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AN AGE STRUCTURED MODEL FOR ASSESSMENT AND MANAGEMENT OF COPPER RIVER CHINOOK SALMON

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A

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ABSTRACT

Chinook salmon in Alaska support human uses through a variety of fisheries. Age-structured assessment models are rarely used for estimating the abundance of exploited stocks. This thesis develops a model for the Copper River chinook salmon population to show its advantages over typical assessment models. Information consists of catch-age data from three fisheries (commercial, recreational, subsistence), and two sources of auxiliary data (escapement index, spawner-recruit relationship). Four approaches utilizing different information sources are explored. Results suggest that an approach utilizing pooled catch-age data with time-varying brood-year proportions produces the best estimates, although retrospective and sensitivity analyses suggest that all four approaches explored are robust. The model should assist managers when making management decisions, because it integrates all sources of information, accounts for uncertainty, and provides estimates of optimal escapement. The model shows promise as a method for assessing and forecasting chinook salmon populations.

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INTRODUCTION

From the large commercial fishery near Cordova, Alaska, to the in-river recreational and subsistence fisheries found in the Copper River Valley, the Copper River supports a variety of important fisheries. While its sockeye (*Onchorynchus nerka*) salmon commercial fishery is the best known, an important chinook (*O. tschawtscha*) salmon population supports commercial, recreational, and subsistence harvests. The Copper River chinook salmon population is made up of a number of different stocks that are spatially and temporally divided during spawning. The total harvest within the last five years (1995-1999) has averaged 75,853 (Taube 2000). A limited understanding of recruitment and population dynamics, as well as the political, geographical, and physical characteristics of the river, have made managing the area-wide drainage for these specific fisheries difficult. Currently the chinook salmon return is managed under a fixed escapement policy. The policy is implemented through two plans, wherein managers with ADF&G depend on in-season sonar counts, weekly anticipated harvest forecasts, and fishery-specific harvests to improve upon previous estimates of run strength. Although there is an established biological escapement goal of 28,000-55,000 chinook salmon, there are no fishery specific harvest guidelines. Furthermore, of the 40 spawning streams identified, only nine are used to provide an indication of total escapement. Imprecision of in-season management coupled with an inaccurate index of escapement places uncertainty on achieving the fixed escapement goal. Therefore, in order to establish acceptable biological escapement goals and sustainable harvest guidelines, a dependable and cost effective method for estimating the abundance of returning chinook salmon is required.

A common assessment approach for salmon populations is known as run reconstruction. This approach utilizes information about catch and escapement over time to estimate the return of salmon at various times throughout the run (Templin et al. 1996). However, one drawback to run reconstruction is the inability to estimate complete brood-year returns in years with incomplete estimates of the return at each age.

Age-structured assessment models are widely used to estimate population parameters and understand population dynamics by combining various information sources about fish populations (Quinn and Deriso 1999, p. 295). The basic model provides estimates of these population parameters based on processes like recruitment, catchability, the spawner-recruit relationship, and fishing and natural mortality. Parameter estimates are determined by optimizing an objective function usually obtained from least squares or maximum likelihood formulations.

Catch-age analysis is one age-structured method that has been used in a variety of ways to estimate current stock abundance of exploited fish (Doubleday 1976; Pope 1977; Dupont 1983; Fournier and Archibald 1982; Deriso et al. 1985, 1989; Kimura 1989, 1990; Methot 1989,1990). Age-structured models up until Agger et al. (1971) were completely deterministic and predicted the observed catch data with no measure of how well the parameters were estimated (Megrey 1989). Furthermore, catch-age data were analyzed one cohort at a time; estimated parameter values from one cohort were not related to other cohorts from the same population (Megrey 1989).

Copper River chinook salmon are different than most age-structured populations because returning salmon are subject to three separate fisheries during migration to their spawning grounds. To handle the complex life history of Pacific salmon and the multiple fisheries they encounter, Kope (1987) used a catch-age model that separates fishing mortality rates into annual fishing effort and vulnerability at age. Dividing the return into three time periods allowed him to partition the fishing mortality between the commercial and recreational fisheries. In my model, brood-year returns are modeled differently by bringing in brood-year proportions, thereby avoiding the necessity of incorporating natural mortality, a totally unknown parameter.

Although Pope (1977) and Doubleday (1976) are recognized as introducing the separability assumption, Pope (1977) gave credit to Agger et al. (1971). Agger et al. (1971) minimized the number of parameters in the model, provided a means to estimate all the parameters simultaneously instead of sequentially, and simultaneously linked data from several cohorts (Megrey 1989). Whether or not Agger et al. (1971) were the first to utilize this assumption, Doubleday (1976) and Pope (1977) demonstrated that catch-age data alone provide an unreliable estimate of stock abundance because of a negative correlation between estimates of fishing mortality and stock abundance. From this point on, studies utilizing catch-age analysis would routinely incorporate the separability assumption and some form of auxiliary information in order to estimate abundance.

Deriso et al. (1985) showed that the addition of auxiliary information such as fishing effort or survey catches is typically required to constrain the catch-at-age analysis and obtain reliable estimates. However, the types and function of auxiliary data need to be thoroughly scrutinized to prevent the inappropriate application of the model to fisheries management (Crone and Sampson 1998). Auxiliary information takes one of two forms: either (1) supplemental data that provides insight into one or more population parameters; or (2) additional assumptions about the underlying population dynamics that provide model structure (Deriso et al. 1985).

A study by Crone and Sampson (1998) showed that stock assessment models based on maximum likelihood techniques with multinomial error structures are more appropriate for describing the variability found in observed catch-age data. Least squares formulations typically assume that observation errors in the catch-age data are lognormally distributed. In other words, the least squares estimators assume the log transformed estimates have constant variance; this dictates that the coefficients of variation (CV's) for the untransformed catch-age estimates must be approximately equal (Kimura 1990). Because the authors found the CV's associated with their untransformed catch-age estimates were not constant, they chose a maximum likelihood format with a multinomial error structure. In contrast, Quinn and Gates (1997) found that the maximum likelihood approach for parameter estimation is difficult to use when the data have different levels of precision and accuracy and contain autocorrelation. Since the age compositions of the four fisheries are based on different levels of sampling, the population parameters in this study will be determined by minimizing a least squares objective function containing elements of catch and escapement. Measurement errors in catch and escapement are known to occur and are provided for in the model.

In practice, parameters found with catch-age models are fitted to catch-at-age data either from a single cohort or from several cohorts at once. Most of the limitations of single cohort analysis, such as the number of parameters equaling the number of data points, can be handled by using multiple cohort techniques (Kope 1987).

The main goal of this study is to establish an integrated assessment environment for the understanding and management of Copper River chinook salmon. A secondary goal is to estimate the total return and escapement each year from catch information and an index of escapement. To accomplish these goals, I achieved the following objectives:

1) to compile catch, escapement, and auxiliary information about the population;
2) to supplement existing age-structured information by sampling recreational and subsistence catches in 1999 and 2000;
3) to develop an age-structured assessment model of the population by year;
4) to determine a robust approach for utilizing the age-composition information;
5) to determine if the proportion of brood-year returns at each age could be estimated annually;
6) to examine sensitivity of the model to various weightings of the data;
7) to forecast the population accurately; and,
8) to determine optimal escapement and the maximum sustainable catch (MSC).

The model combines catch-age analysis with auxiliary information as well as elements of run reconstruction and applies this combination to a returning population of Copper River chinook salmon. The chinook salmon population consisted of several brood-years; therefore, the model contains multiple cohorts. A simple run reconstruction provided initial brood-year return estimates required for the catch-age analysis. Auxiliary information sources included an aerial escapement index providing escapement information and a spawner-recruit relationship constraining the model's recruitment estimates from deviating too far from a particular spawner-recruit relationship.

This model provides an historical perspective of catch and escapement that allows one to predict future returns and estimate population parameters. Prior to the model's development, estimates of escapement, gear selectivity, and exploitation could not be determined with existing information. Furthermore, forecasts of the commercial catch, which are simply the average catch over the last ten years, are of little use to up-river recreational and subsistence fishery managers.

STUDY AREA

The Copper River is a large, glacial river that drains 61,440 square kilometers and is the fifth largest watershed in Alaska (Figure 1). The river originates from the Copper Glacier in the Wrangell-St. Elias Mountains and flows south for 550 km. Along the way it drains a large portion of interior Alaska and carves its way through the Chugach Mountains before entering the Gulf of Alaska near Cordova.

The Copper River supports significant populations of chinook, sockeye, and coho (*O. kisutch*) salmon. Six tributaries of the Copper River — the Klutina, Gulkana, Chitina, Tazlina, Tonsina, and Chistochina Rivers — contain the majority of chinook salmon spawning areas; however, over 40 streams have been reported as areas where spawning occurs. Of the 40 streams identified, only nine streams are utilized when determining the area wide escapement. Biologists establish an aerial index by counting chinook salmon from the air in the nine designated streams. Factors such as weather, water clarity, and riparian cover influence the reliability of the count. Furthermore, attempting to access these spawning streams from land to procure more reliable estimates of escapement would be costly and logistically difficult.

