returns at the 95% level ($p > 0.05$), but estimated effects were

consistent with results from the multinomial model. For example, the proportion of age-1.3s was higher if air temperatures at the freshwater stage were warmer.

Ricker model results

Using measures of spawner age composition or reproductive success in a generalized Ricker model to predict log-survival of sockeye salmon did not consistently improve the model fit. None of the models using the full time series (1960-2002) with measures of age composition to predict log-survival of Ugashik River salmon resulted in a significant improvement over the basic Ricker model. However, when using the post-regime shift period only (1976-2002), a Ricker model using egg production (E) instead of spawner abundance resulted in the best fit ($\Delta\text{AICc} = 0$, Table 5) and explained 32.4% of the variability in log-survival. Nevertheless, all of the Ugashik model fits had very similar AICc values ($\Delta\text{AICc} < 2$, Table 5). Similar to the Ugashik fits, the later part of the time series produced a better fit ($R^2 = 37\%$ for 1976-2002; $R^2 = 6.3\%$ for 1960-2002) to the data from all sockeye salmon systems in Bristol Bay combined and the best baywide model fit only included E as a measure of spawning potential (Table 5).

Discussion

Our model fits suggest a strong relationship between the age composition of sockeye salmon spawners and that of their offspring; however, incorporating age composition information into the stock-recruitment relationship did not improve estimates of recruitment to the fishery. We found that an increase in the proportion of 3-ocean spawners on the spawning grounds was associated with an increase in age-1.3 returns and a concurrent decrease in age-2.2 returns. The impact of spawner age composition on the age composition of returns was more pronounced than the impact of temperature conditions. This relationship supports the hypothesis that, by allowing more 3-ocean fish to spawn, more 3-ocean fish are likely to return. This may be important to the fishery, because fish spending three years in the ocean environment tend to be larger on average

(Quinn 2005; Ruggerone et al. 2009) and contribute more total weight to fishery landings.

Parental effects on age composition

The observed positive relationship between the proportion of 3-ocean spawners and subsequent age-1.3 returns is likely related to parental effects on growth rates and maturation that could have several causes. Differences in growth and maturation determine the age structure of returns and there are two important components to growth for sockeye salmon: growth in freshwater and growth in the marine environment. These may be affected by different factors and interact with each other. Initial growth rates and size of early stages of sockeye salmon may be affected by the quantity (density-dependence) and quality of eggs, and growth rates in both the freshwater and marine environment may be influenced by environmental factors that determine the productivity of these systems such as local temperatures, large-scale climate changes, and habitat dynamics.

Egg size and fecundity are positively correlated with female length for multiple fish species (Healey and Heard 1984; Beacham and Murray 1985; Hendry et al. 1999). If true for sockeye salmon, allowing more 3-ocean fish to escape into a river system may not only increase the number of eggs but also leads to a higher proportion of larger eggs and potentially larger fry. In the absence of strong density-dependence, these larger fry may grow faster in the freshwater environment and hence outmigrate to the ocean as one-year old smolts; however, they would still be significantly smaller than smolts that spent two years in the freshwater system (Moulton 1997). Therefore, a portion of these smaller smolts may need to spend a third year at sea in order to reach an appropriate maturation size, resulting in a larger proportion of age 1.3 fish returning to spawn.

There may also be a genetic component to growth or age at maturation that would result in offspring that have similar rates of growth and maturation as their parents (Habicht et

al. 2007). Habicht et al. (2007) found that genetic diversity plays a role in developing distinct subpopulations in Bristol Bay and they show that this information can be used to improve understanding of managed populations. Genetically determined patterns of growth and maturation may result in offspring with an age composition similar to that of the parents.

The apparent positive effect of total spawner abundance on proportions of both age-1.3 and age-2.2 returns can be interpreted in a number of ways. The number and density of eggs in the streams and lakes of a system increases with the number of spawners and is likely to lead to density-dependent effects on survival. In years where spawner abundance is high, the larger age-1.3 and age-2.2 spawners may be outcompeting age-1.2 spawners, which may in turn lead to more similarly aged returns in the future. The relatively low proportion of age-2.3 spawners may not represent a large enough portion to be strongly affected by spawner abundance. In years following low spawner abundances, the proportion of age-1.2 and age-2.3 returns may increase, due to less competition with the two dominating age classes.

Environmental effects on age composition

Temperature conditions, in addition to parental age structure, appear to affect age composition of returns, most likely through effects on growth. Climate has been shown to effect survival rates in both freshwater and marine environments (Peterman et al. 1998; Botsford et al. 2011), which could drive populations to spend more or less time in either environment and, in turn, change the age composition of a population. The PDO, as an indicator of conditions in the early marine environment, had a negative effect on the proportions of age-1.3 and age-2.2 returns and a positive effect on age 1.2 returns, relative to age 2.3 returns (Table 3). A higher proportion of age 1.2s during the positive (warm) phase of the PDO, which is associated with warm temperatures in coastal Alaska, may result from faster growth during early marine life (Ruggerone et al. 2007) and hence earlier maturation. In contrast, the cool phase of the PDO resulted in more late maturing

fish (1.3s), which may result from reduced growth and delayed maturation when coastal temperatures are cold. However, the effects of the PDO are to some extent confounded with the effects of air temperatures due to coupling of air and ocean temperatures. Ocean temperatures also determine the marine distribution of sockeye salmon (Welch et al. 1998), hence changes in temperature may affect the spatial overlap between sockeye salmon and their prey, which could affect prey availability and therefore growth patterns.

The positive relationship between air temperature and the proportion of age-1.2 and age-1.3 returns may be related to the importance winter climate has on spring conditions. In warmer years ice breakup and hence the freshwater phytoplankton bloom may occur earlier, which results in a longer growing season overall and may increase the overall productivity and growing conditions in the lake systems. Hence sockeye smolts may grow faster and outmigrate to sea after one year in the freshwater system. The proportion of age-1. fish increased with winter air temperature (Table 3), supporting the hypothesis that warmer winters are associated with better growth conditions for fry, which may lead to a larger proportion of offspring outmigrating in their first summer instead of spending a second winter in freshwater. In the Kvichak River system a greater proportion of sockeye salmon smolt left freshwater after one winter when they grew rapidly (Rogers and Poe 1984). In addition, age specific lengths of sockeye salmon smolts in the Kvichak were significantly smaller from 1977-2003 compared to those during 1955-1976 (Ruggerone and Link 2006). The shift in size corresponds with an increase in the proportion of age-1 smolt and with the 1976-1977 ocean regime shift (Ruggerone and Link 2006). It should be noted that size is not the only factor that determines the duration of freshwater residence, because there are some sockeye salmon populations with slow growth that outmigrate as age 1. smolt (e.g. Lake Owichenk, British Columbia) and others that migrate predominately as age 2. smolt (e.g. Egegik River, Bristol Bay) (Burgner 1991).

Another environmental factor that may play a key role in causing variability in age structure is spawning habitat (substrate and hydrology), which was not explicitly considered in our models. Bristol Bay provides sockeye salmon with a large variety of spawning habitats and differences in habitat result in sub-populations that vary in body structure and age composition (Rogers 1987). Spatial and temporal changes in the hydrology of these habitats directly influence spawning success as well as survival and growth of juveniles during their time in freshwater (Hilborn et al. 2003). Moreover, the scale of these habitats is inversely correlated with variability in population age structure (Schindler et al. 2010), such that high variability at small spatial scales (e.g., individual tributaries or reaches) cancels out at the larger spatial scale of the major river systems. The ability to thrive in a diverse set of habitats provides these stocks with a high degree of resilience against environmental perturbations (Quinn 2005; Schindler et al. 2010).

Effects of age composition on recruitment

The Ricker model has been widely used to obtain pre-season forecasts of recruits (Dorner et al. 2008). Total spawner abundance has generally been used as measure of reproductive potential (Myers and Barrowman 1996; Holt and Peterman 2008), although egg production indices have been used in some cases such as lobster in Quebec (Attard and Hudon 1987), but not for sockeye salmon in Bristol Bay. Here we attempted to account for egg production in several ways but doing so did not improve estimates of recruitment. However, although the effect of egg production was not significant, increases in the proportion of 3-ocean spawners was positively related to recruitment, consistent with higher viability of the offspring of 3-ocean fish. Moreover, effects of differences in egg production may be masked at high spawner abundances due to density-dependent effects and egg production may only be important in years of low spawner abundance when density-dependent limitations on survival are less pronounced.

Several other studies have documented the importance of spawner age composition and successfully incorporated this information into stock assessment and management. For

example, the length of female Atlantic cod (*Gadus morhua*) is positively related to both fecundity and egg size (Marteinsdottir and Begg 2002), presumably resulting in a disproportionate contribution of large females to total reproductive success. This is evident in the Northeast Arctic stock of Atlantic cod, where reproductive success and recruitment is influenced not only by spawning stock biomass but also by the number and quality of eggs available (Marshall et al. 1998). Models of Atlantic cod have shown the benefit of older females to the fishery, and how changes in age and size of spawners have more of an impact on the success of the fishery than the timing of spawning events (Murawski et al. 2001, Scott et al. 2006). In contrast, simulations of Pacific ocean perch (*Sebastes alutus*) dynamics showed that reduced survival rates of offspring from younger females had little to no effect on commonly used fishing rate references points (Spencer et al. 2007). More recently, Branch and Hilborn (2010) used a run reconstruction model that incorporates catch, escapement and age composition data to forecast recent runs in three fishing districts of Bristol Bay. They showed how age classes arriving at different times affect the fishery and that changing gear selectivity in the models directly altered the age composition of spawners. These examples show how spawner age composition can have important consequences for the management of age-structured populations.

Further insights and caveats

One of the assumptions of this study is that all or most of the fish that were caught or escaped in a specific river originated in that same river. If catches cannot be allocated reliably, then interpreting changes in age composition may be problematic because of the variable contribution from other systems that may have a very different age structure. We chose to use the Ugashik River data, because it is the southernmost system in Bristol Bay and is less likely to have issues of catch allocation. Based on genetic analyses, on average 90% of the sockeye salmon commercially caught in the Ugashik District from 2006-2008 originated from the Ugashik River (Dann et al. 2009). Therefore, we believe that our results are not affected by catch allocation issues. Further improvements could be achieved by using genetic information to allocate catches.

Our analysis suggests that using measures of egg production that account for differences in age structure instead of the total number of spawners has the potential to improve stock-recruitment relationships and associated reference points for sockeye salmon. While our relatively crude estimate based on average fecundity at age only resulted in a marginal improvement, better information about sockeye salmon fecundity from individual rivers in Bristol Bay would provide refined measures of reproductive success that could be used to develop improved escapement goals. Currently, egg counts are available for few river systems and targeted field studies will be needed to obtain better estimates of fecundity-at-size for each system. Clearly, maternal influences on the growth and survival of offspring that result from size-or age-dependent differences in the quantity and quality of eggs can have important consequences for the fishery (Kjesbu et al. 1996; Marteinsdottir and Begg 2002; Scott et al. 2006). Our study provides evidence that the maternal age structure of sockeye salmon has potentially important consequences for the rate of growth and survival of the resulting brood. Simulation studies will be needed to assess the potential benefits of taking maternal age structure into account in setting escapement goals or determining other biological reference points for sockeye salmon fisheries.

Ours was the first study examining the potential role of variability in spawner age composition to sockeye salmon dynamics, but we anticipate many future applications. For example, these data could be used to improve forecasts of run size (Chasco et al. 2007) and to evaluate management strategies through simulations. Potential simulations might involve changing management schemes (e.g. different escapement goals, targets for age structure on spawning grounds) and predicting the consequences for the abundance and age structure of returns. Another simulation might include environmental variables such as temperature to evaluate the potential consequences of future climate changes for this fishery. This dataset could also be used as a surrogate for other sockeye salmon populations in Alaska or other geographic regions and the methods applied here

could be extended to other river systems within Bristol Bay and around Alaska, as well as to other species of salmon.

Although the Bristol Bay sockeye salmon age composition data represents one of the longest fisheries datasets in Alaska, our results should be interpreted with caution. There have been many changes in the management of sockeye salmon. One example of changes in management is directly related to escapement goals; in the late 1970s Bristol Bay managers started to allow much higher numbers of spawners on the spawning grounds, which had a large impact on the abundance of returns (Hilborn et al. 2003). Field sampling techniques may also have changed through time and user errors could have had different effects on data quality through time. These changes could lead to errors and bias in the analyses and should be acknowledged when interpreting these results.

Implications for management and general conclusions

As long as salmon have been harvested in Bristol Bay, environmental and managerial changes have impacted the health of the sockeye salmon fishery. The current escapement-focused management strategy has produced good returns and has supported a healthy and diverse fishery. In particular, the past several decades have seen unprecedented returns due to a combination of high ocean productivity and precautionary management. This study has advanced our understanding of the impact of age structure on sockeye salmon biology and our results can be used to improve the estimation of biomass returning to Bristol Bay systems. The relationship between spawner age composition and biomass returning to the fishery could have a large influence on how managers interpret age data in the future.

Salmon management faces multiple challenges and should continue to invest in understanding the full potential of environmental and human impacts on the Bristol Bay fishery. In particular, anticipated climate changes may lead to changes in ocean

productivity, in the distribution of salmon in the ocean, and in changes in freshwater habitats. Both freshwater and marine habitats may also be affected by oil and gas development and by ongoing and proposed mining activities. The effects of these changes, individually and in combination, will test our ability to effectively manage sockeye salmon fisheries. Our results provide another tool for better evaluating the potential consequences of such impacts on the age structure and on the future health and diversity of sockeye salmon stocks in Bristol Bay to ensure that the fishery remains healthy.

References

- Anderson, C.J. 2000. Counting tower projects in the Bristol Bay area, 1955-1999. Alaska Department of Fish and Game, Regional Information Report No. 2A00-08, Anchorage.
- Attard, J., and Hudon, C. 1987. Embryonic development and energetic investment in egg production in relation to size of female lobster (*Homarus americanus*). Can. J. Fish. Aquat. Sci. **44**: 1157-1164.
- Baker, T.T. 2006. Review of Salmon Escapement Goals in Bristol Bay, Alaska 2006. Alaska Department of Fish and Game, Commercial Fisheries Memorandum **No. 06-05**: 1-10.
- Beacham, T.D., and Murray, C.B. 1985. Effect of female size, egg size, and water temperature on developmental biology of chum salmon (*Oncorhynchus keta*) from the Nitinat River, British Columbia. Can. J. Fish. Aquat. Sci. **42**: 1755-1765.

- Berkeley, S.A., Chapman, C., and Sogard, S.M. 2004 Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. *Ecology* **85**: 1258-1264.
- Bernard, D.R. 1983. Variance and bias of catch allocation methods that use the age composition of escapements. Alaska Department of Fish and Game Informational Leaflet No. 227, Alaska Department of Fish and Game, Juneau, AK.
- Botsford, L.W., Holland, M.D., Samhour, J.F., White, J.W., and Hastings, A. 2011. Importance of age structure in models of the response of upper trophic levels to fishing and climate change. *ICES J. Mar. Sci.* **68**: 1270-1283.
- Brazil, C.E. 2008. Sonar enumeration of Pacific salmon escapement into the Nushagak River, 2004. Alaska Department of Fish and Game, Fishery Data Series No. 08-31, Anchorage.
- Branch, T.A., Hilborn, R. 2010. A general model for reconstructing salmon runs. *Can. J. Fish. Aquat. Sci.* **67**: 886-904.
- Brunel, T. 2010. Age-structure-dependent recruitment: a meta-analysis applied to Northeast Atlantic fish stocks. *ICES J. Mar. Sci.* **67**: 1921-1930.
- Burgner, R.L. 1980. Some features of ocean migrations and timing of Pacific salmon. *In* Salmonid Ecosystems of the North Pacific. *Edited by* W.J. McNeil, and D. C. Himsworth, Oregon State University Press, Corvallis, OR. pp. 153-164.
- Burgner, R.L. 1991. Life history of sockeye salmon (*Oncorhynchus nerka*). *In* Pacific Salmon Life Histories. *Edited by* C. Groot, and L. Margolis, V.U. Press. pp. 1-117.

- Burnham, K.P., and Anderson, D.R. 1998. Model selection and inference: a practical information-theoretical approach, Springer-Verlag, New York, New York.
- Chasco, B., Hilborn, R., and Punt, A.E. 2007. Run reconstruction of mixed-stock salmon fisheries using age-composition data. *Can. J. Fish. Aquat. Sci.* **64**: 1479-1490.
- Dann, T.H., Habicht, C., and Jasper, J.R. 2009. Genetic stock composition of the commercial harvest of sockeye salmon in Bristol Bay, 2006-2008. Alaska Department of Fish and Game, Fishery Manuscript Series No. 09-06, Anchorage.
- Dorner, B., Peterman, R.M., and Haeseker, S.L. 2008. Historical trends in productivity of 120 Pacific pink, chum, and sockeye salmon stocks reconstructed by using a Kalman filter. *Can. J. Fish. Aquat. Sci.* **65**: 1842-1866.
- Flynn, L., Punt, A.E., and Hilborn, R. 2006. A hierarchical model for salmon run reconstruction and application to the Bristol Bay sockeye salmon (*Oncorhynchus nerka*) fishery. *Can. J. Fish. Aquat. Sci.* **63**: 1564-1577.
- Groot, C., and Margolis, L. 1991. Pacific salmon life histories. University of British Columbia Press, Vancouver, BC.
- Habicht, C., Seeb, L.W., and Seeb, J.E. 2007. Genetic and ecological divergence defines population structure of sockeye salmon populations returning to Bristol Bay, Alaska, and provides a tool for admixture analysis. *Transactions of the American Fisheries Society* **136**: 82-94.
- Healey, M.C., and Heard, W.R. 1984. Inter- and intra-population variation in the fecundity of Chinook salmon (*Oncorhynchus tshawytscha*) and its relevance to life history theory. *Can. J. Fish. Aquat. Sci.* **41**: 476-483.

- Hendry, A.P., Berg, O.K., and Quinn, T.P. 1999. Condition dependence and adaption-by-time: breeding date, life history, and energy allocation within a population of salmon. *Oikos* **85**: 499-514.
- Hilborn, R., Quinn, T.P., Schindler, D.E., and Rogers, D.E. 2003. Biocomplexity and fisheries sustainability. *PNAS* **100**: 6564-6568.
- Hislop, J.R.G. 1988. The influence of maternal length and age on the size and weight of the eggs and relative fecundity of the haddock, *Melanogrammus aeglefinus*, in British waters. *J. Fish Biol.* **32**: 923-930.
- Holt, C.A., and Peterman, R.M. 2004. Long-term trends in age-specific recruitment of sockeye salmon (*Oncorhynchus nerka*) in a changing environment. *Can. J. Fish. Aquat. Sci.* **61**: 2455-2470.
- Holt, C.A., and Peterman, R.M. 2008. Uncertainties in population dynamics and outcomes of regulations in sockeye salmon (*Oncorhynchus nerka*) fisheries: implications for management. *Can. J. Fish. Aquat. Sci.* **65**: 1459-1474.
- Hyun, S.-Y., Hilborn, R., Anderson, J.J., and Ernst, B. 2005. A statistical model for in-season forecasts of sockeye salmon (*Oncorhynchus nerka*) returns to the Bristol bay districts of Alaska. *Can. J. Fish. Aquat. Sci.* **62**: 1665-1680.
- Kjesbu, O.S., Solemdal, P., Bratland, P., and Fonn, M. 1996. Variation in annual egg production in individual captive Atlantic cod (*Gadus morhua*). *Can. J. Fish. Aquat. Sci.* **53**: 610-620.
- Koo, T.S.Y. 1962. Age destination in salmon. Studies of Alaska red salmon. University of Washington Publications in Fisheries **1**: 37-48.

- Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M., Francis, R.C. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society* **78**: 1069-1079.
- Marshall, C.T., Kjesbu, O.S., Yaragina, N.A., Solemdal, P., and Ulltang, Ø. 1998. Is spawner biomass a sensitive measure of the reproductive and recruitment potential of Northeast Arctic cod? *Can. J. Fish. Aquat. Sci.* **55**: 1766-1783.
- Marteinsdottir, G., and Begg, G.A. 2002. Essential relationships incorporating the influence of age, size and condition on variables required for estimation of reproduction potential in Atlantic cod *Gadus morhua*. *Mar. Ecol. Prog. Ser.* **235**: 235-256.
- Maunder, M.N. 2010. Review and evaluation of likelihood functions for composition data in stock-assessment models: estimating the effective sample size. *Fish. Res.* **109**: 311-319.
- McAllister, M.K., and Ianelli, J.N. 1997. Bayesian stock assessment using catch-age data and the sampling-importance resampling algorithm. *Can. J. Fish. Aquat. Sci.* **54**: 284-300.
- Minard, R.E., and Meacham, C.P. 1987. Sockeye salmon management in Bristol Bay, Alaska. *Can. Spec. Publ. Fish. Aquat. Sci.* **96**: 336-342.
- Morgan, M.J., Shelton, P.A., and Bratney, J. 2007. Age composition of the spawning stock does not always influence recruitment. *Journal of Northwest Atlantic Fisheries Science* **38**: 1-12.

- Morstad, S., Jones, M., and Sands, T. 2009. 2009 Bristol Bay area annual management report. 101. Alaska Department of Fish and Game, Anchorage, AK.
- Moulton, L. 1997. Early marine residence, growth, and feeding by juvenile salmon in northern Cook Inlet, Alaska. *Alaska Fishery Research Bulletin* **4**: 154-177.
- Murawski, S.A., Rago, P.J., and Trippel, E.A. 2001. Impacts of demographic variation in spawning characteristics on reference points for fishery management. *ICES J. Mar. Sci.* **58**: 1002-1014.
- Murphy, B., Poetter, A., Tschersich, P., Jackson, J., and Russ, E. 2007. Alaska peninsula, Aleutian islands, and Atka-Amlia islands management areas salmon season summary, 2007. Alaska Department of Fish and Game, Commercial Fisheries Memorandum.
- Myers, R.A., and Barrowman, N.J. 1996. Is fish recruitment related to spawner abundance? *Fishery Bulletin* **94**: 707-724.
- Peterman, R.M., Pyper, B.J., Lapointe, M.F., Adkison, M.D., and Walters, C.J. 1998. Patterns of covariation in survival rates of British Columbian and Alaskan sockeye salmon (*Oncorhynchus nerka*) stocks. *Can. J. Fish. Aquat. Sci.* **55**: 2503-2517.
- Quinn, T.P. 2005. The behavior and ecology of Pacific salmon and trout, University of Washington Press, Seattle, WA.
- R Development Core Team 2010. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>

- Rogers, D.E. 1987. The regulation of age at maturity in wood river sockeye salmon (*Oncorhynchus nerka*). Can. Spec. Publ. Fish. Aquat. Sci. **96**: 78-89.
- Rogers, D.E., and Poe, P.H. 1984. Escapement goals for the Kvichak River system. Final Report to ADFG. FRI-UW-8407. Fisheries Research Institute, University of Washington, Seattle.
- Ruggerone, G., Nielsen, J., and Bumgarner, J. 2007. Linkages between Alaska sockeye salmon abundance, growth at sea, and climate, 1955-2002. Deep Sea Res. II **54**: 2776-2793.
- Ruggerone, G.T., and Link, M.R. 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. 104p.
- Ruggerone, G.T., Nielsen, J.L., and Agler, B.A. 2009. Linking marine and freshwater growth in western Alaska Chinook salmon *Oncorhynchus tshawytscha*. J. Fish Biol. **75**: 1287-1301.
- Schindler, D.E., Hilborn, R., and Chasco, B., 2010. Population diversity and the portfolio effect in an exploited species. Nature **465**: 610-613.
- Scott, B.E., Marteinsdottir, G., Begg, G.A., Wright, P.J., and Kjesbu, O.S. 2006. Effects of population size/age structure, condition and temporal dynamics of spawning on reproductive output in Atlantic cod (*Gadus morhua*). Ecol. Modell. **191**: 383-415.

- Spencer, P., Hanselman, D., and Dorn, M. 2007. The effect of maternal age of spawning on estimation of F_{msy} for Alaska Pacific ocean perch. *Biology, Assessment, and Management of North Pacific Rockfishes*, Alaska Sea Grant, University of Alaska Fairbanks, pp. 513-533.
- Straty, R.R., and Jaenicke, H.W. 1980. Estuarine influence of salinity, temperature, and food on the behavior, growth, and dynamics of Bristol Bay sockeye salmon. *In Salmonid Ecosystems of the North Pacific. Edited by W.J. McNeil, D.C. Himsworth*), Oregon State University Press, Corvallis, OR. pp. 247-265.
- Thompson, G.G. 1995. Plan Team for the Groundfish Fisheries of the Bering Sea and Aleutian Islands. *In Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions as projected for 1996*. North Pacific Fisheries Management Council, Anchorage, AK.
- Welch, D.W., Ishida, Y., and Nagasawa, K. 1998. Thermal limits and ocean migrations of sockeye salmon (*Oncorhynchus nerka*): long-term consequences of global warming. *Can. J. Fish. Aquat. Sci.* **55**: 937-948.
- Yee, W.T. 2010. The VGAM package for categorical data analysis. *Journal of Statistical Software* **32**: 1-34.

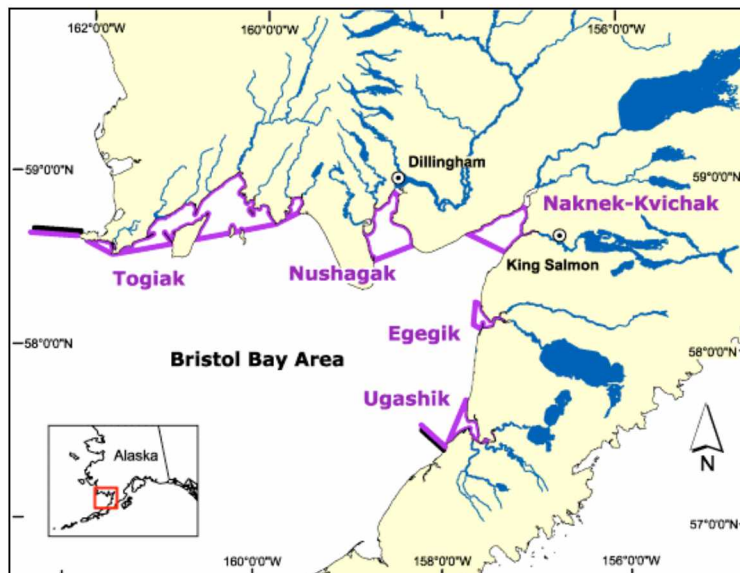
Figures

Figure 1. Map of Bristol Bay Alaska. The purple highlighted areas indicate the five commercial salmon fishing districts of Togiak, Nushagak, Naknek-Kvichak, Egegik and Ugashik.

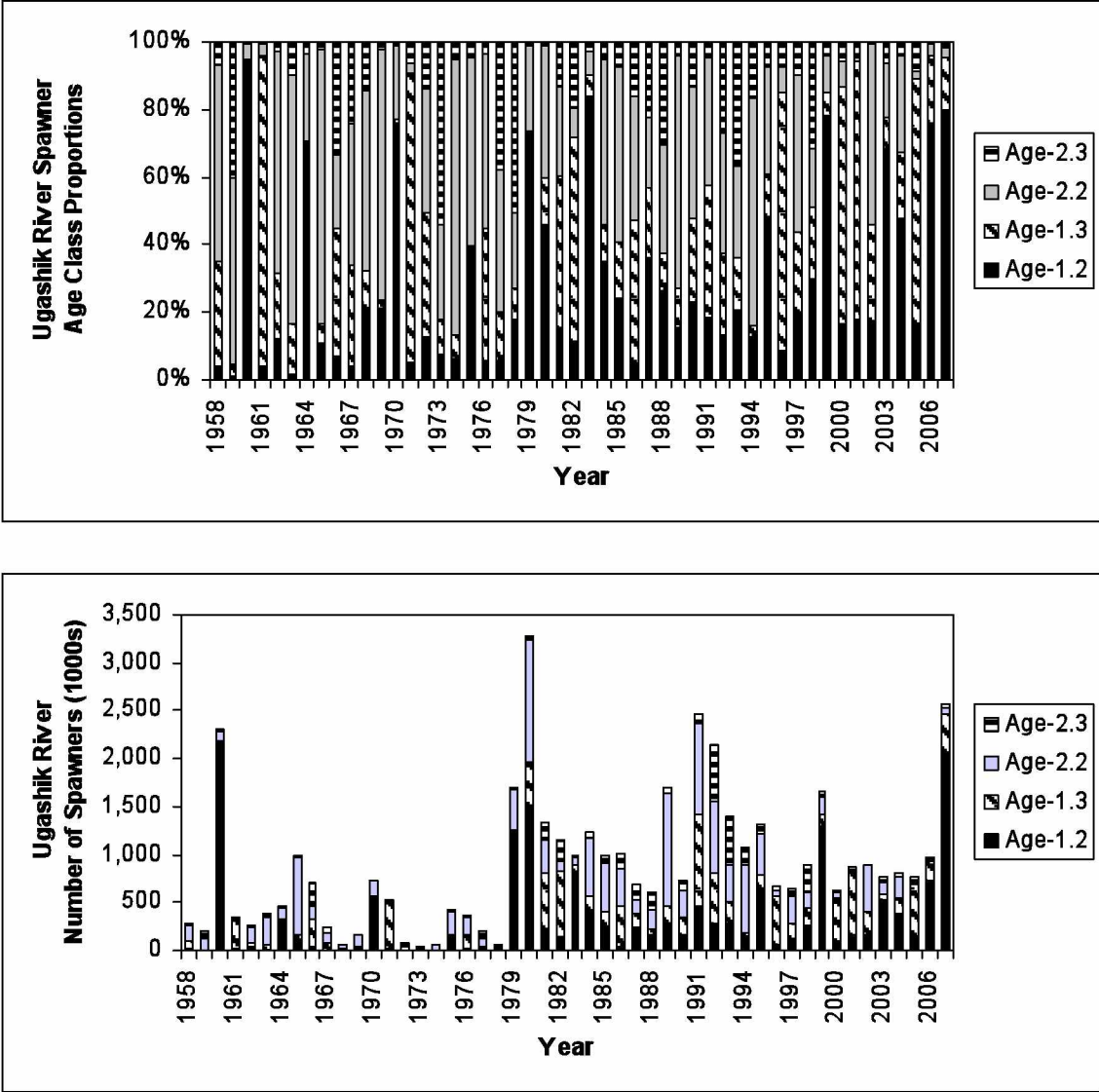


Figure 2. Proportions (top) and absolute numbers of spawners (bottom) by age-class in the Ugashik River, Bristol Bay, Alaska.

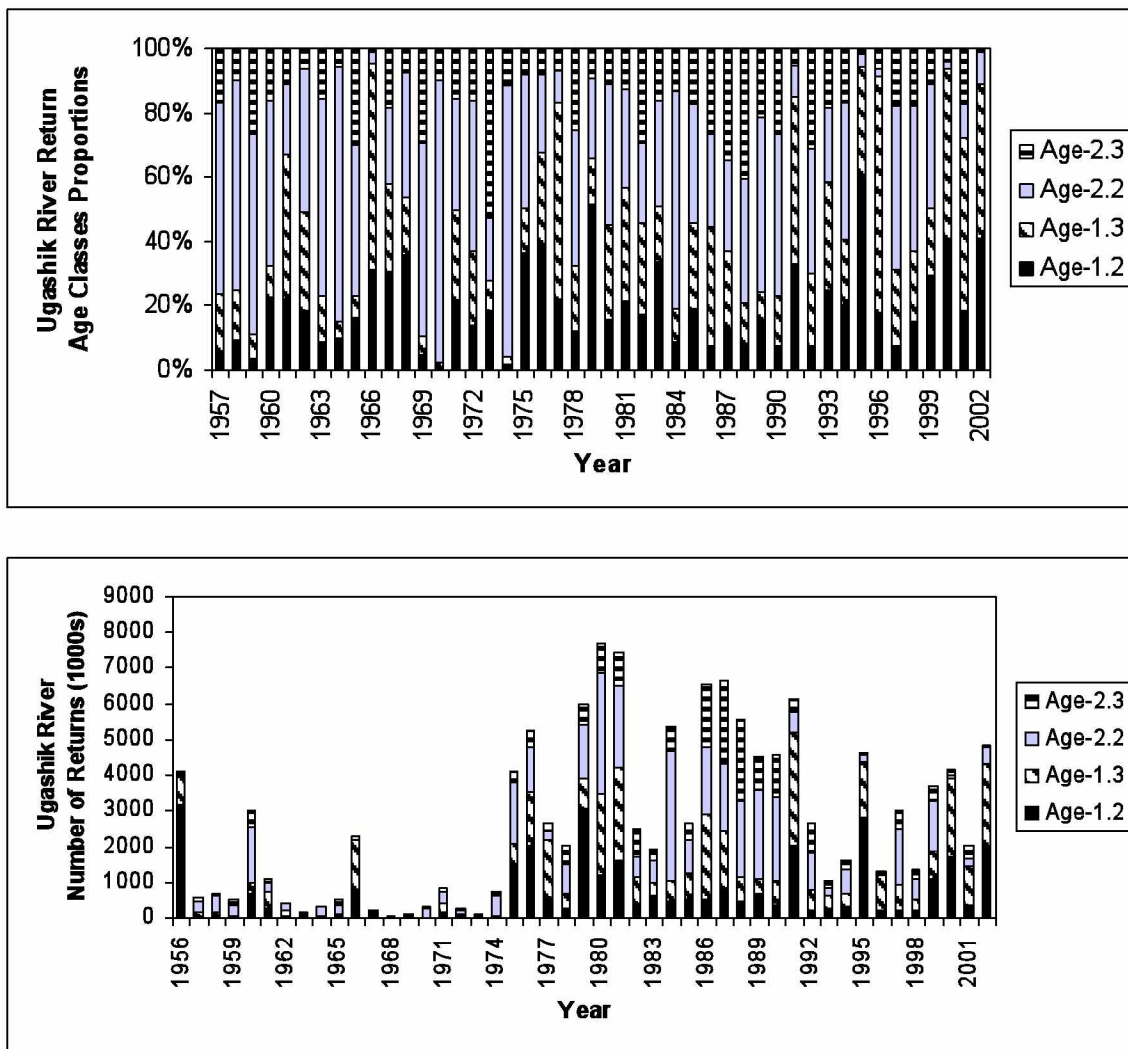


Figure 3. Proportions (top) and absolute numbers of returns (bottom) by age-class in the Ugashik River, Bristol Bay, Alaska.

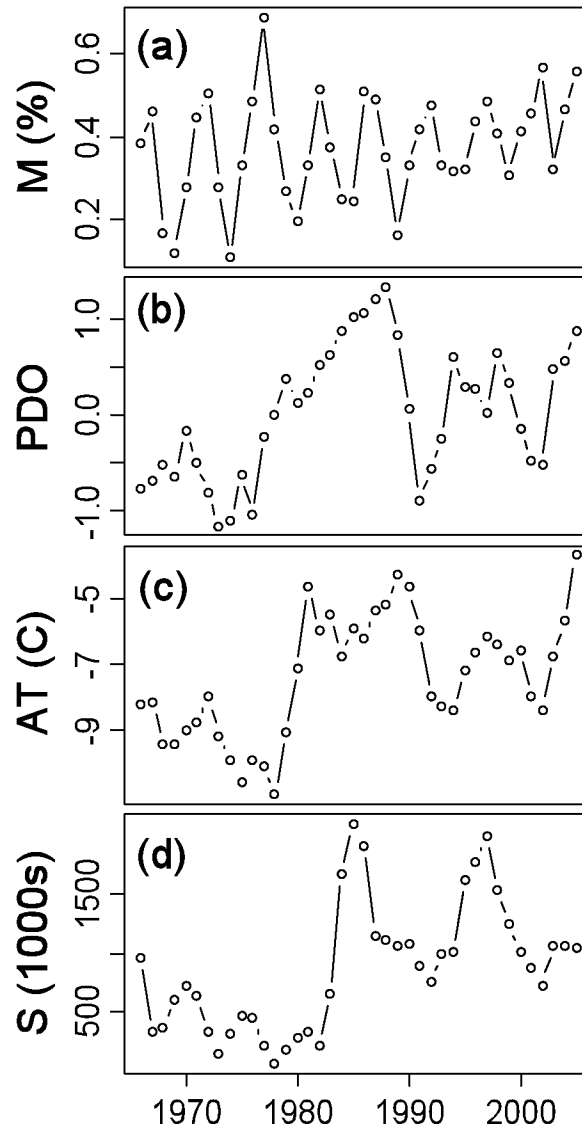


Figure 4. (a) Proportions of Ugashik River 3-ocean spawners, (b) Pacific Decadal Oscillation index, (c) Winter (November through March) average air temperatures at the King Salmon, Alaska, airport, and (d) Ugashik River spawner abundances from 1966 to 2005.