The Copper River supports three fisheries: commercial, subsistence (gillnet/fishwheel and dipnet), and recreational. The commercial fishery, located in the Copper River District, is found at the mouth of the Copper River in waters between and around the barrier islands (Figure 1). The Copper River District is managed in-season

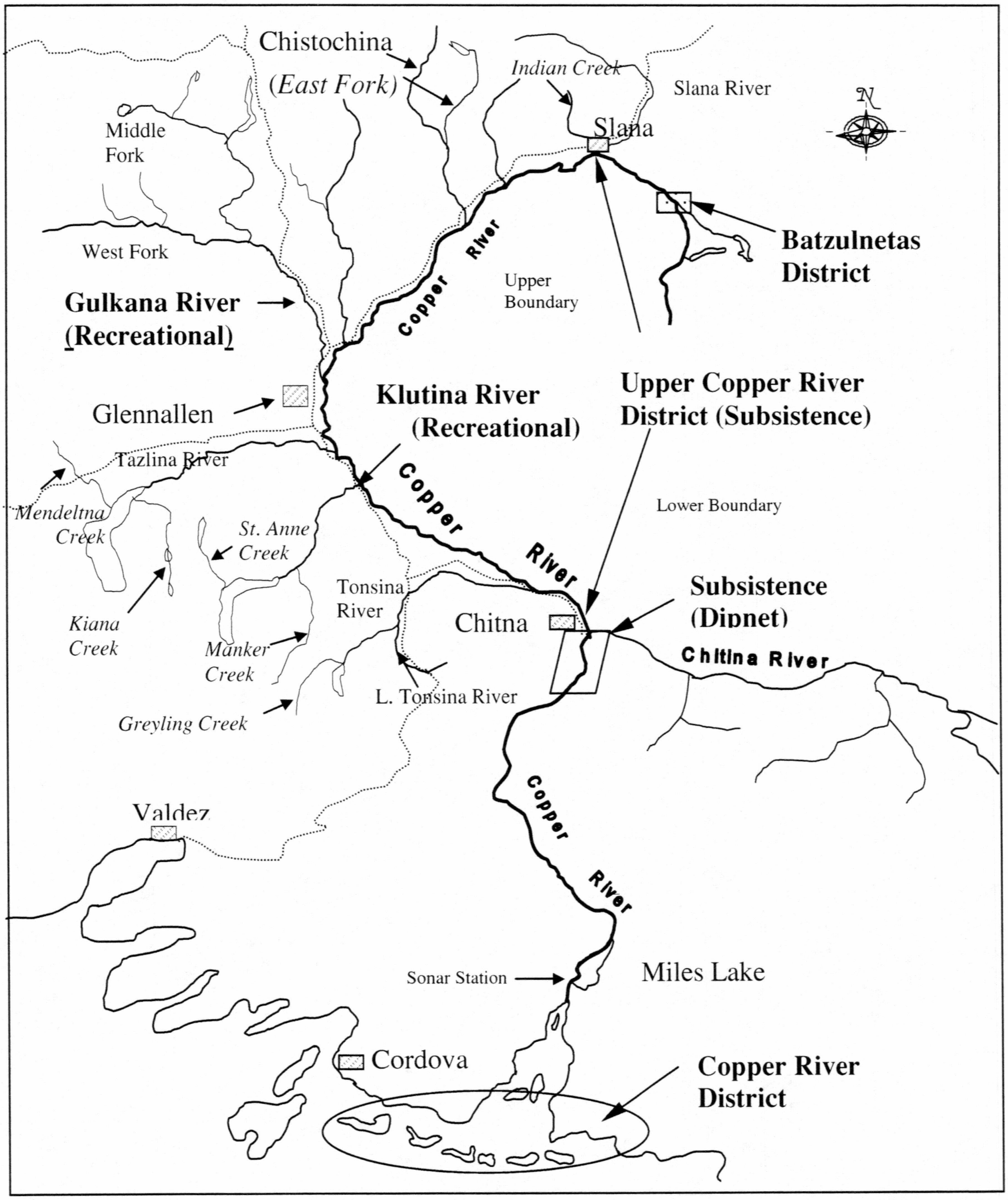


Figure 1. A diagram showing the Copper River Valley, the three fisheries, and the nine index streams.

from three information sources: (1) the number of salmon passing the Miles Lake sonar site; (2) weekly anticipated harvest forecasts; and (3) aerial escapement surveys of the lower Copper River. Historically the sockeye salmon run drove the commercial fishery and chinook salmon were considered an incidental catch. However, in recent years the dramatic increase in price for chinook salmon, from $2.35/lb. in 1989 to $5.35/lb. in 1999, has led commercial fishermen to target chinook salmon during the first few commercial openers. Chinook, sockeye, and coho salmon are the major species harvested using drift gillnets measuring a maximum of 274 m (150 fathoms) with a maximum mesh size of 6 inches. The average commercial harvest for chinook salmon from 1995-1999 was 60,702 with a low of 51,273 in 1997 and a peak of 68,827 in 1998 (Evenson and Savereide 1999). Chinook salmon begin returning to the Copper River in early May with peak migration usually from mid-May to mid-June. Commercial fishing for chinook salmon coincides with the beginning of the peak migration and is essentially over by the 1st of July.

The first subsistence fishery (gillnet and fishwheel) is found in three areas of the Copper River (Figure 1). The first area is located within the commercial fishing district and mandates drift gillnets measuring no more than 91 m (50 fathoms) with a maximum mesh size of 6 inches. The second and largest area is the Upper Copper River District, which runs from the north side of the Chitina-McCarthy Bridge to the village of Slana. The last area, the Batzulnetas District, is small and located at the confluence of the Copper River and Tanada Creek. Fishing in the last two districts is mainly accomplished with shore-positioned fish wheels, but dipnets are allowed also. The subsistence fishing season begins on June 1st and runs through the end of September, but most chinook salmon are harvested by the end of July. The average subsistence harvest of chinook salmon from 1995-1999 was 2,160 with a low of 1,482 in 1995 and a peak of 3,000 in 1999 (Evenson and Savereide 1999).

The subsistence dipnet fishery, historically called the personal use fishery, is located up-river in Wood Canyon just below Chitina, Alaska (Figure 1). Fishermen utilize large dipnets to capture fish from shore or in a drifting boat. The magnitude of the run coupled with the "bottleneck" effect from the canyon walls allows a person to place the dipnet into the water and wait for salmon to swim in as they migrate upstream. Typically, fishing for chinook salmon occurs between early June and late July. The average subsistence dipnet harvest of chinook salmon from 1995-1999 was 5,530 with a low of 3,584 in 1996 and a peak of 7,192 in 1999 (Evenson and Savereide 1999).

Originally, from 1959 to 1980, the personal use fishery was classified as a subsistence fishery. However, in 1980 the passage of the Alaska National Interest Lands Conservation Act (ANILCA) mandated a subsistence fishing preference for "rural" residents. To avoid federal takeover, non-Copper Valley residents were prevented from harvesting fish for personal use. By 1984, the exclusion of non-Copper Valley residents from the fishery led the Alaska Board of Fisheries to establish a personal-use fishery for all Alaska residents on the Copper River. At the present time, the Federal government has claimed jurisdiction over Upper Copper River subsistence fisheries, because a portion of the river abuts national park lands. The State of Alaska disputes Federal jurisdiction not only on the navigability claim but also because the Ahtna Native Corporation privately owns the majority of adjacent lands. The State of Alaska continues to issue subsistence permits and manage the subsistence fishery.

The recreational fisheries for chinook salmon in the Copper River primarily occur in two major tributaries, the Klutina and Gulkana rivers. However, other areas on the Tonsina, Tazlina, and Chistochina rivers support small chinook harvests. The chinook salmon recreational fishery is the most important recreational fishery in the Copper River in terms of effort and economic value (Taube 2000). The increase in tourism coupled with strong returns in previous years has led to a 27 % increase in effort since 1988 (Taube 2000). Chinook salmon typically enter the Gulkana River in early June with a peak occurring toward the end of June. Fishing continues into July, but catches decrease until the fishery closes on July 19th. In contrast, chinook salmon enter the Klutina River towards the end of June and continue into August. Typically, the peak of the run is in the second week of July, but fishing continues until August 10th. The average recreational fishery harvest of chinook salmon from 1995-1999 was 7,673 with a low of 6,709 in 1995 and a peak of 8,937 in 1998 (Evenson and Savereide 1999).

METHODS

Fishery Harvest

The harvest of Copper River chinook salmon is determined in a variety of ways. The commercial catch statistics, such as numbers and weight by species and date harvested, are collected by ADF&G from commercial fish ticket receipts. The catch is updated at the end of each commercial opening and the total catch is known at the end of the season. The subsistence dipnet and fishwheel harvests are also determined from the return of fishery specific harvest permits. The recreational fishery is estimated from the statewide annual harvest survey mailed to resident and non-resident sport fish license holders. Estimates are determined from the surveys returned.

Catch-Age Data

Age composition of the harvest is estimated from scale samples collected by the Sport and Commercial Fish Divisions, ADF&G. Sampling of the three fisheries for age composition has varied greatly. Sampling of the commercial fishery dates back to 1980 and includes large sample sizes; however, scale sampling of the dipnet and fishwheel subsistence fisheries did not begin until 1992 and 1993, respectively, and the sample sizes are relatively small. Moreover, recreational scale samples have been sporadic, with data available in only 6 of 20 years (1988-1991, 1996, and 1999), and small sample sizes.

Beginning in 1997 sampling goals for chinook salmon harvested in the subsistence dipnet fishery changed from a "get what you can" scenario to specific sample sizes. The goal for chinook is to collect 150 scale samples a week for the first five weeks of the subsistence dipnet fishery. Weekly objectives are based on regeneration rates (25% for chinook salmon in 1999) resulting in 20% precision on estimated age compositions.

The subsistence fishwheel scale samples are collected from several privately owned fishwheels located near the lower boundary of the Upper Copper River subsistence fishery. With no specific sampling objectives, fishery technicians can sample only when their schedules allow and the fishwheel owner is present. This coupled with the "get what you can" scenario led me to combine scale samples from the fishwheel and dipnet fisheries to form a single subsistence data set.

The recreational fishery scale samples come from two creel surveys and an unpublished field project. Each creel survey emphasized the amount of fishing effort on the Gulkana and Klutina rivers more than age compositions. AWL (age, weight, length) sampling was done at one site on each river in a systematic manner. However, weekdays were chosen for AWL sampling; fishery technicians were unable to amass any kind of sample size because both fisheries are weekend-oriented. The field project was simply an AWL sampling project with no specific objective other than learning something about what age compositions one might see.

It was clear from the onset of this project that age composition information from the recreational and subsistence fisheries needed to be enhanced in order to successfully model these fisheries. In 1999, additional age samples were collected from recreational fishermen and subsistence fishwheels. I conducted a partial creel survey, collecting scales, sex, and length information, of the recreational fisheries on the Gulkana and Klutina rivers. The goal was to collect as many samples as possible given the distance between the two fisheries (Figure 1), the extensive use of these fisheries, and the fact that I was the only person gathering the information. I also periodically sampled the subsistence fishwheels near the lower boundary of the Upper Copper River District. Again, the sampling goal was to collect as many samples as possible when fishermen were present and I was not sampling the recreational fishery.

Scales are collected from the fourth scale row above the lateral line along the diagonal line between the rear insertion of the dorsal fin and the anterior insertion of the anal fin. Scales are then pressed onto acetate cards and annuli are counted using a microfiche reader. Typically, the aging system for salmon includes the number of freshwater and ocean years of residence. For example, age 1.2 symbolizes one year of freshwater residence followed by two years in the ocean. In this study, ages are reported chronologically from the year of spawning— e.g., a fish denoted as 1.2 has one year of freshwater residence, two years of ocean residence, and one year for the year of spawning for a total of four years. The most common ages found in the Copper River chinook salmon return are 4 (age 1.2), 5 (age 1.3), 6 (age 1.4), and 7 (1.5 and 2.4); however, in the model ages 3 (1.1) and 8 (1.6 and 2.5) are also included.

Estimates of the total catch at age in numbers were determined for chinook salmon in the commercial, subsistence, and recreational fisheries from 1980-1999. The catch at each age is simply the proportion sampled at each age times the total harvest. In years when no age compositions are available for the recreational or subsistence fisheries, the average proportion at each age across years was applied to the fishery-specific total catch to determine the catch at age. Then the previous data was assembled into catch-age matrices containing the catch at each age from 1980-1999 (Tables 1-3).

Run Reconstruction

Typically, run reconstruction methods utilize spatial and temporal abundance distributions of each stock constructed from information about catch and escapement to estimate stock specific catch contributions (Templin et al. 1996). These methods provide valuable information about the population's migratory behavior (Mundy 1982) or the relationship between the resource and the fishery (Schnute and Siebert 1983). In my analysis, run reconstruction was used to obtain initial brood-year estimates for the catch-age analysis. Therefore, a simplified run reconstruction was completed under the following assumptions:

1) the estimated age composition is measured without error;
2) the estimated harvest is measured without error;
3) a constant exploitation rate exists over all ages and years;
4) the sampled proportion at each age is the true population proportion at each age.

For each age a and year t, let

C_t = total catch

$N_{a,t}$ = abundance (return by age and year)

Run_t = total return (or the sum of $N_{a,t}$)

$R_{a,y}$ = return at each age indexed by brood-year y

Table 1. Estimated commercial catch-age composition, including sample size (*n*).

	Age							
Year	3	4	5*	6*	7*	8*	*n*	Total
1980	0	77	2,431	5,324	579	39	219	8,450
1981	0	1,848	8,775	8,621	1,539	0	135	20,783
1982	158	3,706	26,465	16,529	2,304	0	-	49,162
1983	22	1,930	31,916	16,057	97	0	3,165	50,022
1984	0	909	13,137	23,369	1,298	0	2,387	38,713
1985	56	2,859	12,316	26,215	877	0	2,830	42,323
1986	28	2,340	21,853	15,566	883	0	2,766	40,670
1987	24	521	6,177	16,983	1,597	0	2,576	25,302
1988	52	929	7,217	18,017	2,016	0	1,752	28,231
1989	45	852	7,645	19,734	2,585	0	1,545	30,861
1990	119	1,314	5,715	12,211	2,274	67	1,594	21,700
1991	167	1,354	20,002	12,462	770	24	1,596	34,779
1992	50	1,760	5,518	30,064	2,334	79	1,996	39,805
1993	152	1,974	18,913	7,966	721	0	2,043	29,726
1994	62	2,447	18,482	25,703	355	0	1,999	47,049
1995	184	3,869	35,362	25,586	674	0	2,118	65,675
1996	327	3,636	26,302	24,953	323	23	1,729	55,564
1997	129	4,794	29,537	16,503	311	0	1,805	51,274
1998	218	4,586	44,011	19,387	625	0	1,920	68,827
1999	0	6,004	32,617	23,179	537	0	1,696	62,337

* Chinook salmon gear selectivity equals one.

Table 2. Estimated recreational catch-age composition, including sample size (*n*).

	Age							
Year	3	4	5*	6*	7*	8*	*n*	Total
1980	0	178	1,614	301	7	0	-	2,101
1981	0	146	1,319	246	6	0	-	1,717
1982	0	153	1,385	258	6	0	-	1,802
1983	0	219	1,981	370	9	0	-	2,579
1984	0	236	2,141	399	10	0	-	2,787
1985	0	165	1,490	278	7	0	-	1,939
1986	0	311	2,814	525	13	0	-	3,663
1987	0	195	1,768	330	8	0	-	2,301
1988	0	93	988	454	27	0	117	1,562
1989	0	37	589	1,510	83	0	241	2,219
1990	0	506	1,384	312	30	0	150	2,232
1991	0	0	2,388	2,029	10	0	851	4,427
1992	0	339	3,071	573	14	0	-	3,997
1993	0	647	5,855	1,092	27	0	-	7,620
1994	0	546	4,941	922	22	0	-	6,431
1995	0	569	5,155	962	23	0	-	6,709
1996	0	604	5,465	1,020	25	0	12	7,113
1997	0	752	6,813	1,271	31	0	-	8,868
1998	0	758	6,866	1,281	31	0	-	8,937
1999	0	831	4,279	1,632	0	0	219	6,742

* Chinook salmon gear selectivity equals one.

Table 3. Estimated subsistence catch-age composition, including sample size (*n*).

	Age							
Year	3	4	5*	6*	7*	8*	*n*	Total
1980	98	395	2,056	476	10	0	-	3,035
1981	82	313	1,614	393	8	0	-	2,409
1982	94	359	1,853	449	9	0	-	2,764
1983	210	770	3,949	1,001	19	0	-	5,950
1984	79	294	1,511	378	7	0	-	2,269
1985	60	256	1,344	292	7	0	-	1,958
1986	106	396	2,033	508	10	0	-	3,053
1987	133	490	2,510	636	12	0	-	3,781
1988	135	518	2,675	646	13	0	-	3,986
1989	101	395	2,045	487	10	0	-	3,038
1990	122	434	2,211	577	11	0	-	3,355
1991	182	699	3,610	874	18	0	-	5,384
1992	114	541	1,922	2,272	6	0	90	4,854
1993	0	430	2,361	1,209	280	0	68	4,280
1994	0	1,580	1,903	2,186	63	0	62	5,732
1995	0	733	4,400	1,423	43	0	131	6,599
1996	138	276	3,027	1,625	0	0	58	5,066
1997	0	311	6,162	1,517	39	0	143	8,030
1998	0	1,161	5,420	1,980	0	0	114	8,561
1999	37	1,195	6,099	1,632	0	0	517	8,962

* Chinook salmon gear selectivity equals one.

μ_t = exploitation rate

$p_{a,t}$ = proportion of a brood returning at each age.

The total return is estimated by the total catch divided by the exploitation rate, or

$$Run_t = \frac{C_t}{\mu_t} \tag{1}$$

A constant exploitation rate of 0.55 was used, determined from a 1999 mark-recapture experiment and the 1999 commercial catch (Evenson and Wuttig 2000).

The number of fish at each age is simply the total return times the proportion of the brood-year returning at that age, or

$$N_{a,t} = Run_t p_{a,t} . \tag{2}$$

In the run reconstruction, the catch proportion was substituted for the unknown run proportion for lack of other information. The return at each age *a* indexed by brood-year *y*, is identical to the abundance at age a in year *a*+*y*, or

$$R_{a,y} = N_{a,a+y} . \tag{3}$$

For example, the number of 3-year-olds from the 1977 brood-year returned in 1980.