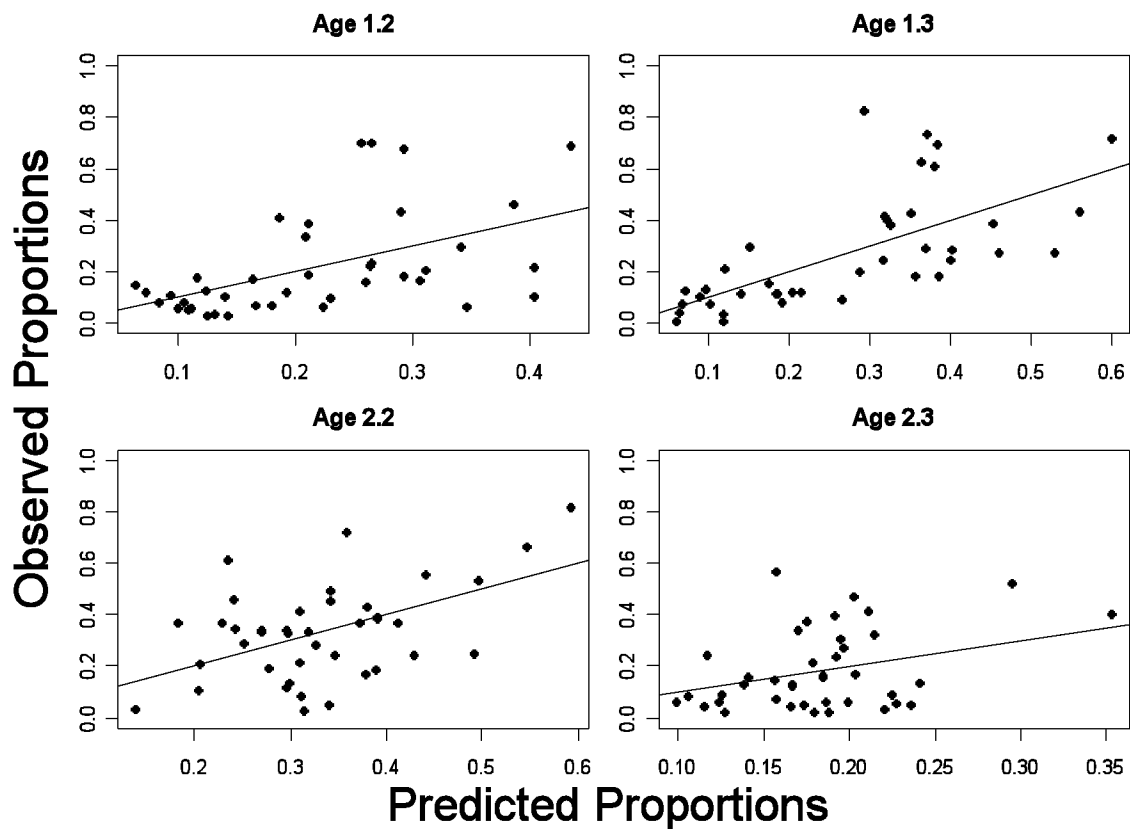


Figure 5. Estimated against observed proportions of major sockeye salmon age classes returning to the Ugashik River system from 1966 to 2005 based on full model (see text). Lines denote 1:1 correspondence (perfect agreement).

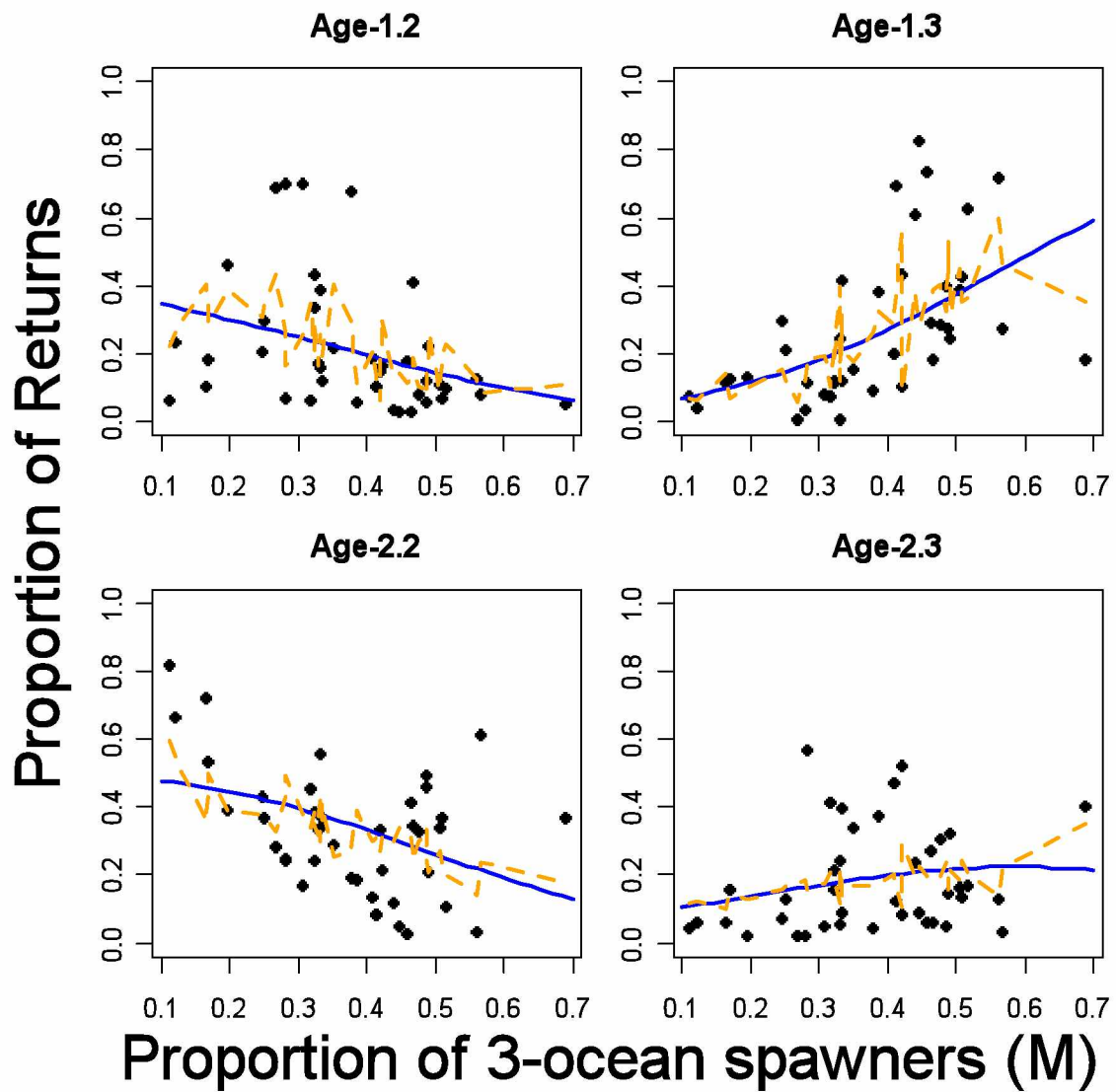


Figure 6. Scatterplots of the proportions of four major age classes of sockeye salmon returns to Bristol Bay (1966 – 2005) against the proportion of 3-ocean spawners of the parental generation. Solid line shows modeled proportions from the best model with the PDO, air temperature, and spawner abundance held constant at their means. Dashed line shows predicted values from a model that accounts for environmental variability.

Tables

Table 1. Matrix of pairwise Pearson's product moment correlations for predictor variables: 3-ocean Spawners (M), air temperature (AT) from November to March, Pacific decadal oscillation (PDO) from November to March, and spawner abundance (S).

Correlations are below diagonal and corresponding p-values are above the diagonal.

Bold values are significant at 95% level.

	M	AT	PDO	S
M		p = 0.557	p = 0.897	p = 0.830
AT	0.097		p < 0.001	p < 0.001
PDO	0.021	0.675		p < 0.001
S	0.035	0.526	0.549	

Table 2. Comparison of multinomial models to predict the age composition of sockeye salmon returns to the Ugashik River and to all of Bristol Bay (Baywide) using different combinations of environmental predictors (M2 = proportion of 2-freshwater spawners, ATS = spring (May-July) air temperature, see Table 1 for other abbreviations). Values represent differences in the AICc value between the best model ($\Delta\text{AICc} = 0$) and models including the listed predictor variable(s). Two-way interactions did not significantly improve the fit (not shown).

Predictors	Ugashik River	Baywide
M, S, AT, PDO	0.0	0.0
M2, S, AT, PDO	116.1	18.4
M, S, ATS, PDO	43.7	22.3
M, S, AT	61.3	36.4
M, S, PDO	43.2	28.5
M, S, ATS	85.3	55.7
M, PDO, AT	6.1	31.1
M, AT	55.7	59.8
S, AT	196.3	52.9
M, S	83.6	61.6
M, PDO	59.1	62.7
S, PDO	182.2	64.4
M	83.9	80.3
S	222.2	98.2
AT	191.2	95.9
PDO	197.7	109.4

Table 3. Signs of coefficients from best Ugashik River multinomial model:

Log-Odds Ratio	M	S	AT	PDO
1.2 / 2.3	-	-	+	+
1.3 / 2.3	+	+	+	-
2.2 / 2.3	-	+	+	-

Table 4. Comparison of binomial models of age-1.3 and age 2.2 sockeye salmon returns to the Ugashik River, Bristol Bay, Alaska (Eq. 7). Values represent differences in the AICc value between the best model ($\Delta\text{AICc} = 0$) and models including the listed predictor variable(s). See Table 2 for abbreviations.

Predictors	Age-1.3 ΔAICc	Age-2.2 ΔAICc
M, S, PDO, AT	0.0	1.7
M, S, PDO	44.6	1.3
M, S, AT	33.9	1.8
M, PDO, AT	2.5	0.0
M, AT	32.0	0.1
S, AT	131.2	38.9
M, S	49.8	7.9
M, PDO	56.5	0.3
S, PDO	145.8	43.4
M	55.2	9.7

Table 5. Comparisons of Ugashik River Ricker models and Bristol Bay generalized Ricker models with different predictor variables (Eq. 2). Values represent differences in the AICc value between the best model ($\Delta\text{AICc} = 0$) and models including the listed predictor variable(s).

Predictors	Ugashik (ΔAICc)		Baywide (ΔAICc)	
	(1960-2002)	(1976-2002)	(1960-2002)	(1976-2002)
S	0.0	1.1	1.7	0.6
M, S	0.2	1.9	2.5	2.1
S2, S3	1.7	0.8	3.4	1.5
E	0.1	0.0	1.9	0.0

Conclusions

The age composition of sockeye salmon spawners has been shown to impact that of their offspring. The models showed a positive relationship between the proportion of 3-ocean spawners and 3-ocean returns. This may prove important to the fishery, because fish spending three years in the ocean environment tend to be larger on average (Quinn 2005; Ruggerone et al. 2009) and contribute more overall to fishery landings in weight. Growth rate and maturation variability may be caused by a combination of parental, environmental and genetics effects.

Potential parental effects include impacts on egg size and fecundity, which are both positively correlated with female length for multiple fish species (Healey and Heard 1984; Beacham and Murray 1985; Hendry et al. 1999). If true for sockeye salmon, allowing more 3-ocean fish to escape into a river system may not only increase the number of eggs but also leads to a higher proportion of larger eggs and potentially larger fry. Genetic influences may be directly related to growth through growth patterns; for example, 2-ocean fish may simply grow at a faster rate than 3-ocean fish and return earlier.

Climate has been shown to effect survival rates in both freshwater and marine environments (Peterman et al. 1998; Botsford et al. 2011), which could drive populations to spend more or less time in either environment and, in turn, change the age composition of a population. Another environmental factor that may play a key role in causing variability in age structure is spawning habitat (substrate and hydrology). Bristol Bay provides sockeye salmon with a large variety of spawning habitats and differences in habitat result in sub-populations that vary in body structure and age composition (Rogers 1987). Spatial and temporal changes in the hydrology of these habitats directly influence spawning success as well as survival and growth of juveniles during their time in freshwater (Hilborn et al. 2003).

As long as salmon have been harvested in Bristol Bay, environmental and managerial changes have impacted the health of the sockeye salmon fishery. The current escapement-focused management strategy has produced good returns and has supported a healthy and diverse fishery. In particular, the past several decades have seen unprecedented returns due to a combination of high ocean productivity and precautionary management. The relationship between spawner age composition and biomass returning to the fishery could have a large influence on how managers interpret age data in the future.

Salmon management faces multiple challenges and should continue to invest in understanding the full potential of environmental and human impacts on the Bristol Bay fishery. In particular, anticipated climate changes may lead to changes in ocean productivity, in the distribution of salmon in the ocean, and in changes in freshwater habitats. Both freshwater and marine habitats may also be affected by oil and gas development and by ongoing and proposed mining activities. The effects of these changes, individually and in combination, will test our ability to effectively manage these fisheries.

Results found in the Ugashik River could potentially be compared to that of other rivers in the region. The fact that models showed consistent relationships in both the Ugashik and baywide models suggests that modeling other rivers might show similar results. Plots of other Bristol Bay river data show how each river is unique in its age structure and dynamic throughout time (Figs. A2-1 through A2-10). For instance, figure A2-4 shows how the Kvichak River returns have generally been dominated by age-2.2 fish while figure A2-10 shows the Togiak River returns being largely represented by age-1.3 over time. Further modeling of these rivers may prove useful in assessing the interpretation of these results.

Literature cited

- Baker, T.T. 2006. Review of salmon escapement goals in Bristol Bay, Alaska 2006. Alaska Department of Fish and Game, Commercial Fisheries Memorandum No. **06-05**: 1-10.
- Beacham, T.D., and Murray, C.B. 1985. Effect of female size, egg size, and water temperature on developmental biology of chum salmon (*Oncorhynchus keta*) from the Nitinat River, British Columbia. *Can. J. Fish. Aquat. Sci.* **42**: 1755-1765.
- Berkeley, S.A., Chapman, C., and Sogard, S.M. 2004a. Maternal age as a determinant of larval growth and survival in a marine fish, *Sebastes melanops*. *Ecology* **85**: 1258-1264.
- Berkeley, S.A., Hixon, M.A., Larson, R.J., and Love, M.S. 2004b. Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries* **29**: 23-32.
- Botsford, L.W., Holland, M.D., Samhour, J.F., White, J.W., and Hastings, A. 2011. Importance of age structure in models of the response of upper trophic levels to fishing and climate change. *ICES J. Mar. Sci.* **68**: 1270-1283.
- Brunel, T. 2010. Age-structure-dependent recruitment: a meta-analysis applied to Northeast Atlantic fish stocks. *ICES J. Mar. Sci.* **67**: 1921-1930.
- Burgner, R.L. 1980. Some features of ocean migrations and timing of Pacific salmon. *In* Salmonid Ecosystems of the North Pacific. *Edited by* W.J. McNeil, and D. C. Himsworth, Oregon State University Press, Corvallis, OR. pp. 153-164.

- Dann, T.H., Habicht, C., and Jasper, J.R. 2009. Genetic stock composition of the commercial harvest of sockeye salmon in Bristol Bay, 2006-2008. Alaska Department of Fish and Game, Fishery Manuscript Series No. 09-06, Anchorage.
- Flynn, L., Punt, A.E., and Hilborn, R. 2006. A hierarchical model for salmon run reconstruction and application to the Bristol Bay sockeye salmon (*Oncorhynchus nerka*) fishery. *Can. J. Fish. Aquat. Sci.* **63**: 1564-1577.
- Groot, C., and Margolis, L. 1991. Pacific salmon life histories. University of British Columbia Press, Vancouver, BC.
- Healey, M.C., and Heard, W.R. 1984. Inter- and intra-population variation in the fecundity of Chinook salmon (*Oncorhynchus tshawytscha*) and its relevance to life history theory. *Can. J. Fish. Aquat. Sci.* **41**: 476-483.
- Hendry, A.P., Berg, O.K., and Quinn, T.P. 1999. Condition dependence and adaption-by-time: breeding date, life history, and energy allocation within a population of salmon. *Oikos* **85**: 499-514.
- Hilborn, R., Quinn, T.P., Schindler, D.E., and Rogers, D.E. 2003. Biocomplexity and fisheries sustainability. *PNAS* **100**: 6564-6568.
- Holt, C.A., and Peterman, R.M. 2004. Long-term trends in age-specific recruitment of sockeye salmon (*Oncorhynchus nerka*) in a changing environment. *Can. J. Fish. Aquat. Sci.* **61**: 2455-2470.
- Hyun, S.-Y., Hilborn, R., Anderson, J.J., and Ernst, B. 2005. A statistical model for in-season forecasts of sockeye salmon (*Oncorhynchus nerka*) returns to the Bristol bay districts of Alaska. *Can. J. Fish. Aquat. Sci.* **62**: 1665-1680.

- Minard, R.E., and Meacham, C.P. 1987. Sockeye salmon management in Bristol Bay, Alaska. *Can. Spec. Publ. Fish. Aquat. Sci.* **96**: 336-342.
- Morgan, M.J., Shelton, P.A., and Bratney, J. 2007. Age composition of the spawning stock does not always influence recruitment. *Journal of Northwest Atlantic Fisheries Science* **38**: 1-12.
- Morstad, S., Jones, M., and Sands, T. 2009. 2009 Bristol Bay area annual management report. 101. Alaska Department of Fish and Game, Anchorage, AK.
- Peterman, R.M., Pyper, B.J., Lapointe, M.F., Adkison, M.D., and Walters, C.J. 1998. Patterns of covariation in survival rates of British Columbian and Alaskan sockeye salmon (*Oncorhynchus nerka*) stocks. *Can. J. Fish. Aquat. Sci.* **55**: 2503-2517.
- Quinn, T.P. 2005. The behavior and ecology of pacific salmon and trout, University of Washington Press, Seattle, WA.
- Rogers, D.E. 1987. The regulation of age at maturity in wood river sockeye salmon (*Oncorhynchus nerka*). *Can. Spec. Publ. Fish. Aquat. Sci.* **96**: 78-89.
- Ruggerone, G.T., Nielsen, J.L., and Agler, B.A. 2009. Linking marine and freshwater growth in western Alaska Chinook salmon *Oncorhynchus tshawytscha*. *J. Fish Biol.* **75**: 1287-1301.
- Scott, B.E., Marteinsdottir, G., Begg, G.A., Wright, P.J., and Kjesbu, O.S. 2006. Effects of population size/age structure, condition and temporal dynamics of spawning on reproductive output in Atlantic cod (*Gadus morhua*). *Ecol. Modell.* **191**: 383-415.

Straty, R.R., and Jaenicke, H.W. 1980. Estuarine influence of salinity, temperature, and food on the behavior, growth, and dynamics of Bristol Bay sockeye salmon. *In* Salmonid Ecosystems of the North Pacific. *Edited by* W.J. McNeil, and D.C. Himsworth, Oregon State University Press, Corvallis, OR, pp. 247-265.

Appendix I: multinomial sample size

To account for overdispersion, we calculated a correction factor to estimate effective sample sizes (McAllister and Ianelli, 1997) based on the assumption that the variance of the observed proportions should match the variance of a multinomial random variable.

The variance of the observed counts of fish at age i in year t (X_{it}) can be written as:

$$\text{var}(X_{it}) = \text{var}(N_t p_{it}) = N_t^2 \text{var}(p_{it})$$

where p_{it} is the observed proportion of age class i in year t and N_t is the observed sample size in year t , which is assumed to be the same across all years (N).

This can also be written as:

$$\text{var}(X_{it}) = N^2 \text{var}(r_{it})$$

because the variance of the residuals, i.e. the difference between observed and predicted proportions ($r_{it} = p_{it} - \hat{p}_{it}$), is given by:

$$\text{var}(r_{it}) = \text{var}(p_{it} - \hat{p}_{it}) = \text{var}(p_{it})$$

where the predicted values \hat{p}_{it} are from fitting the full multinomial logit model (Eq. 1, page 11 of manuscript) and the variance is computed across years for each age class i .