Finally, total brood-year returns are determined by summing the returns at each age, or

$$R_y = \sum_a R_{a,y} . \tag{4}$$

Catch-Age Analysis

The initial brood-year returns from run reconstruction were used just for starting values in the catch-age analysis. The goal was to estimate the total return each year from information about catch and escapement, because the sum of total catch and escapement equals the total return.

The extent to which catch-age models can describe the random properties found in fish populations is based on the validity associated with the model's assumptions and parameters (Megrey 1989). In my model, the separability of each gear exploitation fraction into age and year factors is an extremely important assumption. By letting gear selectivity be $s_{a,g}$ and exploitation fraction be $\mu_{t,g}$, the exploitation fraction for age, year, and gear $\mu_{a,t,g}$ is simply the product of $s_{a,g}$ and $\mu_{t,g}$, or,

$$\mu_{a,t,g} = s_{a,g}\mu_{t,g} \; . \tag{5}$$

If the catch is in direct proportion to abundance, then $s_{a,g} = 1$. In this case, the majority of the catch is between 5 and 8 years; therefore, these fish are assumed to be fully selected. The separability assumption is important in catch-age analysis because it simplifies the parameter estimation by reducing the number of unknown exploitation fractions and selectivity parameters from 120 (20 years and 6 ages) to 22 (20 μ's plus 2 selectivities at ages 3 and 4).

The other important assumption that reduces the number of parameters to be estimated is that the proportion of a brood returning over time, $p_{a,t}$, is assumed constant ($p_{a,t} = p_a$), reducing the number of parameters from 120 to 6 (for p). The age composition of the total return is not known, because age composition and total escapement are both unknown. Nevertheless, to determine how reasonable this constant proportion assumption is, I compiled catch proportions by brood. These observed catch proportions of a brood returning for salmon ages 3 through 8 are shown in Figure 2 for those broods with complete data.

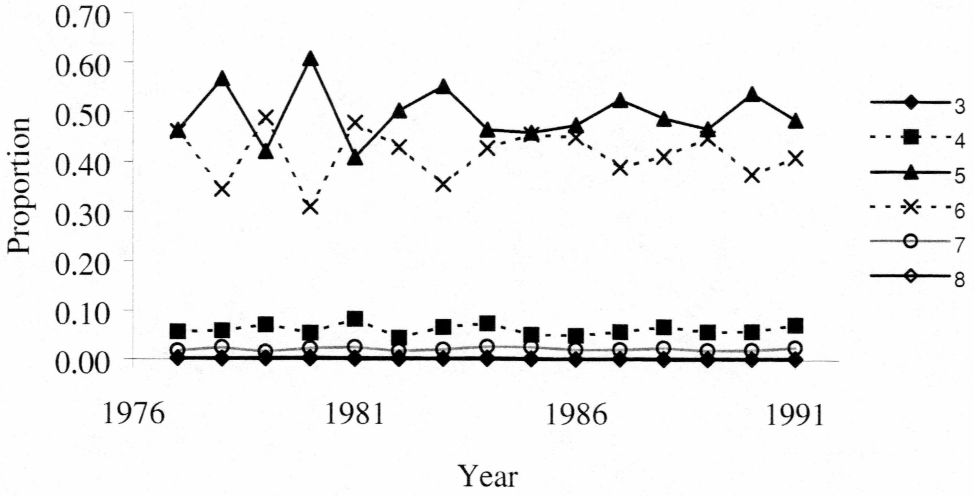


Figure 2. The observed proportion in the catch of a brood-year returning for salmon ages 3 through 8.

The proportions vary over time, especially for ages 5 and 6, and they reflect changes in both the return and exploitation intensity. All the same, the variation in catch proportions opens the possibility that the run proportions may also vary in time. Therefore, in attempts to relax this assumption an additional configuration of the model (approach IV below) let the proportion of a brood returning vary across years.

Additional assumptions necessary to specify the model included:

1) returning salmon face a commercial (*c*), subsistence (*s*), and recreational (*r*) fishery when migrating to their spawning grounds;
2) age composition estimates of the catch are from sampling and may differ from the true number;

3) an index of escapement obtained from aerial surveys is proportional to the true escapement;
4) returning salmon not caught migrate to their spawning grounds, spawn, and die; and,
5) no natural mortality occurs before or during spawning.

For each age *a*, year *t*, and gear *g*, let

$C_{a,t,g}$ = catch

$S_{a,t,g}$ = escapement

γ= proportion of the total escapement observed during aerial surveys.

The abundance of returning fish in a given year is just the total return from the appropriate brood-year times the proportion returning in that year for each age, or

(6) $$N_{a,t} = R_y p_{a,t}$$

where brood-year $y = t-a$. The catch in each fishery, which stems from extensions of the Baranov catch equation (Quinn and Deriso 1999, p. 333), is the abundance times the exploitation fraction, or from the separability assumption (5),

(7) $$C_{a,t,g} = N_{a,t}\mu_{a,t,g} = N_{a,t}s_{a,g}\mu_{t,g}\,.$$

The escapement (spawning abundance) is simply the number of fish left after fishing, or from assumptions 1, 4, and 5,

(8) $$S_{a,t,g} = N_{a,t} - \sum_g C_{a,t,g} = N_{a,t} - C_{a,t,c} - C_{a,t,r} - C_{a,t,s}$$

A schematic diagram shows the temporal structure of an Alaskan chinook salmon population for a single brood (Figure 3).

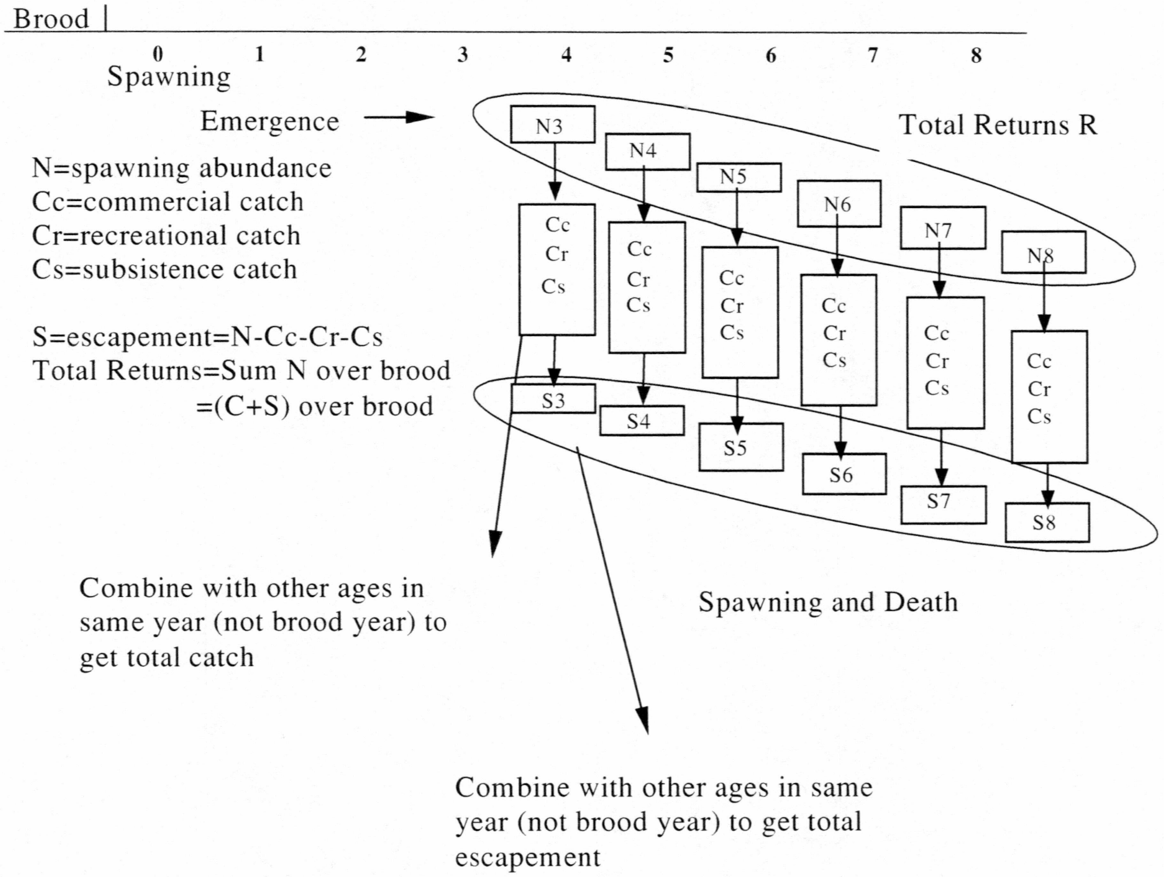


Figure 3. Schematic showing the temporal structure of an Alaskan chinook salmon population for a single brood. Events shown are spawning of eggs, emergence the following year, and the returns of maturing parts of the brood from ages 3-8. During the return fish encounter commercial, recreational, and subsistence fisheries. Those that escape will spawn and die.