Because fish sampled for aging generally do not comprise a simple random sample of independently sampled fish from the population, the effective sample size is often much smaller than the actual sample size. Under the assumption that the number of fish in each age class, X_{it} , follow a multinomial distribution, the expected variance of X_{it} is:

$$\text{var}(X_{it}) = N \cdot \hat{p}_{it} (1 - \hat{p}_{it})$$

Hence we wish to find a corrected or effective sample size $N_{corr} = fN$ such that the observed variance is equal to the multinomial variance, where f is a correction factor:

$$N_{corr}^2 \text{var}(r_{it}) = N_{corr} \cdot \hat{p}_{it}(1 - \hat{p}_{it})$$

$$\text{var}(r_{it}) = \frac{\hat{p}_{it}(1 - \hat{p}_{it})}{N_{corr}}$$

$$\text{var}(r_{it}) = \frac{\hat{p}_{it} \cdot (1 - \hat{p}_{it})}{f N}$$

$$\text{var}(r_{it}) \frac{N}{\hat{p}_{it} \cdot (1 - \hat{p}_{it})} = \frac{1}{f}$$

or

$$\text{var}\left(r_{it} \cdot \sqrt{\frac{N}{\hat{p}_{it} \cdot (1 - \hat{p}_{it})}}\right) = \frac{1}{f}$$

$$f = \left(\text{var}\left(r_{it} \cdot \sqrt{\frac{N}{\hat{p}_{it} \cdot (1 - \hat{p}_{it})}}\right)\right)^{-1} \quad (\text{Eq. A1})$$

We initially assumed an effective sample size for N corresponding to the square root of the average number of fish that were aged per year. That is, counts in year t (X_{it}) were adjusted such that $X_{it} = p_{it} * N$, where the p_{it} were the observed proportions of each age class. The full multinomial logit model, including predictors M, S, AT and PDO, was then fit to the adjusted counts to compute predicted proportions and residuals. A correction factor was then computed from Eq. A1 and was used to compute an updated sample size as $N^* = fN$. The sample size was updated iteratively until it converged to an estimated effective sample size of $N = 37$ for each sampling year, for a total sample size of 1480 observations across the 40 year time series. Using the same approach, baywide models had an effective annual sample size of $N = 44$.

Appendix II: age data summary for Bristol Bay

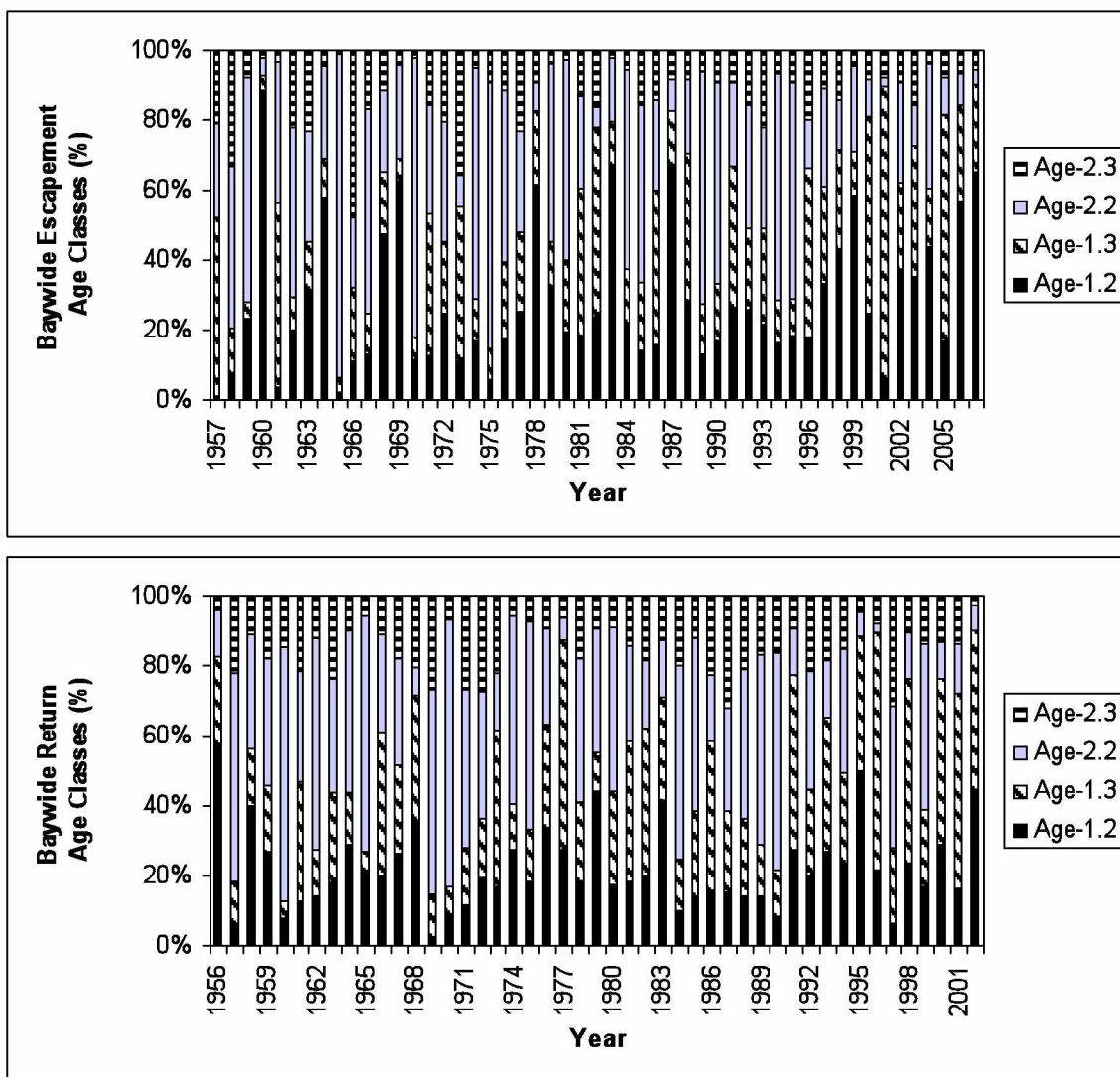


Figure A2-1. Percentages of escapement (top) and return (bottom) age classes for the entire Bristol Bay area, Alaska.

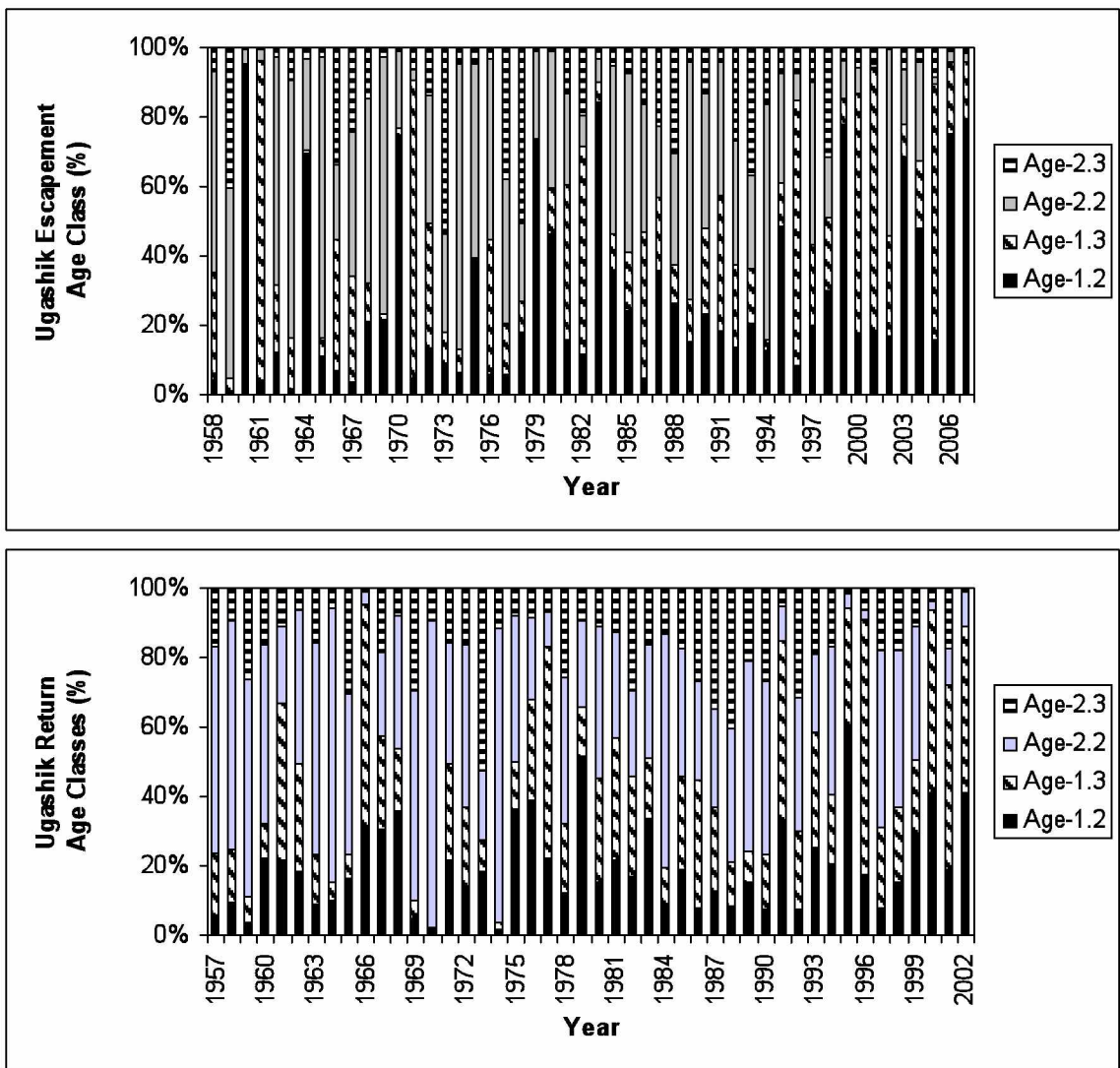


Figure A2-2. Percentages of escapement (top) and return (bottom) age classes in the Ugashik River, Bristol Bay, Alaska.

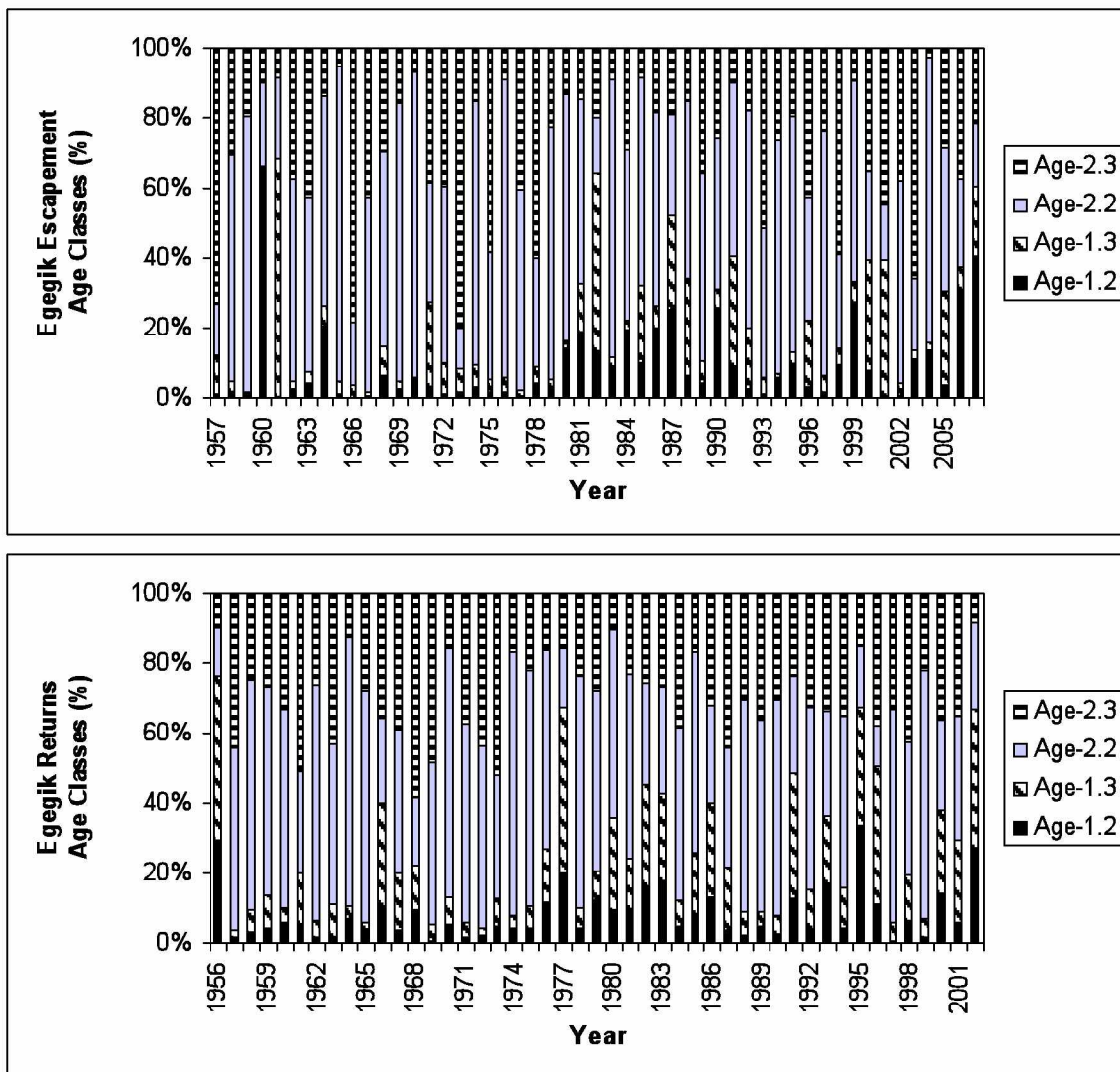


Figure A2-3. Percentages of escapement (top) and return (bottom) age classes in the Egegik River, Bristol Bay, Alaska.

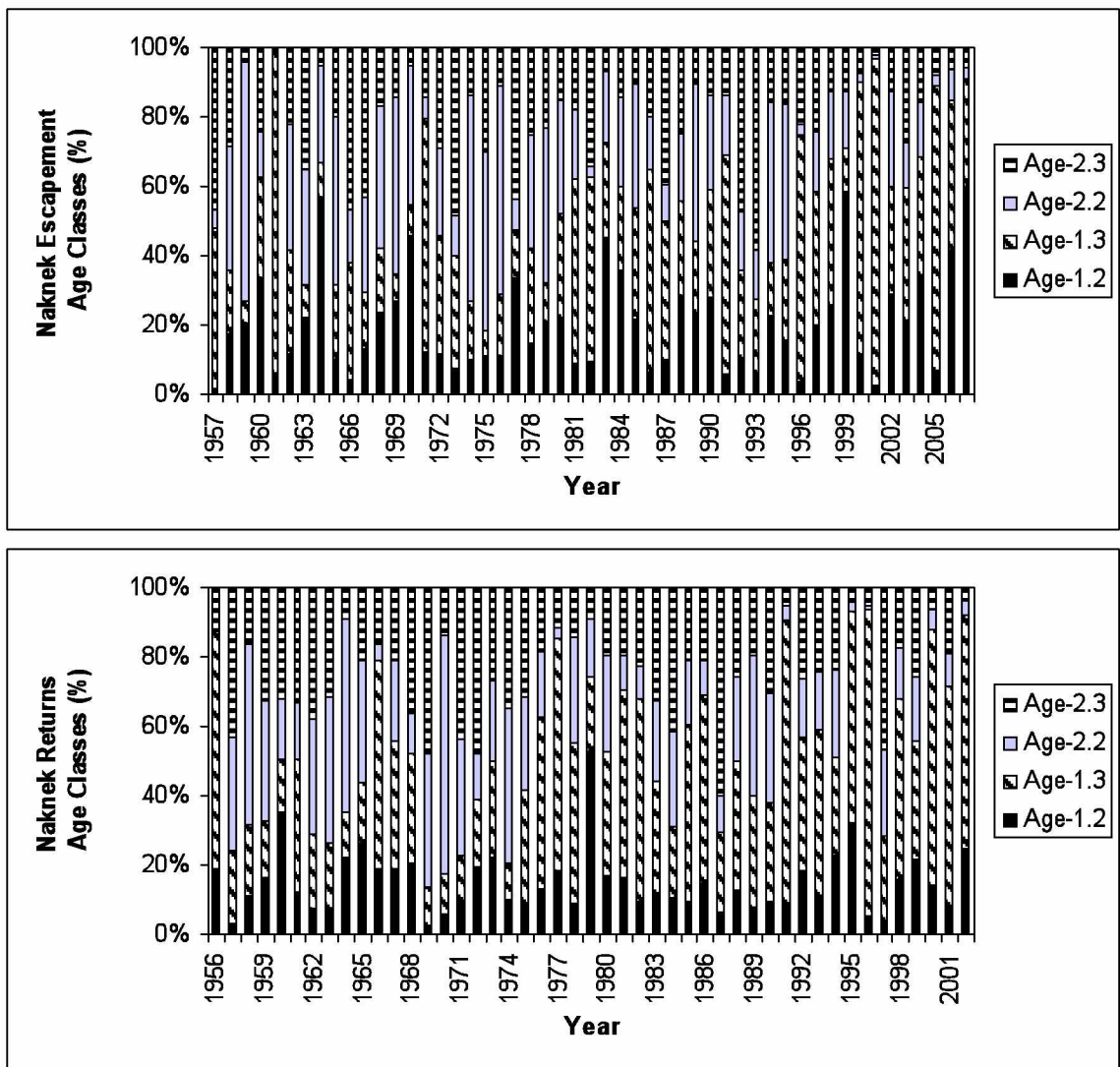


Figure A2-4. Percentages of escapement (top) and return (bottom) age classes in the Naknek River, Bristol Bay, Alaska.

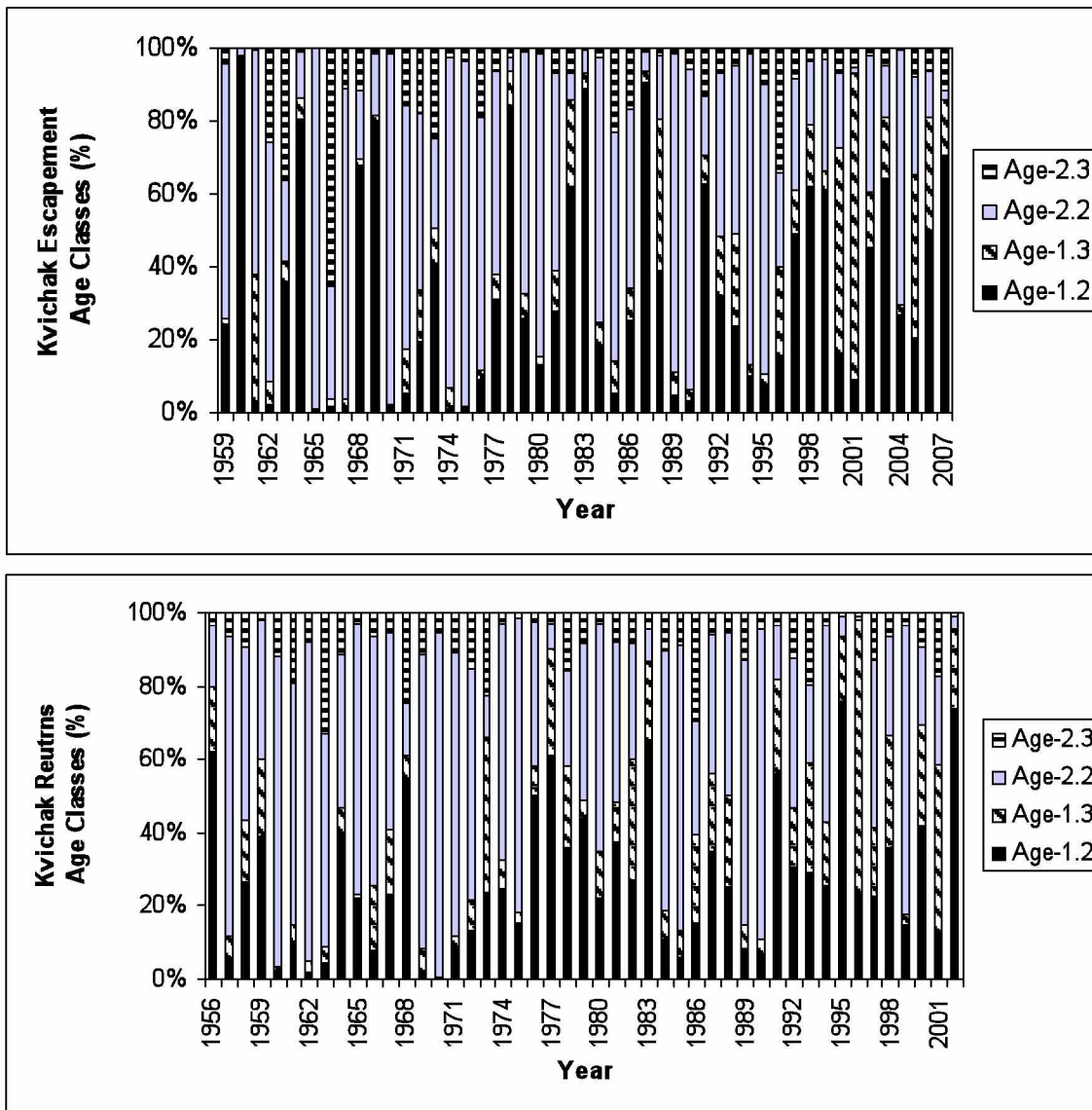


Figure A2-5. Percentages of escapement (top) and return (bottom) age classes in the Kvichak River, Bristol Bay, Alaska.

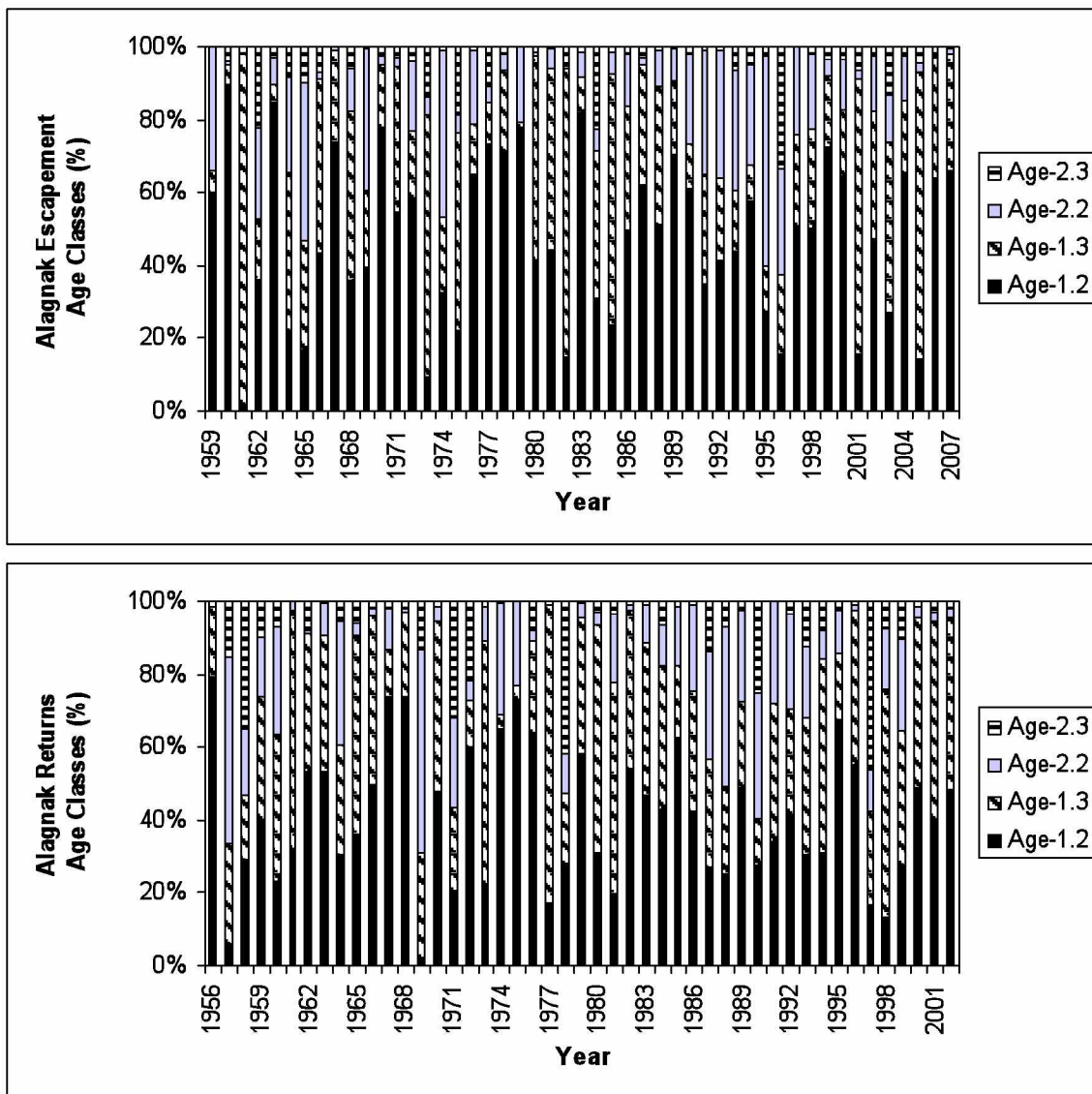


Figure A2-6. Percentages of escapement (top) and return (bottom) age classes in the Alagnak River, Bristol Bay, Alaska.

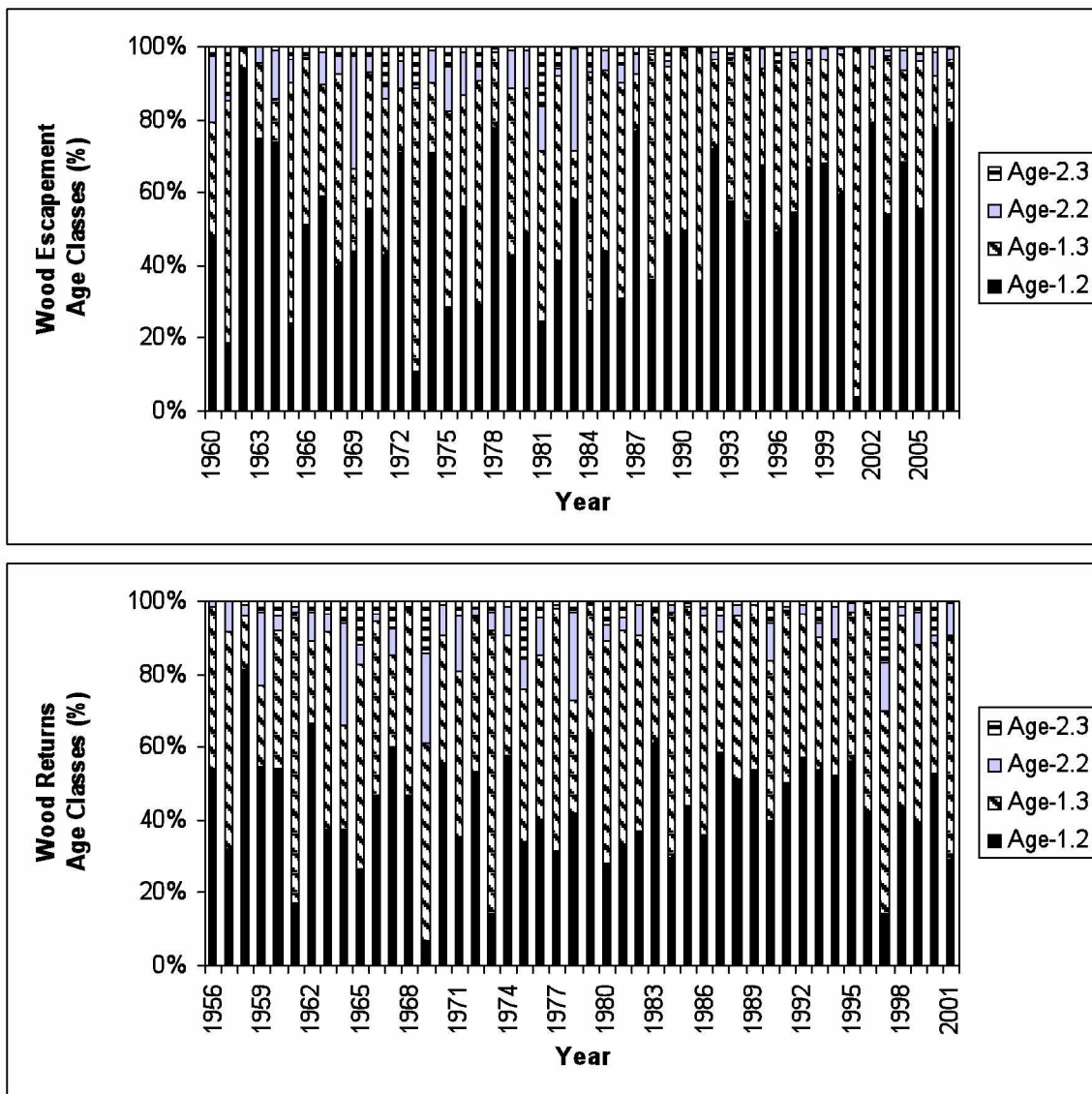


Figure A2-7. Percentages of escapement (top) and return (bottom) age classes in the Wood River, Bristol Bay, Alaska.

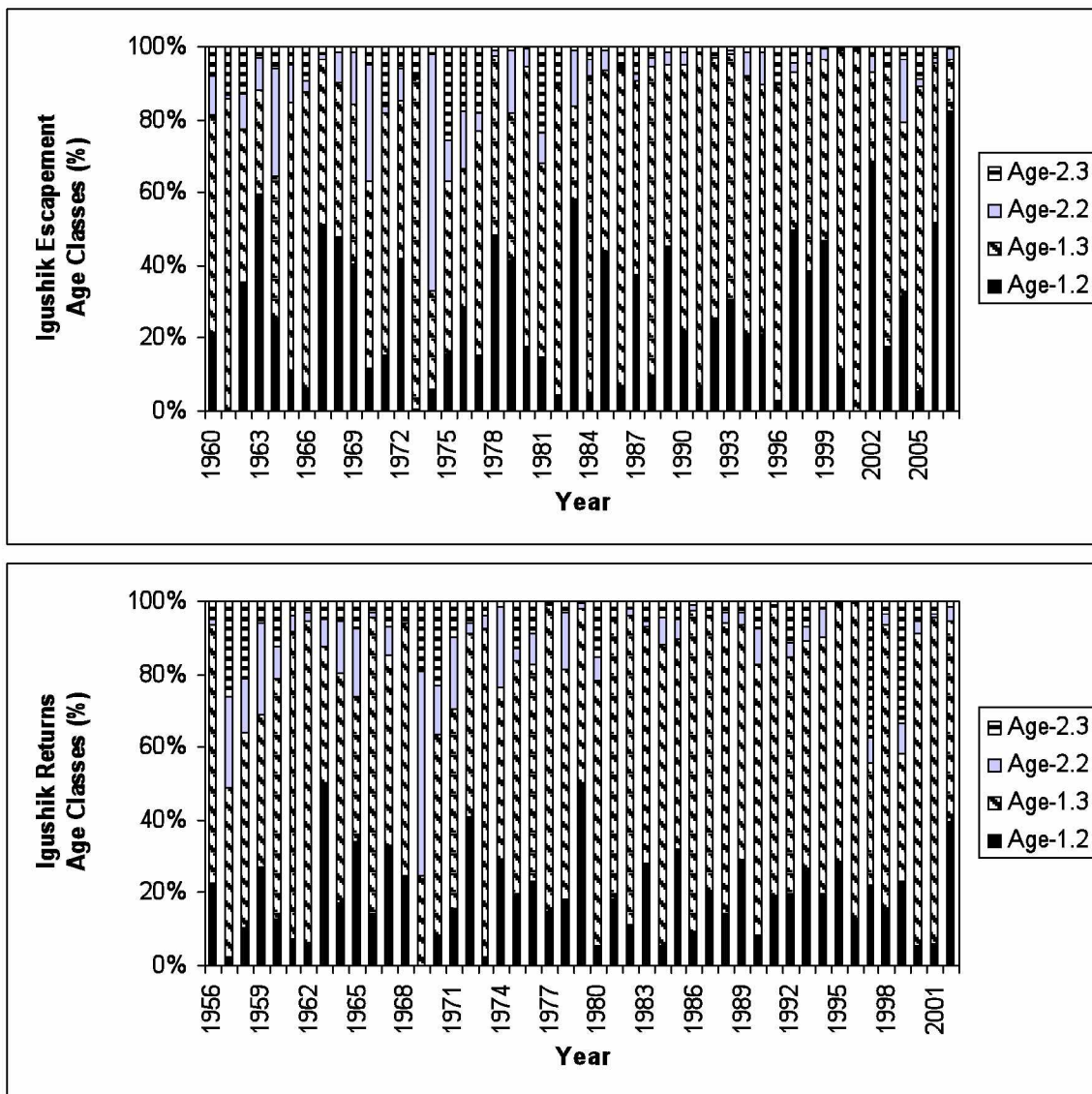


Figure A2-8. Percentages of escapement (top) and return (bottom) age classes in the Igushik River, Bristol Bay, Alaska.

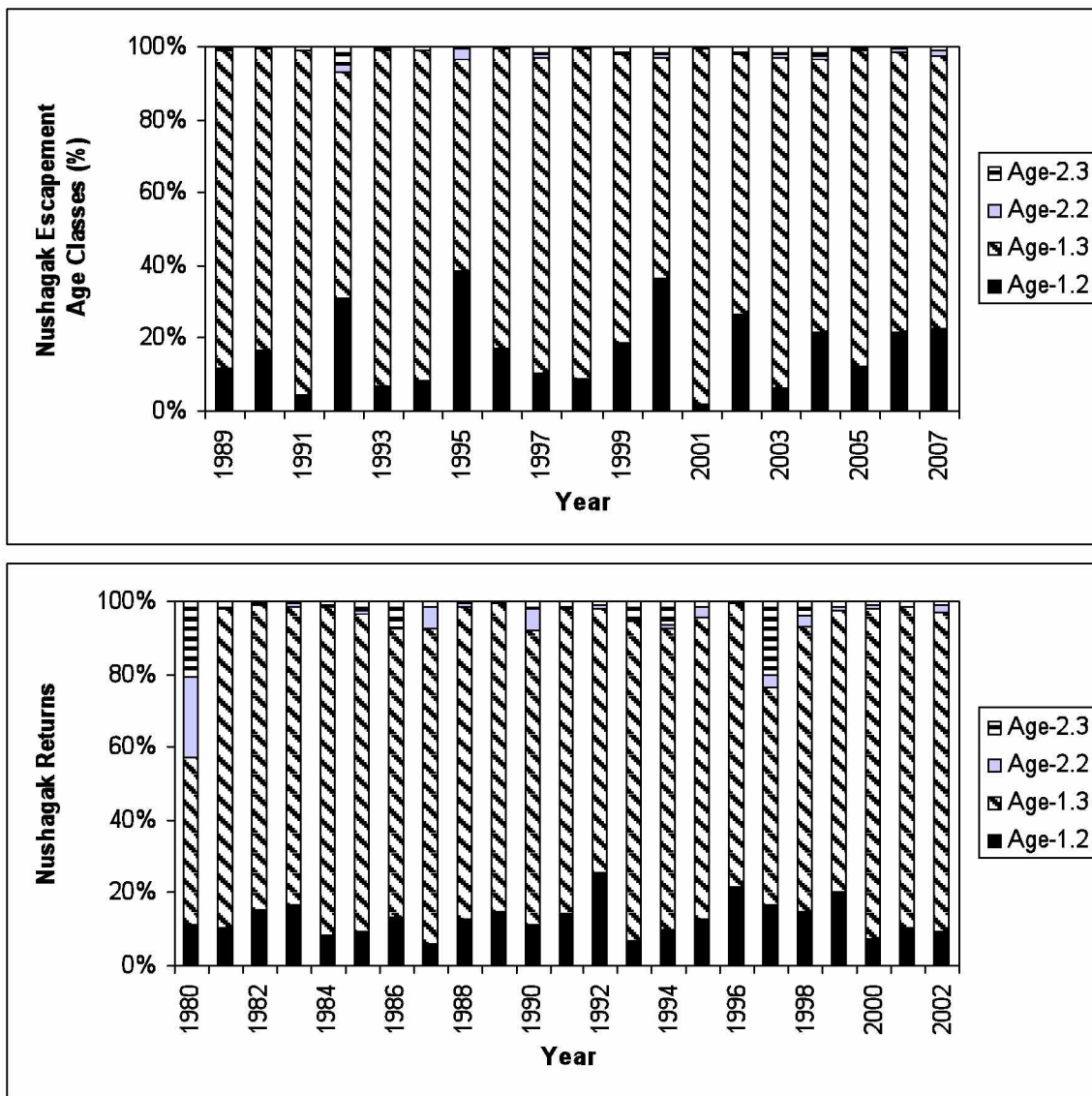


Figure A2-9. Percentages of escapement (top) and return (bottom) age classes in the Nushagak River, Bristol Bay, Alaska.