The addition of auxiliary information into catch-age models occurs in a variety of forms. Quinn et al. (1998) advocated specifying as many auxiliary parameters as possible since a variety of parameter combinations can explain observed data equally well. Paloheimo (1980) and Dupont (1983) incorporated fishing effort into their catch-age models under the assumption that effort was proportional to full-recruitment fishing mortality. However, this assumption has major limitations; catchability is likely to vary from year to year, and effective fishing effort is rarely known precisely (Deriso et al. 1985). Fournier and Archibald (1982) relaxed this assumption by modeling differences between fishing mortality and effort in a lognormal framework. They also developed formulae incorporating spawner-recruit relationships and aging error into their objective function. Following Fournier and Archibald (1982) and Deriso et al. (1985), I assumed that recruitment is dependent upon the spawning abundance through a Ricker spawner-recruit relationship but subject to error, or

$$R_y = \alpha S_y e^{-\beta S_y + \varepsilon_y} \tag{9}$$

where α is the productivity parameter, β measures the level of density dependence, and returns from brood-year *y* come from spawners in year *y*. Throughout the analysis a Ricker spawner-recruit function was employed; however, the Beverton-Holt relationship $[R=\alpha S/(1+\beta S)]$ was also explored.

At this point, the maximum sustained catch (MSC) and its related exploitation rate were determined from the Ricker relationship. To do this for the Ricker model the quantity $\alpha(1-\beta S_m)\, e^{-\beta S_m}$ must be equal to one where S_m equals the optimal escapement.

This equation cannot be solved directly for S_m; therefore, the Microsoft Excel® application Solver was used to set $\alpha\,(1\text{-}\beta S_m)\, e^{-\beta S m} = 1$ by changing the value of S_m.

In addition to the spawner-recruit relationship, I included an escapement index as auxiliary information. From assumption 3, the annual escapement index I_t is the proportion of the escapement observed through aerial sampling times the total escapement, or

(10) $$I_t = \gamma \sum_a S_{a,t} = \gamma\, S_t$$

(where the absence of a subscript denotes summation over the subscript).

Objective Function and Error Structure

In order to address the variability associated with sample estimates of catch-age data and factors that influence fish population abundance, the inclusion of an error structure into the model's objective function is required. Earlier approaches utilized lognormal deviations with likelihood (Fournier and Archibald 1982) and least squares (Deriso et al. 1985) formulations to describe assumed differences between observed and model catch due to measurement error. More recent approaches have dealt with measurement and process error (errors in the population dynamics process) in a likelihood (Gudmundsson 1994; Schnute and Richards 1995) or Bayesian (McAllister et al. 1994; McAllister and Ianelli 1997) framework. Furthermore, if measurement error were due to aging error coupled with variation due to simple random sampling for catch, then a reasonable alternative to the lognormal distribution would be a multinomial distribution (Deriso and Quinn 1999).

In contrast to the previous studies, my analysis utilized a least squares framework and assumed an underlying root normal distribution (Quinn 1985; Quinn et al. 1998) to accommodate measurement errors in catch and escapement. Catch observations are denoted as $C'_{a,t,g}$ and the observed escapement index is I'_t. The total brood-year return R_y is not denoted this way because the brood-year return comes from the model. There is a difference between brood-year return estimates from the model and from the spawner-recruit relationship. For a particular spawning year *y*, the predicted total brood-year return would be the number of recruits accumulated over years *y*+3, *y*+4,…*y*+8. Because some of the run reconstruction brood-year returns are incomplete, the addition of a spawner-recruit relationship allowed me to estimate with some stability complete brood-year returns in years with incomplete observations.

A simple least squares objective function would be the combination of catch, escapement index, and spawner-recruit residual sums of squares (RSS), or

$$(11)\quad RSS = \sum_{a,t,g}\left(\sqrt{C'_{a,t,g}} - \sqrt{C_{a,t,g}}\right)^2 + \lambda_I \sum_t \left(\sqrt{I'_t} - \sqrt{I_t}\right)^2 + \lambda_F \sum_y \left(\sqrt{R_y} - \sqrt{F(S_y)}\right)^2$$

where *F* represents a spawner-recruit relationship and λ_I and λ_F are weighting terms which control the influence of the escapement index and spawner-recruit relationship respectively.

Square root transformations were used for several reasons. The square root transformation is appropriate for count data distributed according to a Poisson distribution in order to stabilize variance. While much fishery data is more clustered than a Poisson, it is a reasonable starting point for count data. Compared to logarithmic transformations, square root transformations are capable of handling zero values and their less aggressive nature doesn't overly dilute the influence that large catches may have on estimates of returns. Quinn et al. (1998) showed an underlying root normal distribution will provide more reliable convergence of the objective function.

Initial Model Parameters

Population parameters include total brood-year returns R_y, annual return proportions $p_{a,t}$, selectivities $s_{a,g}$, exploitation fractions $\mu_{t,g}$, the proportion of escapement observed through aerial sampling (γ), and the α and β terms in the Ricker spawner-recruit relationship. Initial brood-year returns and selectivities for ages that are not fully selected were provided by run-reconstruction. In addition, the exploitation rate used during the run reconstruction served as the preliminary exploitation fractions $\mu_{t,g}$. The proportion seen through aerial sampling was determined from personal communication with Tom Taube, an area manager for the ADF&G who conducts the aerial surveys. Finally, realistic values were chosen for the α and β terms in the Ricker spawner-recruit function.

Model Approaches

In this study, the catch-age information was analyzed with four different approaches. Approach I (commercial) allowed for measurement error in the commercial data but treated the catch from the recreational and subsistence fisheries as being measured without error. The model predicts the number at each age, subtracts the predicted commercial catch at age from the model, and then subtracts the observed recreational and subsistence catch at age.

Approach II (pooled) assumed that selectivities were constant among gear types and pooled the data, effectively treating the pooled data as being measured with error. The sum of the commercial and corrected recreational and subsistence catch at age completed the pooled catch-age matrix.

Approach III (stratified) is known as stratified catch-age analysis, in which the previous model was generalized to allow for measurement error in multiple gear types. If selectivities vary over gear types, the separability assumption in the previous model will be grossly violated. Deriso et al. (1989) showed the selectivity issue could be resolved by defining a separate selectivity for each gear type. Stratified catch-age analysis makes no common assumptions about gear selectivities among gear types and has a separate sum of squares (SSQ) term for each fishery; therefore, the filled-in age-compositions in Tables 2 and 3 were not used. The total SSQ for each fishery includes a SSQ term based on years with available catch-age information and when catch-age data was unavailable, a SSQ term based on the total catch. This way the model utilized all of the information available from a specific fishery. Each fishery and SSQ value has its own weighting term, λ, to control the influence of these fisheries on the objective function.

Approach IV (time-varying) is the same as approach II, except that annual proportions ($p_{a,t}$) were modeled as a dynamic process. Proportions for salmon ages 3, 4, 7, and 8 remained constant because there is relatively little variation in these age classes (Figure 2). In contrast, the model estimated annual age 5 proportions and set age 6 to 1 minus the sum of the remaining age classes, so that proportions for both ages varied over time.

Approaches I and II utilize 54 parameters to optimize the objective function, which is comprised of 140 observations. In contrast, approach III utilizes 98 parameters based on 224 observations. Approach IV has the same number of observations as approaches I and II but 72 parameters are used in the parameter string. The observed data includes the catch-age matrix (or matrices) and aerial index vector. Each catch-age matrix has six age groups over six, eight, and 20 years for a total of 36, 48, and 120 observations from the recreational, subsistence, and commercial fisheries, respectively. The aerial index has one count for each year for a total of 20.

Parameter Estimation

Estimates of model parameters were determined by minimizing the objective function (equation 11) using a Microsoft Excel® spreadsheet. The Excel® application Solver, which is based on a quasi-Newton optimization algorithm (Chong and Zak 1996), was set to minimize the RSS by changing the values found in specified cells. The specified cells contain a parameter string that includes all of the population parameters to be estimated. The following constraints were placed on Solver to ensure reasonable population parameter estimates: (1) annual proportions across ages must sum to one; (2) commercial exploitation rates are less than or equal to 70%; (3) total exploitation rates are less than or equal to 85%; (4) brood-year returns are greater than or equal to 10,000; and (5) all population parameters must be positive.

The total RSS was minimized by estimating all of the population parameters at the same time except for the proportion counted through aerial sampling or gamma (γ).

Interim convergence of the objective function is required to ensure that Solver is not so removed from the solution that it cannot obtain a global minimum. Therefore, the weighting of each auxiliary data source and the separate fisheries found in approach III was brought into the analysis one at a time. In other words, the initial parameter string for approaches I , II, and IV was estimated with an aerial weighting and again by incorporating a spawner-recruit weighting.

The procedure for approach III is similar to the others but with a weighting term for each fishery. In this case, the initial parameter string was estimated with a commercial catch and aerial weighting. Then the spawner-recruit relationship was brought in and finally the recreational and subsistence fisheries. After Solver had obtained interim convergence, all parameters, including gamma, were run at once to obtain the final population parameter estimates.

Diagnostics

Quinn and Deriso (1999, p. 339) suggest a variety of diagnostic checks to assure reasonable estimates. As with any model, the results should be insensitive to initial parameter values, and residuals from catch and auxiliary data should display no pattern in age, time, or as a function of predicted catch. They also recommend running the model with different values for the weighting terms, λ, to provide insight into the robustness of parameter estimates. In this study, all of the above mentioned diagnostic tools are utilized as well as retrospective analysis (see below).