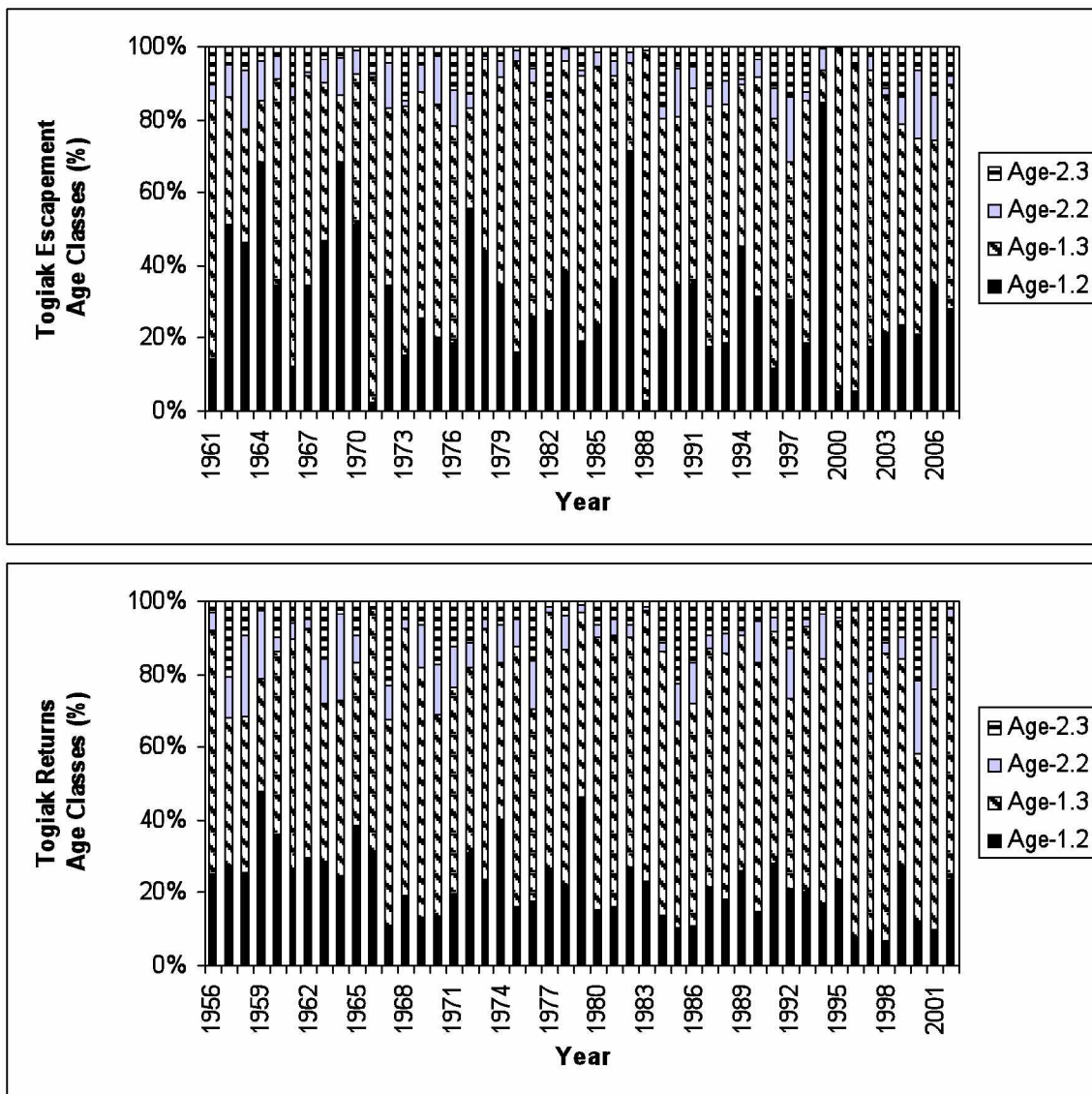


Figure A2-10. Percentages of escapement (top) and return (bottom) age classes in the Togiak River, Bristol Bay, Alaska.

Table A2-1. Bristol Baywide spawner age class data (1956-2007).

Bristol Baywide Spawners by Age Class (in thousands)							
Year	Age Classes						Total
	1.2	1.3	2.2	2.3	Major	Other	
1956							14967
1957	51	1970	1030	810	3860	873	4734
1958	101	164	588	428	1281	1,503	2783
1959	1109	214	3063	375	4761	3,513	8274
1960	19726	964	1174	502	22365	245	22610
1961	218	3244	2479	197	6137	42	6179
1962	1125	532	2742	1238	5637	40	5677
1963	1216	527	1208	887	3839	174	4013
1964	2955	550	1349	247	5100	221	5322
1965	560	1248	26679	297	28785	71	28856
1966	887	1733	1616	3863	8099	90	8190
1967	771	681	3426	997	5875	132	6007
1968	2378	884	1155	582	4998	213	5211
1969	7398	709	3219	476	11802	611	12413
1970	2150	1209	14855	346	18561	108	18669
1971	775	2476	1924	953	6128	100	6228
1972	735	605	1013	608	2962	18	2981
1973	180	696	149	565	1590	84	1675
1974	1614	1152	6208	509	9483	116	9598
1975	1132	1630	14378	1826	18965	359	19324
1976	966	1243	2745	641	5595	314	5909
1977	1201	1056	1372	1087	4716	88	4804
1978	5758	1994	722	913	9387	575	9962
1979	5901	2235	9184	626	17945	503	18448
1980	7356	7764	21908	1008	38036	645	38681
1981	1589	3618	2263	1143	8613	200	8813
1982	1597	3711	407	1098	6812	239	7051
1983	5587	1009	1521	190	8307	202	8509
1984	3442	2524	9148	960	16074	275	16350
1985	1815	2565	6492	2030	12903	216	13119
1986	1224	3379	1954	1108	7665	227	7892
1987	7597	1745	1020	936	11298	119	11417
1988	2559	3754	1899	757	8969	430	9399
1989	1932	2171	9839	958	14900	395	15295
1990	2318	2269	7964	1349	13900	583	14483
1991	4132	6293	3700	1443	15568	453	16021
1992	3224	2891	4396	2006	12518	675	13194
1993	2322	2939	3122	2389	10772	553	11325
1994	2359	1780	9500	991	14629	554	15184
1995	2977	1696	9954	1548	16176	226	16401
1996	1287	3444	940	1439	7110	235	7345
1997	2127	1799	1784	726	6435	238	6674
1998	3503	2317	1161	1150	8132	272	8403
...							

Table A2-1 continued...

Bristol Baywide Spawners by Age Class (in thousands)							
	Age Classes						
Year	1.2	1.3	2.2	2.3	Major	Other	Total
1999	8200	1797	3407	645	14049	94	14142
2000	1915	4390	805	659	7768	26	7794
2001	436	6499	196	606	7737	274	8011
2002	2352	1590	1820	590	6351	226	6578
2003	3880	4153	1257	1737	11027	576	11603
2004	7421	2881	6155	594	17051	171	17222
2005	2411	9313	1513	1155	14392	381	14773
2006	8056	3881	1256	972	14165	272	14438
2007	9663	3668	581	873	14785	200	14985

Table A2-2. Bristol Baywide return age class data (1956-2004).

Bristol Baywide Returns by Age Class (in thousands)							
Year	Age Classes						Total
	1.2	1.3	2.2	2.3	Major	Other	
1956	32851	14611	7538	2419	57419	131	57550
1957	559	1106	5405	2029	9099	195	9294
1958	2563	1038	2116	705	6422	40	6462
1959	2175	1580	2925	1475	8155	66	8221
1960	5674	3620	53759	11042	74095	319	74414
1961	1357	3611	3361	2286	10615	103	10718
1962	1468	1394	6293	1286	10441	148	10589
1963	1246	1737	2265	1618	6866	124	6990
1964	3593	1870	5800	1230	12493	285	12778
1965	11684	2718	36282	3030	53714	655	54369
1966	3719	7672	5187	2030	18608	131	18739
1967	1799	1713	2072	1237	6821	79	6900
1968	1233	1246	275	707	3461	50	3511
1969	282	1516	6978	3230	12006	474	12480
1970	1952	1891	17693	1590	23126	628	23754
1971	1500	2082	5715	3434	12731	233	12964
1972	1644	1428	3061	2308	8441	178	8619
1973	1650	4346	1554	2148	9698	102	9800
1974	11102	5153	21758	2272	40285	511	40796
1975	11409	9237	36798	4661	62105	496	62601
1976	13150	12181	10901	3840	40072	371	40443
1977	5899	13037	1320	1412	21668	406	22074
1978	4679	5741	10409	4575	25404	147	25551
1979	29100	7547	23364	6173	66184	260	66444
1980	6472	10042	17517	3364	37395	729	38124
1981	4900	10473	7191	3686	26250	425	26676
1982	3356	7021	3275	3036	16688	689	17377
1983	14040	9932	5522	4331	33825	999	34824
1984	5200	7422	28545	10192	51359	897	52257
1985	5443	10374	20495	4938	41250	1017	42266
1986	7538	20432	9141	10713	47824	2219	50044
1987	8362	12859	16428	17896	55546	2340	57886
1988	6192	9934	19002	9247	44376	1566	45942
1989	7556	7973	29094	8996	53618	1240	54859
1990	4792	7678	35785	9404	57659	1375	59034
1991	10503	19352	5179	3585	38620	612	39231
1992	4202	5275	7098	4618	21192	1092	22283
1993	4207	6118	2586	2876	15787	406	16194
1994	6543	7532	9930	4407	28412	313	28725
1995	22298	17085	3118	2091	44593	457	45050
1996	5964	18597	692	2241	27494	766	28260
1997	1013	3543	6533	5096	16185	1182	17367
1998	5044	11093	2807	2175	21119	333	21452
...							

Table A2-2 continued...

Bristol Baywide Returns by Age Class (in thousands)							
	Age Classes						
Year	1.2	1.3	2.2	2.3	Major	Other	Total
1999	6794	8781	19015	5562	40152	706	40858
2000	14274	23474	5314	6554	49616	872	50488
2001	4818	16480	4207	3995	29500	908	30408
2002	15631	15729	2676	907	34943	512	35455
2003	23239	23381	2588				
2004	14690						

Table A2-3. Ugashik River spawner age class data (1956-2007).

Ugashik River Spawners by Age Class (in thousands)							
Year	Age Classes						Total
	1.2	1.3	2.2	2.3	Major	Other	
1956							425
1957							215
1958	11	86	159	19	275	5	280
1959	2	8	113	83	206	13	219
1960	2185	5	99	15	2304	0	2304
1961	15	320	11	2	348	1	349
1962	31	50	167	7	255	0	255
1963	7	57	286	37	387	1	388
1964	322	5	121	15	463	10	473
1965	109	55	806	25	995	2	997
1966	48	267	151	236	702	2	704
1967	9	72	100	57	238	1	239
1968	13	7	33	9	62	9	71
1969	34	3	117	4	158	2	160
1970	550	15	161	8	734	1	735
1971	26	453	17	33	529	1	530
1972	10	29	29	11	79	0	79
1973	3	4	11	21	39	0	39
1974	4	4	50	3	61	1	62
1975	168	1	239	20	428	1	429
1976	20	139	184	12	355	1	356
1977	12	29	84	76	201	1	202
1978	12	6	15	34	67	15	82
1979	1247	4	433	15	1699	8	1707
1980	1515	440	1284	36	3275	60	3335
1981	208	597	346	177	1328	0	1328
1982	133	697	102	224	1156	30	1186
1983	835	61	67	30	993	8	1001
1984	429	138	597	62	1226	44	1270
1985	242	165	513	76	996	10	1006
1986	48	427	370	164	1009	7	1016
1987	245	140	142	153	680	7	687
1988	160	66	194	183	603	51	654
1989	263	201	1171	71	1706	7	1713
1990	166	179	283	96	724	25	749
1991	460	954	945	108	2467	15	2482
1992	289	514	764	581	2148	47	2195
1993	289	215	377	511	1392	21	1413
1994	138	34	724	176	1072	23	1095
1995	633	166	415	100	1314	7	1321
1996	58	517	51	51	677	15	692
1997	128	149	297	64	638	19	657
1998	267	188	153	280	888	37	925
...							

Table A2-3 continued...

Ugashik River Spawners by Age Class (in thousands)							
	Age Classes						
Year	1.2	1.3	2.2	2.3	Major	Other	Total
1999	1290	117	183	63	1653	9	1662
2000	107	445	45	38	635	3	638
2001	154	656	9	42	861	5	866
2002	153	259	479	7	898	8	906
2003	524	71	121	49	765	25	790
2004	388	157	232	33	810	5	815
2005	124	569	16	67	776	24	800
2006	727	197	32	8	964	39	1003
2007	2050	412	76	37	2575	24	2599

Table A2-4. Ugashik River return age class data (1956-2004).

Ugashik River Returns by Age Class (in thousands)							
Year	Age Classes						Total
	1.2	1.3	2.2	2.3	Major	Other	
1956	3165	837	80	35	4117	15	4132
1957	35	105	354	100	594	9	603
1958	63	105	444	66	678	0	678
1959	18	38	310	132	498	1	499
1960	674	296	1563	487	3020	11	3031
1961	240	500	247	120	1107	7	1114
1962	77	130	185	27	419	4	423
1963	13	21	91	23	148	0	148
1964	31	16	245	18	310	12	322
1965	86	38	249	162	535	4	539
1966	723	1478	90	21	2312	3	2315
1967	56	50	44	34	184	0	184
1968	14	7	15	3	39	0	39
1969	4	5	53	26	88	4	92
1970	4	2	256	28	290	5	295
1971	178	236	290	130	834	1	835
1972	35	58	119	41	253	5	258
1973	16	8	17	46	87	5	92
1974	13	15	602	83	713	12	725
1975	1484	575	1721	325	4105	11	4116
1976	2027	1527	1248	437	5239	70	5309
1977	585	1614	266	186	2651	41	2692
1978	247	413	863	523	2046	19	2065
1979	3076	851	1471	562	5960	46	6006
1980	1183	2309	3371	850	7713	68	7781
1981	1603	2632	2278	933	7446	22	7468
1982	423	713	606	737	2479	29	2508
1983	650	342	632	319	1943	22	1965
1984	472	568	3635	709	5384	80	5464
1985	508	721	978	469	2676	19	2695
1986	503	2427	1874	1750	6554	142	6696
1987	828	1626	1875	2310	6639	106	6745
1988	463	692	2144	2252	5551	99	5650
1989	694	391	2479	955	4519	54	4573
1990	345	709	2302	1218	4574	37	4611
1991	2034	3167	597	326	6124	27	6151
1992	191	597	1013	827	2628	75	2703
1993	265	352	241	198	1056	30	1086
1994	333	327	689	274	1623	37	1660
1995	2808	1562	185	82	4637	49	4686
1996	231	978	36	81	1326	62	1388
1997	234	701	1553	534	3022	39	3061
1998	204	292	603	241	1340	9	1349
...							

Table A2-4 continued...

Ugashik River Returns by Age Class (in thousands)							
	Age Classes						
Year	1.2	1.3	2.2	2.3	Major	Other	Total
1999	1088	769	1425	399	3681	44	3725
2000	1711	2186	92	162	4151	28	4179
2001	382	1088	210	356	2036	70	2106
2002	1973	2323	491	44	4831	43	4874
2003	4648	1390	156				
2004	1429						

Table A2-5. Egegik River spawner age class data (1956-2007).

Egegik River Spawners by Age Class (in thousands)							
Year	Age Classes						Total
	1.2	1.3	2.2	2.3	Major	Other	
1956							1104
1957	4	42	57	280	384	7	391
1958	2	9	150	70	231	15	246
1959	11	1	711	173	896	177	1072
1960	1155	6	409	174	1744	55	1799
1961	1	480	161	58	701	1	702
1962	26	24	590	380	1019	8	1027
1963	37	33	466	394	930	68	998
1964	167	46	484	111	807	42	850
1965	14	53	1298	75	1440	4	1445
1966	2	29	141	618	790	15	804
1967	2	9	332	255	598	39	637
1968	20	26	179	94	319	20	339
1969	25	17	741	148	931	84	1016
1970	45	6	766	59	876	43	920
1971	16	157	214	241	627	7	634
1972	7	47	273	215	542	4	546
1973	4	22	37	257	320	9	329
1974	42	78	957	195	1271	5	1276
1975	16	35	370	591	1011	162	1174
1976	8	18	371	39	435	74	509
1977	3	12	384	273	672	20	693
1978	36	40	259	502	837	58	896
1979	26	28	726	229	1009	23	1032
1980	139	23	704	128	994	67	1061
1981	129	96	363	103	692	3	695
1982	128	527	166	203	1025	10	1035
1983	61	29	628	69	787	6	792
1984	219	30	557	331	1137	28	1165
1985	106	232	624	91	1053	42	1095
1986	227	70	629	211	1136	16	1152
1987	318	339	367	241	1265	8	1274
1988	99	428	774	232	1533	80	1613
1989	65	98	850	566	1579	33	1612
1990	554	115	919	548	2136	56	2192
1991	230	868	1342	277	2717	70	2787
1992	50	322	1169	335	1876	69	1946
1993	15	73	618	752	1458	59	1517
1994	106	15	1187	472	1780	118	1898
1995	118	44	827	236	1225	42	1267
1996	31	192	363	431	1017	60	1076
1997	18	50	739	254	1061	43	1104
1998	95	53	274	603	1025	86	1111
...							

Table A2-5 continued...

Egegik River Spawners by Age Class (in thousands)							
	Age Classes						
Year	1.2	1.3	2.2	2.3	Major	Other	Total
1999	469	100	986	163	1719	10	1728
2000	82	325	258	359	1024	8	1032
2001	5	364	145	419	933	36	969
2002	6	38	572	379	995	41	1036
2003	96	25	182	583	886	267	1152
2004	171	27	1031	33	1263	28	1290
2005	56	413	631	437	1536	85	1622
2006	428	89	348	511	1376	89	1465
2007	553	272	242	292	1358	74	1433

Table A2-6. Egegik River return age class data (1956-2004).

Egegik River Returns by Age Class (in thousands)							
Year	Age Classes						Total
	1.2	1.3	2.2	2.3	Major	Other	
1956	2025	3190	925	685	6825	21	6846
1957	37	43	1096	927	2103	132	2235
1958	42	73	817	308	1240	21	1261
1959	73	164	1037	467	1741	40	1781
1960	447	328	4447	2560	7782	129	7911
1961	82	229	446	791	1548	42	1590
1962	22	69	950	375	1416	58	1474
1963	16	112	538	506	1172	86	1258
1964	126	69	1454	242	1891	92	1983
1965	104	72	2016	845	3037	67	3104
1966	249	752	600	890	2491	20	2511
1967	60	257	665	622	1604	8	1612
1968	41	56	87	258	442	17	459
1969	12	111	1096	1141	2360	395	2755
1970	59	89	796	175	1119	121	1240
1971	45	109	1477	970	2601	132	2733
1972	57	61	1508	1264	2890	69	2959
1973	76	135	578	851	1640	39	1679
1974	131	99	2224	496	2950	75	3025
1975	148	241	2449	797	3635	29	3664
1976	612	789	3003	846	5250	67	5317
1977	823	1969	688	655	4135	82	4217
1978	398	510	6071	2184	9163	45	9208
1979	712	520	3036	1659	5927	20	5947
1980	803	2225	4576	917	8521	54	8575
1981	544	953	3284	1438	6219	97	6316
1982	988	1874	1796	1638	6296	43	6339
1983	1748	2763	3235	2822	10568	78	10646
1984	608	978	6539	5029	13154	374	13528
1985	567	1404	4358	1262	7591	80	7671
1986	1850	3733	3912	4515	14010	321	14331
1987	886	4561	8863	11239	25549	402	25951
1988	413	1278	11061	5650	18402	483	18885
1989	513	456	6063	3979	11011	250	11261
1990	403	867	9598	4721	15589	150	15739
1991	1397	3939	3113	2607	11056	107	11163
1992	335	1117	4963	3099	9514	187	9701
1993	497	573	880	992	2942	60	3002
1994	368	982	4228	3071	8649	109	8758
1995	3151	3175	1644	1455	9425	60	9485
1996	497	1791	515	1727	4530	87	4617
1997	34	322	3572	1971	5899	775	6674
1998	104	206	602	684	1596	41	1637
...							

Table A2-6 continued...

Egegik River Returns by Age Class (in thousands)							
	Age Classes						
Year	1.2	1.3	2.2	2.3	Major	Other	Total
1999	249	676	9686	3010	13621	253	13874
2000	1726	2907	3224	4444	12301	86	12387
2001	294	1221	1797	1822	5134	73	5207
2002	1464	2201	1350	475	5490	108	5598
2003	2731	3634	2067				
2004	2815						

Table A2-7. Naknek River spawner age class data (1956-2007).

Naknek River Spawners by Age Class (in thousands)							
Year	Age Classes						Total
	1.2	1.3	2.2	2.3	Major	Other	
1956							1773
1957	10	293	34	297	634	1	635
1958	45	47	91	72	255	23	278
1959	449	140	1509	93	2192	40	2232
1960	279	239	109	201	828	1	828
1961	17	327	1	3	348	3	351
1962	84	209	257	156	706	17	723
1963	199	83	298	317	898	8	905
1964	760	135	376	68	1339	10	1350
1965	70	155	345	142	713	5	718
1966	45	336	156	475	1012	5	1016
1967	99	120	205	320	744	11	756
1968	237	180	407	168	993	30	1023
1969	347	98	659	180	1284	47	1331
1970	332	65	292	40	729	4	733
1971	110	626	62	130	928	8	936
1972	68	202	148	169	586	0	587
1973	26	115	41	171	352	4	357
1974	122	204	728	165	1219	22	1241
1975	217	153	1025	605	2000	27	2027
1976	147	231	787	147	1312	9	1321
1977	364	147	97	474	1082	4	1086
1978	117	219	263	203	802	12	813
1979	190	101	406	213	910	15	925
1980	580	793	857	397	2628	17	2645
1981	157	955	363	318	1792	4	1796
1982	110	604	34	389	1137	19	1156
1983	391	232	177	60	860	28	888
1984	436	300	311	176	1222	20	1242
1985	397	585	657	192	1832	18	1850
1986	123	1157	297	394	1971	7	1978
1987	104	418	114	411	1048	14	1062
1988	287	270	197	246	999	39	1038
1989	256	247	514	118	1135	27	1162
1990	587	640	578	281	2086	7	2093
1991	207	2234	617	485	3544	34	3579
1992	157	369	254	696	1476	131	1607
1993	96	310	209	867	1483	53	1536
1994	213	141	433	146	933	58	991
1995	157	271	501	178	1108	4	1111
1996	39	762	37	234	1072	6	1078
1997	192	373	168	231	963	62	1026
1998	292	499	232	145	1169	33	1202
...							

Table A2-7 continued...

Naknek River Spawners by Age Class (in thousands)							
	Age Classes						
Year	1.2	1.3	2.2	2.3	Major	Other	Total
1999	943	209	258	207	1617	9	1625
2000	158	1077	37	104	1375	0	1375
2001	49	1694	15	40	1798	33	1830
2002	344	377	325	152	1198	66	1264
2003	362	720	234	499	1815	16	1831
2004	649	676	304	304	1933	6	1940
2005	184	2200	78	213	2675	70	2745
2006	797	827	170	122	1916	37	1953
2007	1755	909	100	170	2934	12	2945

Table A2-8. Naknek River return age class data (1956-2004).

Naknek River Returns by Age Class (in thousands)							
Year	Age Classes						Total
	1.2	1.3	2.2	2.3	Major	Other	
1956	473	1701	3	304	2481	18	2499
1957	53	329	505	674	1561	11	1572
1958	112	211	539	168	1030	9	1039
1959	349	351	742	705	2147	7	2154
1960	1408	625	696	1278	4007	15	4022
1961	239	744	315	640	1938	14	1952
1962	76	230	351	397	1054	20	1074
1963	136	390	833	627	1986	16	2002
1964	447	264	1135	177	2023	37	2060
1965	540	360	732	437	2069	51	2120
1966	728	2304	167	630	3829	10	3839
1967	326	625	401	356	1708	9	1717
1968	152	234	83	269	738	7	745
1969	47	307	976	1211	2541	11	2552
1970	154	318	1845	370	2687	31	2718
1971	397	559	1428	1844	4228	45	4273
1972	245	241	161	599	1246	18	1264
1973	494	618	524	598	2234	0	2234
1974	232	228	1026	783	2269	15	2284
1975	425	1746	1393	1641	5205	21	5226
1976	1084	4048	1575	1491	8198	57	8255
1977	635	2272	95	401	3403	89	3492
1978	331	1695	1121	530	3677	18	3695
1979	2438	973	792	408	4611	25	4636
1980	723	1505	1192	828	4248	27	4275
1981	782	2568	473	937	4760	29	4789
1982	185	1172	191	457	2005	38	2043
1983	163	484	336	480	1463	14	1477
1984	469	911	1214	1828	4422	55	4477
1985	656	3533	1293	1441	6923	111	7034
1986	1981	7167	1276	2817	13241	424	13665
1987	336	1251	565	3225	5377	129	5506
1988	273	796	516	544	2129	55	2184
1989	226	930	1154	566	2876	11	2887
1990	405	1236	1345	1316	4302	73	4375
1991	546	5209	250	343	6348	60	6408
1992	268	552	250	379	1449	35	1484
1993	293	1390	473	692	2848	37	2885
1994	503	631	553	526	2213	38	2251
1995	2067	3896	156	280	6399	80	6479
1996	345	6117	83	354	6899	114	7013
1997	119	854	824	1596	3393	39	3432
1998	625	2099	598	690	4012	20	4032
...							

Table A2-8 continued...

Naknek River Returns by Age Class (in thousands)							
	Age Classes						
Year	1.2	1.3	2.2	2.3	Major	Other	Total
1999	854	1339	712	1009	3914	23	3937
2000	1187	6091	479	546	8303	84	8387
2001	401	2973	463	884	4721	69	4790
2002	1425	3914	268	203	5810	114	5924
2003	3928	5370	244		9542	8	9550
2004	606						

Table A2-9. Kvichak River spawner age class data (1956-2007).

Kvichak River Spawners by Age Class (in thousands)							
Year	Age Classes						Total
	1.2	1.3	2.2	2.3	Major	Other	
1956							9443
1957	37	1635	938	233			2843
1958	43	21	187	267			535
1959	155	13	451	27	647	27	674
1960	14267	29	299	0	14595	7	14602
1961	78	1317	2290	20	3706	0	3706
1962	57	156	1697	670	2580	1	2581
1963	121	19	75	122	337	2	339
1964	670	45	105	11	830	127	957
1965	98	141	24082	2	24323	2	24326
1966	60	85	1148	2452	3745	10	3755
1967	35	85	2735	348	3204	13	3216
1968	1657	35	462	279	2433	124	2557
1969	6328	151	1358	113	7951	444	8394
1970	228	85	13425	186	13925	11	13935
1971	119	296	1588	383	2386	2	2387
1972	198	141	489	182	1010	0	1010
1973	90	21	53	54	217	9	227
1974	41	269	3970	110	4391	43	4434
1975	212	10	12428	454	13103	37	13140
1976	159	40	1220	329	1747	218	1965
1977	411	92	738	86	1327	14	1341
1978	3245	364	139	101	3848	301	4149
1979	2832	745	7222	135	10933	286	11218
1980	2888	555	18552	397	22391	115	22505
1981	486	194	954	116	1749	5	1754
1982	658	250	79	73	1059	76	1135
1983	3109	158	218	18	3502	68	3570
1984	1907	657	7639	268	10471	20	10491
1985	397	633	4510	1651	7190	21	7211
1986	296	104	577	200	1177	3	1179
1987	5488	194	308	73	6063	3	6066
1988	1557	1679	700	74	4011	54	4065
1989	389	510	7246	135	8280	37	8318
1990	211	234	6102	398	6945	25	6970
1991	2584	338	678	539	4139	84	4223
1992	1498	745	2088	324	4655	70	4726
1993	911	974	1777	188	3849	176	4025
1994	813	254	7053	151	8271	85	8356
1995	799	266	7957	1006	10027	11	10039
1996	207	370	373	496	1446	5	1451
1997	734	174	458	128	1494	10	1504
1998	1395	381	387	83	2246	50	2296
...							

Table A2-9 continued...

Naknek River Spawners by Age Class (in thousands)							
	Age Classes						
Year	1.2	1.3	2.2	2.3	Major	Other	Total
1999	3715	408	1889	182	6193	3	6197
2000	300	1027	374	127	1828	0	1828
2001	99	918	14	58	1088	7	1095
2002	313	104	255	16	687	17	704
2003	1031	268	236	72	1608	79	1687
2004	1473	155	3820	37	5484	16	5500
2005	470	1017	615	176	2278	42	2320
2006	1532	938	395	185	3051	17	3068
2007	1975	434	68	324	2800	10	2810

Table A2-10. Kvichak River return age class data (1956-2004).

Kvichak River Returns by Age Class (in thousands)							
Year	Age Classes						Total
	1.2	1.3	2.2	2.3	Major	Other	
1956	24246	6968	6472	1308	38994	14	39008
1957	243	244	3333	259	4079	12	4091
1958	76	48	135	26	285	3	288
1959	212	117	206	11	546	1	547
1960	1314	563	46746	6472	55095	151	55246
1961	334	190	2287	679	3490	6	3496
1962	104	152	4675	408	5339	18	5357
1963	49	50	639	366	1104	15	1119
1964	2232	407	2341	647	5627	124	5751
1965	9853	471	32951	1239	44514	512	45026
1966	497	1086	4262	385	6230	33	6263
1967	349	272	812	86	1519	7	1526
1968	293	34	77	132	536	7	543
1969	129	321	4221	595	5266	38	5304
1970	43	13	14463	848	15367	465	15832
1971	244	93	2169	303	2809	20	2829
1972	255	159	1206	297	1917	23	1940
1973	576	1028	274	543	2421	37	2458
1974	6328	2009	16725	763	25825	355	26180
1975	5683	1232	30263	599	37777	310	38087
1976	5298	826	4115	273	10512	63	10575
1977	1934	935	208	99	3176	63	3239
1978	1835	1157	1318	817	5127	33	5160
1979	18331	2234	17931	3512	42008	134	42142
1980	2889	1641	8076	413	13019	29	13048
1981	789	231	931	167	2118	12	2130
1982	445	544	524	139	1652	34	1686
1983	8596	3010	1195	573	13374	17	13391
1984	2532	1924	16952	2483	23891	59	23950
1985	1024	1282	13465	1560	17331	90	17421
1986	688	1079	1390	1332	4489	69	4558
1987	4179	2519	4499	700	11897	148	12045
1988	2503	2470	4385	557	9915	76	9991
1989	2147	1679	18841	3316	25983	220	26203
1990	1542	1192	21105	1162	25001	109	25110
1991	2688	1232	699	170	4789	13	4802
1992	429	226	567	175	1397	23	1420
1993	852	890	624	574	2940	15	2955
1994	1811	1204	3777	250	7042	34	7076
1995	7736	1810	600	76	10222	22	10244
1996	369	1202	19	16	1606	13	1619
1997	130	107	263	75	575	7	582
1998	323	278	245	58	904	15	919
...							

Table A2-10 continued...

Naknek River Returns by Age Class (in thousands)							
	Age Classes						
Year	1.2	1.3	2.2	2.3	Major	Other	Total
1999	1070	244	5769	253	7336	90	7426
2000	1808	1179	912	408	4307	13	4320
2001	529	1842	979	690	4040	41	4081
2002	2633	775	139	28	3575	12	3587
2003	2756	1485	60		4301	21	4322
2004	4299						

Table A2-11. Alagnak River spawner age class data (1956-2007).

Alagnak River Spawners by Age Class (in thousands)							
Year	Age Classes						Total
	1.2	1.3	2.2	2.3	Major	Other	
1956							784
1957							127
1958							95
1959	492	51	278	0	820	5	825
1960	1,110	69	13	48	1,241	0	1,241
1961	2	87	0	2	90	0	90
1962	32	15	22	20	88	2	91
1963	172	10	15	6	203	0	203
1964	53	103	63	20	239	10	249
1965	26	46	67	15	155	20	175
1966	75	84	3	12	174	0	174
1967	146	50	2	0	197	6	203
1968	67	87	22	11	186	8	194
1969	66	36	66	1	169	14	182
1970	131	29	4	4	168	9	177
1971	99	72	5	5	180	7	187
1972	89	28	29	6	151	0	151
1973	3	25	2	5	34	1	35
1974	69	44	97	3	213	2	215
1975	22	54	5	18	100	1	100
1976	53	11	17	1	82	0	82
1977	70	11	4	10	95	5	100
1978	150	46	9	5	210	20	229
1979	206	7	55	1	268	26	294
1980	114	153	3	4	274	24	298
1981	35	40	5	0	80	2	82
1982	35	187	0	14	236	3	239
1983	76	9	6	1	93	4	96
1984	67	87	13	48	215	0	215
1985	28	81	7	2	118	0	118
1986	114	77	33	4	229	1	230
1987	94	50	3	5	152	2	154
1988	98	73	19	2	191	3	195
1989	137	39	18	1	195	2	197
1990	103	21	41	4	169	0	169
1991	97	83	94	3	277	1	278
1992	91	50	77	2	220	4	225
1993	150	58	113	21	343	5	348
1994	138	26	67	12	242	0	243
1995	57	26	122	5	211	5	216
1996	47	66	88	101	302	4	307
1997	109	56	53	0	218	0	218
1998	123	67	51	5	246	6	252
...							

Table A2-11 continued...

Alagnak River Spawners by Age Class (in thousands)							
	Age Classes						
Year	1.2	1.3	2.2	2.3	Major	Other	Total
1999	333	92	20	16	460	3	464
2000	289	82	63	14	448	3	451
2001	42	196	7	17	261	6	267
2002	357	264	113	19	753	14	767
2003	961	1653	453	472	3538	138	3676
2004	3532	1047	654	143	5376	21	5397
2005	598	3313	112	182	4205	14	4219
2006	1123	582	9	42	1757	17	1774
2007	1624	794	26	17	2460	6	2466

Table A2-12. Alagnak River return age class data (1956-2004).

Alagnak River Returns by Age Class (in thousands)							
Year	Age Classes						Total
	1.2	1.3	2.2	2.3	Major	Other	
1956	1885	459	0	38	2382	8	2390
1957	5	23	43	13	84	1	85
1958	43	26	27	52	148	0	148
1959	302	265	122	76	765	3	768
1960	105	185	135	31	456	0	456
1961	89	185	7	0	281	12	293
1962	129	91	3	19	242	20	262
1963	199	140	34	1	374	1	375
1964	100	98	113	17	328	8	336
1965	104	161	10	17	292	7	299
1966	282	262	12	11	567	13	580
1967	291	51	46	7	395	18	413
1968	127	40	2	3	172	8	180
1969	4	54	105	25	188	1	189
1970	73	71	6	2	152	0	152
1971	26	28	31	40	125	7	132
1972	91	19	8	33	151	1	152
1973	105	317	44	6	472	1	473
1974	730	47	341	6	1124	17	1141
1975	1099	62	342	3	1506	39	1545
1976	1111	433	52	138	1734	70	1804
1977	367	1768	0	22	2157	85	2242
1978	259	177	103	385	924	4	928
1979	1208	779	85	9	2081	20	2101
1980	272	545	33	24	874	7	881
1981	145	452	140	28	765	5	770
1982	463	370	12	8	853	2	855
1983	393	349	86	9	837	1	838
1984	420	385	111	61	977	5	982
1985	947	300	245	22	1514	10	1524
1986	910	704	509	20	2143	5	2148
1987	415	449	454	210	1528	8	1536
1988	413	388	719	113	1633	3	1636
1989	919	445	477	43	1884	19	1903
1990	697	324	873	628	2522	7	2529
1991	526	586	432	0	1544	10	1554
1992	259	187	165	22	633	6	639
1993	326	404	212	130	1072	16	1088
1994	419	717	106	108	1350	10	1360
1995	1875	516	324	69	2784	25	2809
1996	1057	815	28	20	1920	14	1934
1997	174	273	117	486	1050	32	1082
1998	369	1704	467	197	2737	12	2749
...							

Table A2-12 continued...

Alagnak River Returns by Age Class (in thousands)							
	Age Classes						
Year	1.2	1.3	2.2	2.3	Major	Other	Total
1999	991	1316	895	374	3576	97	3673
2000	4234	4064	252	129	8679	77	8756
2001	732	988	49	51	1820	34	1854
2002	1652	1635	71	75	3433	22	3455
2003	2655	5146	10				
2004	922						

Table A2-13. Wood River spawner age class data (1956-2007).

Wood River Spawners by Age Class (in thousands)							
Year	Age Classes						Total
	1.2	1.3	2.2	2.3	Major	Other	
1956							773
1957							289
1958							960
1959							2209
1960	488	316	187	23	1014	2	1016
1961	84	300	6	59	449	11	461
1962	823	48	3	0	874	0	874
1963	529	146	30	0	705	16	721
1964	793	128	147	9	1076	0	1076
1965	162	442	45	22	671	4	675
1966	620	543	8	35	1207	2	1209
1967	305	155	47	7	514	2	516
1968	257	336	33	15	640	9	649
1969	263	133	185	16	596	8	604
1970	640	434	53	27	1155	7	1162
1971	364	361	30	90	845	6	851
1972	304	77	32	17	430	1	431
1973	35	254	4	33	325	5	330
1974	1205	330	155	14	1704	5	1709
1975	356	670	154	69	1249	21	1270
1976	456	248	96	12	812	5	817
1977	163	343	24	29	559	3	562
1978	1724	459	24	10	2217	50	2267
1979	727	778	181	15	1701	5	1706
1980	1438	1178	298	30	2945	24	2969
1981	306	573	152	201	1233	1	1233
1982	401	487	18	57	963	13	976
1983	794	178	382	7	1361	0	1361
1984	277	655	15	55	1002	1	1003
1985	411	465	48	10	935	4	939
1986	252	486	39	40	817	1	819
1987	1027	208	75	27	1336	1	1337
1988	307	532	7	9	854	12	867
1989	559	554	19	44	1176	11	1186
1990	517	514	6	5	1042	27	1069
1991	410	730	6	2	1149	11	1160
1992	912	317	23	19	1271	15	1286
1993	671	458	12	24	1165	11	1176
1994	758	675	7	10	1450	22	1472
1995	993	390	78	7	1470	13	1482
1996	805	753	11	63	1632	18	1650
1997	807	620	36	19	1481	31	1512
1998	1177	515	53	7	1753	3	1756
...							

Table A2-13 continued...

Wood River Spawners by Age Class (in thousands)							
	Age Classes						
Year	1.2	1.3	2.2	2.3	Major	Other	Total
1999	1030	429	47	7	1512	0	1512
2000	770	499	19	8	1296	4	1300
2001	59	1381	1	10	1451	8	1459
2002	999	206	61	6	1271	13	1284
2003	786	625	22	16	1449	11	1460
2004	1054	387	83	12	1536	7	1543
2005	808	586	23	32	1449	48	1497
2006	3079	615	257	50	4000	8	4008
2007	1189	276	46	5	1516	12	1528

Table A2-14. Wood River return age class data (1956-2004).