Data Weighting and Sensitivity Analysis

In fisheries management the decision-making process is influenced by the personal perceptions of the fisheries manager. Information of unknown precision and accuracy is utilized to develop models that describe some population process; because these uncertainties cannot be removed, managers have perceptions of the various data resources and the plausibility of estimates, which often leads to intuitive judgments in their decision-making (Merritt and Quinn 2000). Weighting according to perceptions is not commonly found in abundance estimation; however, the uncertainty surrounding the auxiliary information warrants incorporating perceptions of accuracy from knowledgeable individuals.

The commercial (or pooled) catch weighting term (λ_{Comm}) is set to one without loss of generality. The weighting terms for the aerial escapement index (λ_I), the spawner-recruit relationship (λ_F), and the separate fisheries (λ_{Rec} and λ_{Sub}) are related to the ratio of commercial catch variance to variance of each other data source. Weather conditions from year to year influenced the quality of the aerial escapement index and required weighting the data source by survey quality and utilizing only one of the nine index streams.

Past and present ADF&G Copper River Area managers believe the Gulkana River is the least susceptible to factors negatively influencing the aerial count; therefore, the index stream chosen was the Gulkana River. Every year each aerial survey was given a number grade based on weather, water, and flight conditions. The survey is graded 1-5, with 1 being the best quality and 5 being the worst. The average quality of all the surveys from a particular year was transformed into an annual survey weight by exponentiating the average survey quality, dividing one by this value, and then multiplying by 100 — e.g., an average aerial survey quality of 2.5 would convert to an annual survey weight of 8.2, or the annual survey weight = $(1/e^{2.5})*100$. The sum of the product of the aerial index residuals squared and the survey weights equals the escapement index RSS.

In contrast, there is little known about the spawner-recruit relationship. Possibly no relationship exists, in which case the weight would be zero.

The criteria used to choose the most appropriate weighting scenario included: (1) the model's ability to track the trends in catch; (2) the model's ability to track the trends in the aerial escapement index without taking away from the catch fit; (3) no pattern in average root residuals across ages and time; (4) robust parameter estimates across approaches; (5) a reasonable visual fit to the particular spawner-recruit (S-R) relationship chosen; and (6) plausible brood-year returns (Merritt and Quinn 2000). My investigation looked at various weighting scenarios for the auxiliary data sources and also the separate fisheries found in approach III.

Retrospective Analysis

The precision of abundance estimates produced by bootstrapping catch-age analyses may not be realistic, because bootstrap estimates are themselves based on the assumption that model residuals are independent and identically distributed (Parma 1993). Consequently, parameter estimates can deviate greatly from true values due to persistent autocorrelation. Therefore, comparing retrospective estimates to corresponding reference estimates will assess the errors in brood-year return estimates. Sinclair et al. (1991) defined reference estimates as those estimates determined from the longest time series of data; retrospective estimates are those estimates obtained by running the model retrospectively to different segments of the time series database. In other words, one eliminates one year of data as if it never existed and re-runs the catch-age model based on this reduced data set. In my analysis, the catch-age model was applied to data collected through 1994, 1995, 1996, 1997, and 1998. Furthermore, retrospective data sets are referred to as reduced models and the reference data set is the full model.

Final Estimation

Once the diagnostic tests and forecasting were complete, standard errors were determined. The standard errors of estimated model parameters, predicted catch, brood-year return, total return, escapement, and forecast estimates were calculated using the bootstrap technique, described by Efron and Tibshirani (1993) and applied to catch-age data by Deriso et al. (1985). This procedure involved resampling residuals with replacement and then adding these residuals to the predicted values in order to create bootstrap data sets. Then the least squares objective function was minimized with each set of bootstrap data. The difference between the mean of 1000 bootstrap estimates, θ^*, and the original estimate, $\hat{\theta}$, is an estimate of bias. The standard deviation of the bootstrap estimates is an estimate of the standard error of the original estimate. Finally, 95 % confidence intervals were determined from the bootstrap estimates using the percentile method (Efron and Tibshirani 1993).

Choosing the Best Model

The criteria used to choose the best of the four approaches included: (1) a good fit to catch and escapement data; (2) no pattern in average root residuals across ages and time; (3) parameter estimates with low estimated bias and variability; (4) a reasonable fit to the spawner-recruit relationship chosen; (5) robust and plausible parameter estimates; and (6) significant differences between the mean squared errors (MSE's) among approaches. Parameter uncertainty is expressed in the form of the coefficients of variation (CV's) and the root mean square error (RMSE), which is a measure of the model's bias and variability,

$$RMSE = \sqrt{SE^2 + Bias^2}\ . \tag{13}$$

Criddle and Havenner (1991) suggested an asymptotic test they attributed to Lehmann (1959) for the equality of MSE's. The MSE's of alternative models are judged to be different if the correlation between the sums and differences of the errors is significantly different from zero. The correlation of errors is determined with the following formula,

$$r = \frac{\sum_{t=1}^{T}(e_{it} + e_{jt})(e_{it} - e_{jt})}{\sqrt{\sum_{t=1}^{T}(e_{it} + e_{jt})^2 \sum_{t=1}^{T}(e_{it} - e_{jt})^2}}\ , \tag{14}$$

where i and j index the alternative models and T equals the total number of observations involved in the MSE. The correlation coefficient can then be converted into a t-statistic by

$$t = \frac{r\sqrt{T-2}}{\sqrt{(1-r^2)}} \tag{15}$$

with T-2 degrees of freedom. The pairwise comparison are formulated as two-tailed t-tests at a 95% confidence level:

H_o: $r = 0$ the MSE for model j is not significantly different than the MSE for model i

H_a: $r \neq 0$ the MSE for model j is significantly different than the MSE for model i

Critical values for r are determined by $t/\sqrt{(T-2)+t^2}$, where t is the critical value of a t-distribution with T-2 degrees of freedom at a significance level α. If the t-statistic is greater than t-critical, reject H_o. If the t-statistic is less than t-critical, do not reject H_o.

Forecasting Future Returns

In this analysis, data from the 1998 retrospective analysis (reduced model) was used to forecast the total return for 1999 and 2000; then the reference data set (full model) was used to forecast the total return for 2000. This allowed me to compare the 1999 and 2000 return forecasts from the reduced model to the 1999 estimate and 2000 forecast from the full model.

The total returns were projected by applying the model's proportion of a brood returning at each age to corresponding brood-year returns in order to estimate the number at each age. This corresponds to how returns were estimated within the catch-age model (equation 6). Yet salmon aged 3 in 1999 and 3 and 4 in 2000 are from brood-years 1996 and 1997, but the reduced and full model's final brood-year estimate is for 1995 and 1996, respectively. Therefore, brood-years 1996 and 1997 were forecasted by applying the model's Ricker spawner-recruit relationship to the spawning abundance in 1996 and 1997. Then I summed the number at each age for a forecast of the total return in a given year.

RESULTS

Run Reconstruction

The final brood table from run reconstruction contains the brood-year return estimates for 1972-1996 (Table 4). Some brood-years (1972-1976) are incomplete because no age composition information prior to 1980 exists, and other years (1992-1996) are incomplete because all the fish from these brood-years have yet to return. The catch-age model below estimates brood-year returns under completely different assumptions than the ones found in run reconstruction. For this reason, incomplete broods cannot be compared between the two approaches.

Data Weighting and Sensitivity Analysis

A thorough investigation of the weighting scenarios revealed the following combinations influenced the constant proportion models, which includes approaches I (commercial), II (pooled), and III (stratified), in a variety of ways. When there is no λ_I (spawner index) or λ_F (S-R relationship) influence, trends in the catch are well explained; however, the brood-year returns in recent years are unreasonably high — greater than 250,000. In contrast, when the λ_I influence is less than one or the λ_F influence is less than 0.1, the model's ability to track the trends in the aerial index is diminished, but brood-year returns are plausible. When the λ_I influence is greater than one or the λ_F influence is greater than 0.5, the model is unable to describe the trends in catch and an obvious pattern is seen in the residuals.

Table 4. Brood-year return estimates from run reconstruction.

	Age						
Year	3	4	5	6	7	8	Total
1972						44	44
1973					677	0	677
1974				6,921	2,294	0	9,215
1975			6,922	13,676	3,728	0	24,326
1976		738	17,291	27,702	205	0	45,936
1977	112	3,406	47,738	28,490	2,134	0	81,880
1978	121	6,779	61,871	39,183	1,483	0	109,437
1979	404	4,772	27,245	44,601	1,417	0	78,440
1980	380	2,336	25,227	25,974	3,852	0	57,769
1981	128	5,461	41,781	42,751	3,411	0	93,532
1982	193	4,767	24,903	31,719	4,172	97	65,851
1983	210	2,872	18,052	33,855	3,356	34	58,380
1984	375	2,555	16,015	18,997	1,135	118	39,195
1985	310	2,000	13,500	21,855	3,511	0	41,176
1986	228	3,268	36,982	49,091	1,338	0	90,907
1987	349	2,920	15,680	13,369	639	0	32,957
1988	497	3,938	35,322	41,748	1,123	34	82,662
1989	244	3,972	36,699	42,404	484	0	83,803
1990	198	6,626	68,093	39,805	522	0	115,244
1991	90	7,840	54,577	26,453	954	0	89,914
1992	279	5,858	58,296	32,922	808		98,163
1993	696	8,032	81,837	39,075			129,641
1994	177	9,456	62,229				71,862
1995	317	11,567					11,884
1996	47						47

The model was also run under the same weighting scenarios as above but with a Beverton-Holt spawner-recruit relationship instead of the Ricker. Inspection of the model's output versus the Beverton-Holt curve revealed a much poorer fit than the Ricker relationship; therefore, the Ricker spawner-recruit function was chosen as the better relationship to describe the Copper River chinook salmon population.