Wood River Returns by Age Class (in thousands)							
Year	Age Classes					Other	Total
	1.2	1.3	2.2	2.3	Major		
1956	774	627	24	0	1425	48	1473
1957	136	257	35	0	428	21	449
1958	2145	389	75	32	2641	2	2643
1959	979	398	359	55	1791	14	1805
1960	1474	1039	106	105	2724	10	2734
1961	255	1183	24	20	1482	14	1496
1962	992	340	116	43	1491	12	1503
1963	536	769	76	46	1427	1	1428
1964	452	347	338	74	1211	9	1220
1965	472	999	90	213	1774	12	1786
1966	974	988	46	69	2077	44	2121
1967	642	269	75	80	1066	26	1092
1968	514	565	5	19	1103	5	1108
1969	57	445	201	116	819	14	833
1970	1539	1002	231	26	2798	2	2800
1971	456	576	198	49	1279	22	1301
1972	779	631	32	27	1469	45	1514
1973	213	1148	74	44	1479	5	1484
1974	2956	1698	421	71	5146	18	5164
1975	1592	1977	406	734	4709	76	4785
1976	2278	2589	572	265	5704	16	5720
1977	1029	2173	40	26	3268	22	3290
1978	1364	1029	784	96	3273	15	3288
1979	2643	1491	24	13	4171	11	4182
1980	453	978	72	101	1604	1	1605
1981	626	1137	60	86	1909	0	1909
1982	522	765	121	14	1422	16	1438
1983	1940	1154	15	75	3184	10	3194
1984	586	1340	32	23	1981	17	1998
1985	1127	1390	29	12	2558	30	2588
1986	1179	1970	70	64	3283	47	3330
1987	1334	756	98	92	2280	78	2358
1988	1613	1425	90	34	3162	31	3193
1989	2293	1922	13	39	4267	23	4290
1990	1104	1208	286	169	2767	27	2794
1991	2633	2466	54	71	5224	86	5310
1992	2398	1674	90	49	4211	71	4282
1993	1715	1161	129	191	3196	29	3225
1994	2747	1993	448	91	5279	13	5292
1995	3524	2594	149	35	6302	67	6369
1996	2705	3675	3	13	6396	58	6454
1997	174	675	164	203	1216	96	1312
1998	2910	3516	176	104	6706	23	6729
...							

Table A2-14 continued...

Wood River Returns by Age Class (in thousands)							
	Age Classes						
Year	1.2	1.3	2.2	2.3	Major	Other	Total
1999	1778	2239	403	144	4564	59	4623
2000	3184	2181	120	578	6063	36	6099
2001	2059	4390	599	50	7098	67	7165
2002	5704	1821	257	31	7813	51	7864
2003	4596	1728	37				
2004	3656						

Table A2-15. Igushik River spawner age class data (1956-2007).

Igushik River Spawners by Age Class (in thousands)							
Year	Age Classes						Total
	1.2	1.3	2.2	2.3	Major	Other	
1956							400
1957							130
1958							107
1959							644
1960	106	296	53	40	495	0	495
1961	1	250	3	39	294	1	294
1962	5	6	2	2	15	0	16
1963	55	27	8	3	92	0	92
1964	33	50	38	7	128	0	129
1965	21	132	19	9	181	0	181
1966	13	167	7	19	206	1	206
1967	145	127	4	6	281	0	282
1968	92	83	16	3	194	1	195
1969	206	225	72	9	512	0	512
1970	43	189	120	18	371	0	371
1971	32	140	4	34	210	1	211
1972	25	26	5	4	60	0	60
1973	0	54	0	5	60	0	60
1974	21	97	231	7	356	2	359
1975	37	114	27	61	240	1	241
1976	52	71	29	33	185	1	186
1977	15	59	4	18	96	0	96
1978	257	260	8	5	530	6	536
1979	358	344	148	10	860	0	860
1980	348	1523	101	11	1982	5	1988
1981	87	312	52	138	589	2	591
1982	18	357	3	41	419	5	424
1983	105	46	27	2	180	0	180
1984	9	161	8	7	185	0	185
1985	93	106	11	2	212	0	212
1986	21	269	1	17	308	0	308
1987	64	90	4	12	169	0	169
1988	17	143	4	5	170	1	170
1989	209	229	16	6	460	1	462
1990	78	264	13	6	360	6	366
1991	44	695	2	12	753	3	756
1992	77	213	1	8	300	5	305
1993	123	270	3	4	400	6	406
1994	94	317	27	7	445	1	446
1995	100	324	40	7	472	2	473
1996	12	347	0	40	400	1	401
1997	63	55	3	6	126	1	128
1998	83	123	6	4	216	0	216
...							

Table A2-15 continued...

Igushik River Spawners by Age Class (in thousands)							
	Age Classes						
Year	1.2	1.3	2.2	2.3	Major	Other	Total
1999	207	224	12	2	446	0	446
2000	47	364	2	2	413	0	413
2001	0	403	0	3	407	3	410
2002	83	30	6	3	121	2	123
2003	34	149	1	9	193	1	194
2004	34	51	19	4	108	2	110
2005	20	305	7	33	366	0	366
2006	158	134	4	9	305	1	305
2007	340	61	10	3	414	2	415

Table A2-16. Igushik River return age class data (1956-2004).

Igushik River Returns by Age Class (in thousands)							
Year	Age Classes						Total
	1.2	1.3	2.2	2.3	Major	Other	
1956	169	523	12	36	740	3	743
1957	2	35	19	20	76	0	76
1958	14	71	20	28	133	0	133
1959	101	155	93	22	371	0	371
1960	61	310	44	57	472	1	473
1961	33	364	20	17	434	2	436
1962	20	280	9	9	318	8	326
1963	254	190	36	25	505	3	508
1964	162	585	133	49	929	1	930
1965	371	436	203	80	1090	0	1090
1966	66	383	6	15	470	0	470
1967	57	90	13	12	172	3	175
1968	43	120	0	10	173	2	175
1969	1	131	301	103	536	2	538
1970	26	170	41	71	308	1	309
1971	48	164	60	30	302	1	303
1972	89	109	6	13	217	12	229
1973	19	650	25	29	723	2	725
1974	441	750	346	25	1562	12	1574
1975	783	2556	137	503	3979	2	3981
1976	551	1411	194	215	2371	23	2394
1977	294	1689	9	9	2001	14	2015
1978	96	330	84	15	525	1	526
1979	422	406	13	5	846	0	846
1980	20	271	25	56	372	0	372
1981	188	779	8	49	1024	1	1025
1982	57	434	9	10	510	9	519
1983	151	353	8	29	541	3	544
1984	41	641	56	36	774	6	780
1985	515	938	86	79	1618	15	1633
1986	236	2231	27	30	2524	33	2557
1987	158	587	7	29	781	25	806
1988	189	1056	41	36	1322	5	1327
1989	508	1119	59	53	1739	22	1761
1990	159	1429	183	146	1917	8	1925
1991	318	1314	3	20	1655	6	1661
1992	44	148	8	26	226	3	229
1993	132	316	20	35	503	3	506
1994	238	846	92	26	1202	1	1203
1995	653	1599	15	13	2280	21	2301
1996	171	1237	1	4	1413	4	1417
1997	34	52	10	58	154	24	178
1998	143	732	28	30	933	9	942
...							

Table A2-16 continued...

Igushik River Returns by Age Class (in thousands)							
	Age Classes						
Year	1.2	1.3	2.2	2.3	Major	Other	Total
1999	206	310	71	297	884	7	891
2000	104	1656	71	100	1931	4	1935
2001	64	1002	13	37	1116	14	1130
2002	343	477	36	13	869	8	877
2003	1266	2545	6				
2004	857						

Table A2-17. Nushagak River spawner age class data (1973-2007).

Nushagak River Spawners by Age Class (in thousands)							
Year	Age Classes						Total
	1.2	1.3	2.2	2.3	Major	Other	
1973							185
1974							185
1975							752
1976							470
1977							553
1978							664
1979							499
1980							3317
1981							1012
1982							601
1983							404
1984							593
1985							498
1986							990
1987							388
1988							483
1989	31	233	1	2	267	246	513
1990	45	226	1	1	273	407	680
1991	11	255	0	3	270	223	493
1992	113	225	7	18	364	331	695
1993	33	457	1	3	495	220	715
1994	22	243	1	3	269	241	509
1995	54	82	4	1	141	140	281
1996	66	315	0	3	384	120	504
1997	31	266	4	6	307	66	373
1998	38	375	1	2	415	44	459
1999	47	203	1	3	254	58	312
2000	144	241	5	7	397	7	404
2001	12	619	2	2	635	176	811
2002	67	179	1	3	251	65	316
2003	36	492	3	12	543	38	581
2004	88	307	5	10	409	83	492
2005	118	827	2	6	953	96	1049
2006	105	374	3	3	486	62	548
2007	103	345	7	5	460	58	518

Table A2-18. Nushagak River return age class data (1980-2003).

Nushagak River Returns by Age Class (in thousands)							
Year	Age Classes						Total
	1.2	1.3	2.2	2.3	Major	Other	
1980	84	344	162	156	746	537	1284
1981	170	1476	2	32	1680	246	1926
1982	164	894	2	7	1067	496	1563
1983	114	553	6	3	676	845	1521
1984	51	566	2	6	625	287	912
1985	64	612	6	16	698	653	1351
1986	114	676	0	64	854	1145	1999
1987	36	535	36	10	618	1429	2047
1988	214	1426	12	8	1661	797	2457
1989	124	703	1	4	831	604	1436
1990	36	253	18	7	314	933	1247
1991	172	1010	3	19	1205	286	1491
1992	228	650	9	11	897	654	1551
1993	63	803	1	49	916	208	1124
1994	81	665	6	53	805	66	872
1995	143	923	34	15	1116	120	1236
1996	502	1795	3	5	2305	69	2374
1997	71	254	14	86	425	158	583
1998	312	1633	64	80	2089	197	2286
1999	421	1598	25	26	2070	121	2191
2000	233	2892	23	35	3183	536	3719
2001	294	2566	7	43	2910	528	3438
2002	196	1856	39	19	2110	140	2250
2003	414	1360					

Table A2-19. Togiak River spawner age class data (1956-2007).

Togiak River Spawners by Age Class (in thousands)							
Year	Age Classes						Total
	1.2	1.3	2.2	2.3	Major	Other	
1956							225
1957							25
1958							72
1959							210
1960							163
1961	17	86	5	13	121	1	122
1962	31	22	5	3	61	1	62
1963	53	36	18	8	115	1	116
1964	71	17	11	4	104	1	105
1965	33	54	6	2	96	0	96
1966	13	76	3	11	103	2	104
1967	28	46	1	6	80	1	81
1968	23	22	3	2	49	0	50
1969	79	21	12	3	116	1	117
1970	102	84	12	2	200	3	203
1971	5	177	2	15	198	2	200
1972	27	38	9	4	78	1	79
1973	16	72	2	15	106	1	107
1974	26	64	7	5	102	1	104
1975	36	113	23	4	177	3	181
1976	35	113	19	22	189	1	189
1977	88	44	6	21	159	4	163
1978	134	158	4	7	303	3	306
1979	70	112	9	8	198	0	198
1980	84	420	15	5	525	2	527
1981	79	197	13	18	306	1	307
1982	77	161	3	38	279	9	289
1983	81	123	7	1	212	0	213
1984	28	105	3	9	144	7	151
1985	36	109	6	2	153	0	153
1986	72	110	8	8	197	6	203
1987	197	66	7	4	276	3	278
1988	9	295	0	3	306	3	309
1989	22	59	3	17	101	3	104
1990	56	77	22	10	165	2	166
1991	88	136	16	13	253	1	254
1992	37	136	11	23	207	2	210
1993	35	123	12	18	187	1	189
1994	76	75	3	15	168	6	174
1995	66	126	10	8	210	1	211
1996	21	124	16	20	182	5	187
1997	46	56	27	20	149	3	152
1998	33	115	5	21	173	2	175
...							

Table A2-19 continued...

Togiak River Spawners by Age Class (in thousands)							
Year	Age Classes						Total
	1.2	1.3	2.2	2.3	Major	Other	
1999	165	17	12	1	195	1	196
2000	18	332	2	0	352	0	352
2001	17	269	1	15	302	1	303
2002	31	134	7	4	176	2	179
2003	50	149	5	26	231	2	232
2004	31	74	9	19	133	2	136
2005	33	83	28	10	154	2	156
2006	106	125	38	41	311	1	312
2007	75	167	7	21	269	1	270

Table A2-20. Togiak River return age class data (1956-2004).

Togiak River Returns by Age Class (in thousands)							
Year	Age Classes						Total
	1.2	1.3	2.2	2.3	Major	Other	
1956	114	306	22	13	455	5	460
1957	48	70	20	36	174	8	182
1958	68	115	59	25	267	3	270
1959	141	92	56	7	296	0	296
1960	191	274	22	52	539	2	541
1961	85	216	15	19	335	5	340
1962	48	102	4	8	162	7	169
1963	43	65	18	24	150	2	152
1964	43	84	41	6	174	1	175
1965	154	181	31	37	403	2	405
1966	200	419	4	9	632	8	640
1967	18	99	16	40	173	8	181
1968	49	190	6	13	258	4	262
1969	28	142	25	13	208	8	216
1970	54	226	55	70	405	2	407
1971	106	317	62	68	553	5	558
1972	93	150	21	34	298	4	302
1973	151	442	18	31	642	12	654
1974	271	307	73	45	696	6	702
1975	195	848	87	59	1189	10	1199
1976	189	558	142	175	1064	5	1069
1977	232	617	14	14	877	9	886
1978	149	430	65	25	669	13	682
1979	270	293	12	5	580	4	584
1980	45	224	10	19	298	6	304
1981	53	245	15	16	329	14	343
1982	109	255	14	26	404	21	425
1983	285	924	9	21	1239	8	1247
1984	21	109	4	17	151	15	166
1985	35	194	35	77	341	9	350
1986	77	445	83	121	726	33	759
1987	190	575	31	81	877	15	892
1988	111	403	34	53	601	16	617
1989	132	328	7	41	508	38	546
1990	101	460	75	37	673	30	703
1991	189	429	28	29	675	16	691
1992	50	124	33	30	237	38	275
1993	64	229	6	15	314	8	322
1994	43	167	31	8	249	5	254
1995	341	1010	11	66	1428	13	1441
1996	87	987	4	21	1099	345	1444
1997	43	305	16	87	451	12	463
1998	54	633	24	91	802	6	808
...							

Table A2-20 continued...

Togiak River Returns by Age Class (in thousands)							
	Age Classes						
Year	1.2	1.3	2.2	2.3	Major	Other	Total
1999	137	290	29	50	506	12	518
2000	87	318	141	152	698	9	707
2001	63	410	90	62	625	12	637
2002	241	727	25	19	1012	14	1026
2003	245	723	8		976	2	978
2004	106						

Table A3-1 continued...

Monthly mean temperature (degree Fahrenheit)												
King Salmon Airport												
Year	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
1995	19.48	23.07	17.37	40.27	46.39	53.15	57.23	54.76	52.43	35.06	18.43	25.02
1996	15.18	13.93	33.08	34.88	46.48	51.92	55.27	52.87	43.53	29.34	25.53	6.26
1997	12.73	30.29	20.79	37.63	47.76	54.02	59.81	57.42	50.43	27.6	26.37	7.79
1998	12.65	22.07	33.03	36.87	42.31	51.67	56.02	51.63	47.12	35.08	28.37	9.6
1999	10.97	4.36	14.02	31.77	40.05	50.92	54.42	53.92	47.52	28.39	18.65	1.6
2000	4.21	30.31	30.37	34.87	42.47	50.62	54.19	54.23	45.85	34.66	32.75	33.9
2001	25.18	28.41	25.52	35.77	40.52	53.02	54.48	55.55	48.45	27.71	18.92	7.53
2002	23.26	19.27	26.89	33.35	45.92	52.33	55.79	55.21	48.73	42.81	34.43	20.9
2003	28.5	35.6	19.9	37.7	44.3	52.4	56.9	56.6	45.9	37	26.3	11.6
2004	9.8	28.4	20.7	36.6	48	54.5	58.9	58.8	46	40.1	29.7	23.8
2005	23.2	23.6	29	31	47.5	53.7	57.3	56.3	49.1	35.1	10.7	27
2006	0.4	22.6	17.7	30.1	44.9	51.3	54.7	52.4	48.5	39.7	15.2	10.4
2007	10.8	21.3	5.7	38.3	43.2	50.6	55.2	56.8	49.6	34.8	31.4	18.5
2008	6.5	8.9	23.4	28.7	42.6	48.5	52.6	53.9	47.9	28.5	14.8	20.7

Table A3-2 continued...

Monthly Pacific Decadal Oscillation												
University of Washington												
Year	JAN	FEB	MAR	APR	MAY	JUN	JUL	AUG	SEP	OCT	NOV	DEC
1986	1.12	1.61	2.18	1.55	1.16	0.89	1.38	0.22	0.22	1	1.77	1.77
1987	1.88	1.75	2.1	2.16	1.85	0.73	2.01	2.83	2.44	1.36	1.47	1.27
1988	0.93	1.24	1.42	0.94	1.2	0.74	0.64	0.19	-0.37	-0.1	-0.02	-0.43
1989	-0.95	-1.02	-0.83	-0.32	0.47	0.36	0.83	0.09	0.05	-0.12	-0.5	-0.21
1990	-0.3	-0.65	-0.62	0.27	0.44	0.44	0.27	0.11	0.38	-0.69	-1.69	-2.23
1991	-2.02	-1.19	-0.74	-1.01	-0.51	-1.47	-0.1	0.36	0.65	0.49	0.42	0.09
1992	0.05	0.31	0.67	0.75	1.54	1.26	1.9	1.44	0.83	0.93	0.93	0.53
1993	0.05	0.19	0.76	1.21	2.13	2.34	2.35	2.69	1.56	1.41	1.24	1.07
1994	1.21	0.59	0.8	1.05	1.23	0.46	0.06	-0.79	-1.36	-1.32	-1.96	-1.79
1995	-0.49	0.46	0.75	0.83	1.46	1.27	1.71	0.21	1.16	0.47	-0.28	0.16
1996	0.59	0.75	1.01	1.46	2.18	1.1	0.77	-0.14	0.24	-0.33	0.09	-0.03
1997	0.23	0.28	0.65	1.05	1.83	2.76	2.35	2.79	2.19	1.61	1.12	0.67
1998	0.83	1.56	2.01	1.27	0.7	0.4	-0.04	-0.22	-1.21	-1.39	-0.52	-0.44
1999	-0.32	-0.66	-0.33	-0.41	-0.68	-1.3	-0.66	-0.96	-1.53	-2.23	-2.05	-1.63
2000	-2	-0.83	0.29	0.35	-0.05	-0.44	-0.66	-1.19	-1.24	-1.3	-0.53	0.52
2001	0.6	0.29	0.45	-0.31	-0.3	-0.47	-1.31	-0.77	-1.37	-1.37	-1.26	-0.93
2002	0.27	-0.64	-0.43	-0.32	-0.63	-0.35	-0.31	0.6	0.43	0.42	1.51	2.1
2003	2.09	1.75	1.51	1.18	0.89	0.68	0.96	0.88	0.01	0.83	0.52	0.33
2004	0.43	0.48	0.61	0.57	0.88	0.04	0.44	0.85	0.75	-0.11	-0.63	-0.17
2005	0.44	0.81	1.36	1.03	1.86	1.17	0.66	0.25	-0.46	-1.32	-1.5	0.2
2006	1.03	0.66	0.05	0.4	0.48	1.04	0.35	-0.65	-0.94	-0.05	-0.22	0.14
2007	0.01	0.04	-0.36	0.16	-0.1	0.09	0.78	0.5	-0.36	-1.45	-1.08	-0.58
2008	-1	-0.77	-0.71	-1.52	-1.37	-1.34	-1.67	-1.7	-1.55	-1.76	-1.25	-0.87
2009	-1.4	-1.55	-1.59	-1.65	-0.88	-0.31	-0.53	0.09	0.52	0.27	-0.4	0.08