In the end, weights of 1.0 and 0.1 were used in approaches I (commercial), II (pooled) and III (stratified) for λ_I and λ_F, respectively. These weights were chosen based on the ability to track trends without apparent patterns in the residuals.

When two models utilize the same information, as in approaches II and IV, it is appropriate to weight each information source equally for comparison purposes. Therefore, various considerations of λ were modeled and the results were compared to the observed harvest and examined for patterns in the residuals. The sensitivity analysis for approach IV revealed that the weights used in approaches I, II, and III display slight patterns in the catch residuals and tended to over-fit the aerial index. To induce more variability into the aerial index estimates, I decreased the λ_I to 0.3, which eliminated the trends in catch residuals and relaxed the model's fit to the aerial index data set. I also increased λ_F to 0.2, which further removed a trend in the catch residuals. However, the CV's surrounding the escapement estimates were unreasonably high — greater than 40%, and a λ_I of 0.3 and a λ_F of 0.2 in approach II diminished the model's ability to describe the catch data without strong residual patterns and unreasonable brood year returns. Therefore, weights of 1.0 and 0.1 were provisionally used in approach IV (time-varying) for λ_I and λ_F, respectively, pending a final sensitivity analysis after model comparisons were made.

In approach III, the weights associated with the recreational and subsistence fisheries needed to be determined. With the commercial fishery weight set to one, the recreational and subsistence fisheries' influence was set to 0.1 and increased in increments of 0.2 until the trends from all three fisheries were explained. The resulting weights $\lambda_{CatchAgeRec}$ and $\lambda_{CatchAgeSub}$ when catch age information was available were both 0.9. In years with no catch age data, the resulting weights $\lambda_{RecCatch}$ and $\lambda_{SubCatch}$ were both 0.7. The influence is less for years without catch age data because the SSQ term is based on only the total catch instead of a sampled age composition.

Throughout the sensitivity analysis, the model was unable to estimate a reasonable value for brood-year 1996. In most cases the value would equal the constraint of 10,000 placed on the model's brood-year returns. This was an undesirable situation; in order to forecast returns, a reliable estimate of the most recent brood-year return is required. The model struggled with this, because initial brood-year values were based on incomplete brood returns from the run-reconstruction. In other words, values from the earliest and latest years of the run-reconstruction brood-year string were extremely small; therefore, the model was unable to estimate a complete brood-year return from incomplete brood-years. To solve this problem, information from a 1996 weir count on the Gulkana River and a 2000 telemetry study on a majority of the Copper River drainage was incorporated into the model.

The Gulkana River weir was built to provide a count of the spawning abundance upstream from Sourdough Creek, which is approximately 51 km from the confluence of the Gulkana and Copper Rivers (Figure 1). A total of 11,684 adult chinook salmon passed through the weir; however, after adjusting for the catch upstream and downstream of the weir, the in-river return equaled 13,840 (LaFlamme 1997). The proportion of Gulkana River chinook salmon that comprise the entire return is approximately 25% (Wuttig and Evenson 2000). Combining these two sources of data generates an escapement estimate of 55,360; however, this estimate doesn't account for the recreational catch. So, attempting to be conservative, I subtracted 15,000 for the recreational catch and assumed one recruit would accrue per spawner, thereby producing a 1996 brood-year return of approximately 40,000. In this way, the model was constrained to provide a 1996 brood-year estimate greater than or equal to this derived quantity. By using this constraint, the model was able to converge to a value above 40,000.

A comparison of estimates between the catch-age analysis and run reconstruction is found in Figure 4. Figure 4 illustrates why run reconstruction is only useful for starting values because there isn't enough information to provide complete brood-year estimates for the earliest and latest years. The major assumption and drawback of run reconstruction is a constant exploitation fraction. Catch-age models that estimate annual exploitation fractions will consistently have a lower RSS about the catch-age data. The deviations between run reconstruction and catch-age analysis results are due to changes

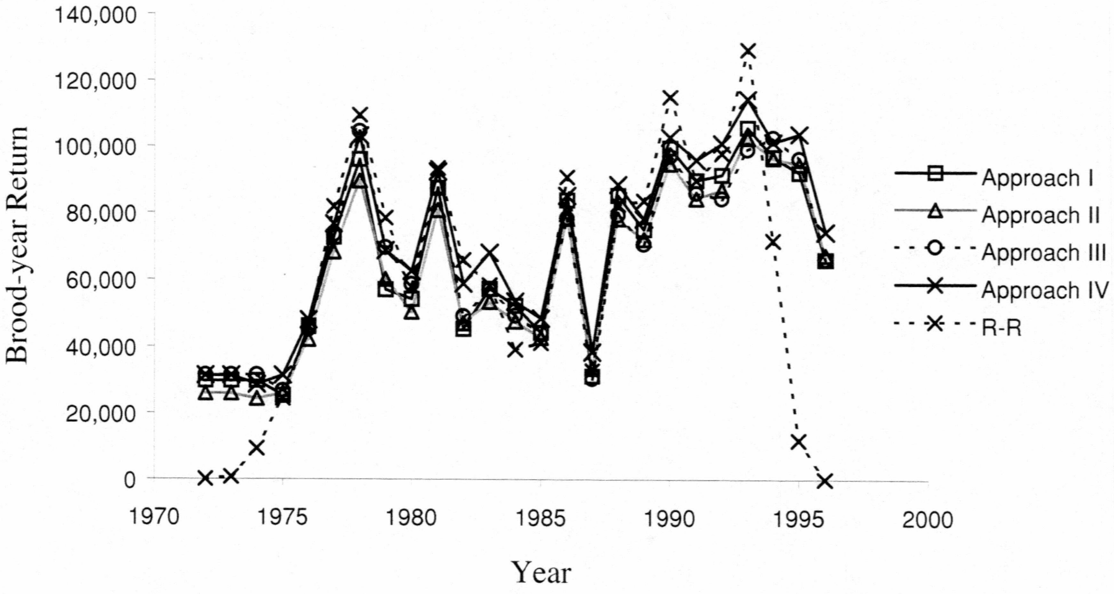


Figure 4. A comparison of brood-year estimates across all approaches including run reconstruction.

in estimated exploitation fractions over time. The catch-age model is more realistic in this regard, and the exploitation fraction estimates are plausible.

Retrospective Analysis

Brood-year returns in 1972 and 1973 were set to the median of the returns in the following three brood-years, thereby decreasing the total number of parameters to be estimated by two. The retrospective analysis exposed an incongruity between the 1972 and 1973 brood-year returns and the proportion of 7 and 8 year olds returning ($p_{a,t}$). This is because salmon aged 7 and 8 are poorly represented in the data set; the only occurrences of brood-years 1972 and 1973 are at age 8 in 1980 and ages 7 and 8 in 1981, respectively. The significant autocorrelation in the brood-year return estimates from approaches II, III, and IV justified using the median approach (First-order autocorrelations equaled 0.51 with p=0.01, 0.43 with p=0.04, and 0.49 with p=0.02 for approaches II, III, and IV, respectively.)

Figure 5 contains the results of the retrospective analysis after the median adjustment. For all approaches, the estimates from early years converge to stable values. For later years, estimates tend to vary from one year to the next but do not display any persistent patterns that would invalidate the model.

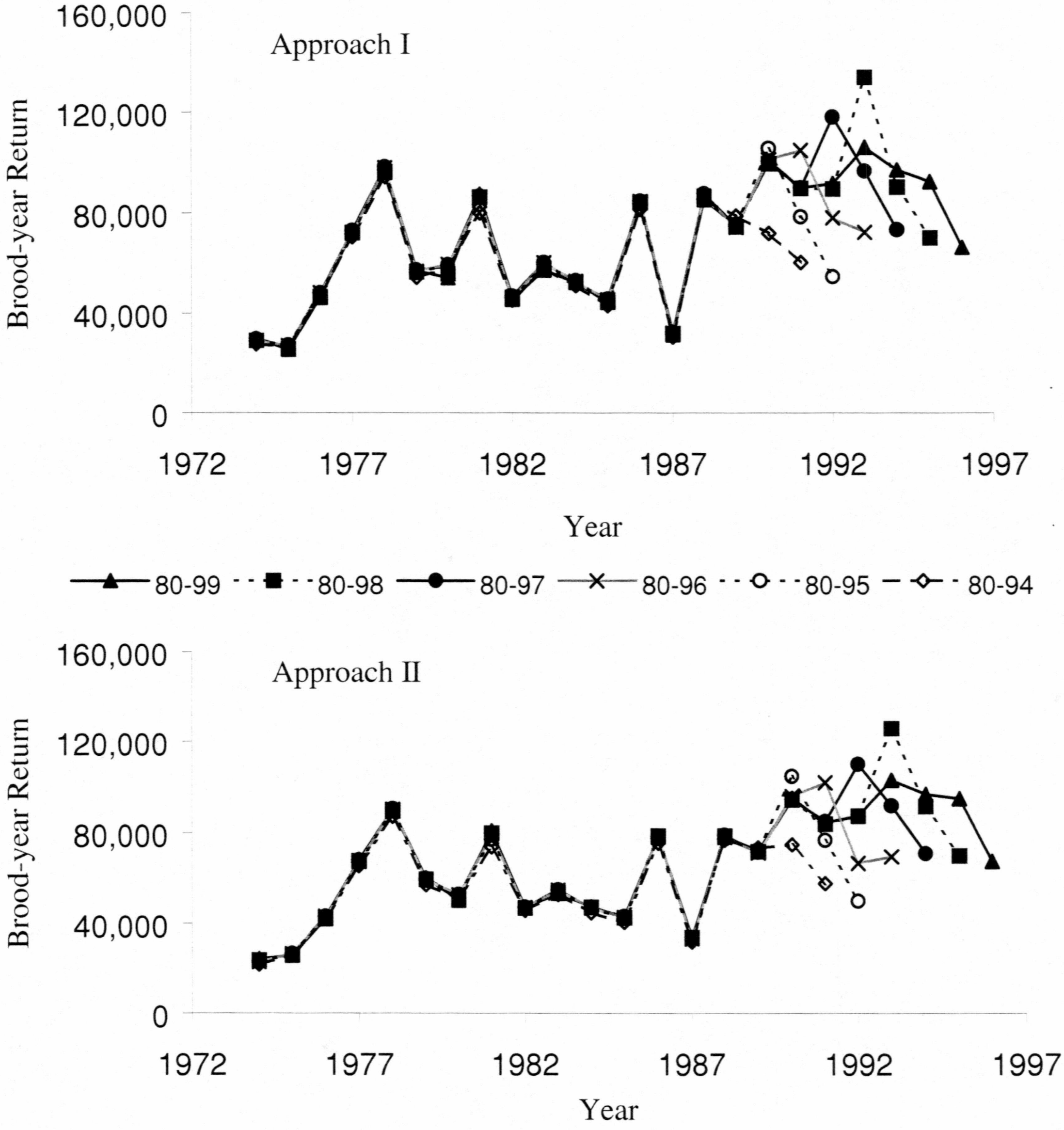


Figure 5. Brood-year returns from the retrospective analysis, (a) approach I, (b) approach II, (c) approach III, (d) approach IV.

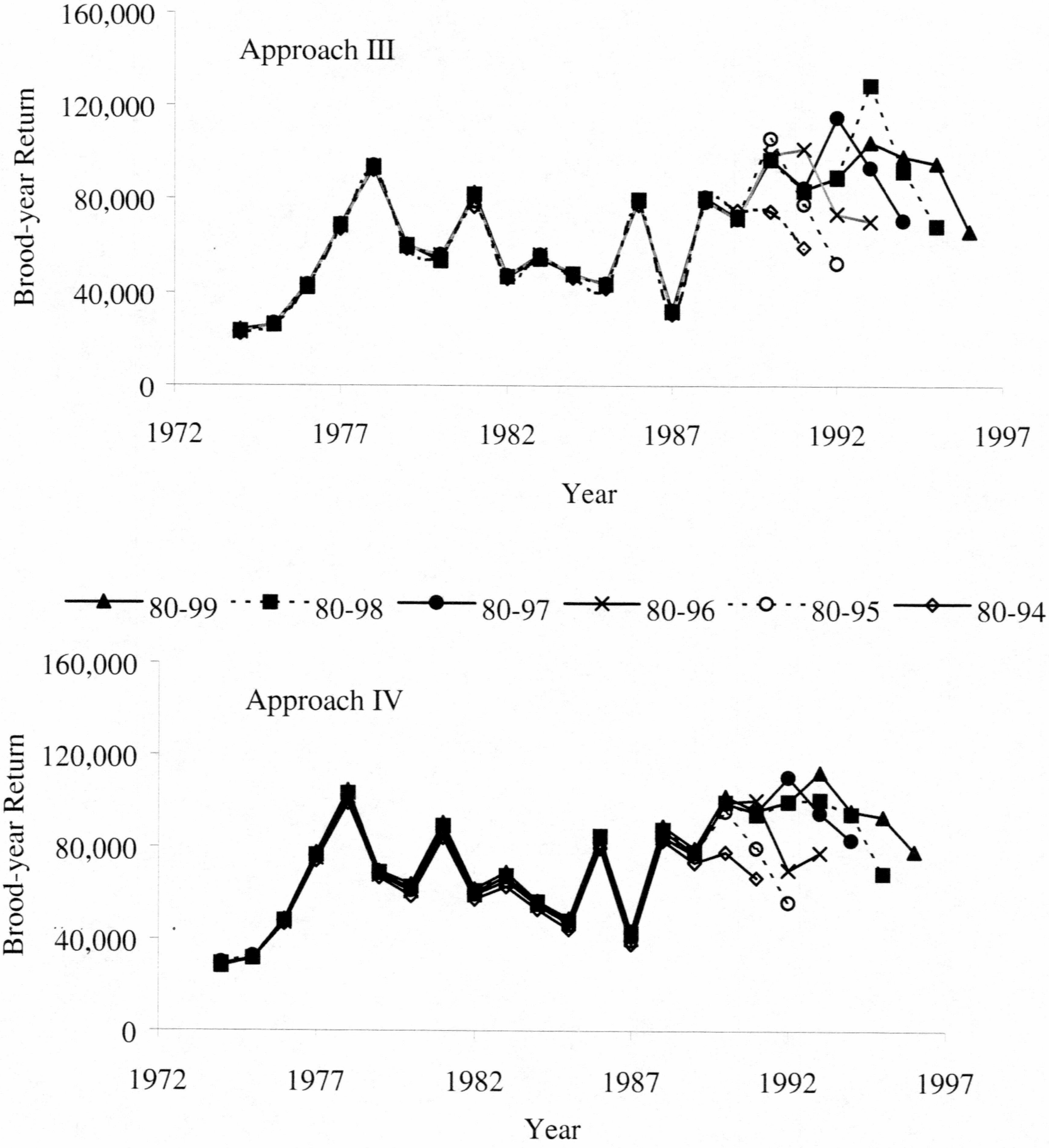


Figure 5, continued.

Final Estimation

To compare the model's output across approaches, a series of figures and tables display all population estimates of interest including: (1) brood-year returns (1972-1996); (2) aerial index (1980-1999); (3) catch (1980-1999); (4) escapement (1980-1999); and (5) total returns (1980-1999). The final population parameter string from approaches I and II contains 56 parameters, whereas approaches III and IV contain 100 and 74, respectively. The residual sum of squares (RSS), estimates, and their standard errors are found in Tables 5-8 for approaches I-IV, respectively.

Parameter estimates across approaches are mostly similar with some minor differences between exploitation rates, γ (the proportion seen in aerial sampling), and the spawner-recruit parameter α. In contrast, approach III's gear selectivities are substantially different from approaches I, II and IV. The commercial (or total) gear selectivity is 1.0 and 0.88 for ages 3 and 4, respectively. In the other approaches, the selectivities are 1.0, suggesting no difference in vulnerability for any age. I believe approach III's selectivity estimate for age 4 salmon is unrealistic, but notice the substantial standard error around the estimate (Table 7).

In approach III, the subsistence selectivities are 0.87 for age 3 and 1.0 for age 4 and the recreational selectivities are 0.08 and 1.0 for ages 3 and 4, respectively. This makes sense because subsistence dipnets have small mesh sizes capable of catching any age fish and fishwheels utilize a large, rotating basket that selects every fish that swims into it. In contrast, the recreational fishery is strictly hook and line and the gear restrictions typically constrain the catch to larger individuals, which tend to be the older

Table 5. The residual sum of squares, population parameter estimates and standard errors from approach I.

Parameter	Description	Estimate	SE	Parameter	Description	Estimate	SE
1	p_3,80	0.002	0.005	29	R_1972	29,723	9,211
2	p_4,80	0.053	0.024	30	R_1973	29,723	9,211
3	p_5,80	0.461	0.022	31	R_1974	29,723	14,477
4	p_6,80	0.460	0.022	32	R_1975	25,252	8,721
5	p_7,80	0.024	0.006	33	R_1976	46,093	11,080
6	p_8,80	0.001	0.000	34	R_1977	72,598	12,659
7	u_80	0.332	0.093	35	R_1978	96,046	16,624
8	u_81	0.549	0.089	36	R_1979	57,025	11,811
9	u_82	0.606	0.080	37	R_1980	54,210	11,578
10	u_83	0.700	0.050	38	R_1981	87,500	16,414
11	u_84	0.501	0.072	39	R_1982	45,399	10,874
12	u_85	0.700	0.064	40	R_1983	57,291	12,477
13	u_86	0.397	0.069	41	R_1984	52,308	12,563
14	u_87	0.566	0.083	42	R_1985	44,258	10,772
15	u_88	0.576	0.084	43	R_1986	83,931	12,975
16	u_89	0.436	0.080	44	R_1987	31,293	8,259
17	u_90	0.457	0.084	45	R_1988	85,364	12,492
18	u_91	0.545	0.077	46	R_1989	75,067	11,675
19	u_92	0.654	0.069	47	R_1990	99,887	13,430
20	u_93	0.503	0.072	48	R_1991	90,018	14,636
21	u_94	0.559	0.066	49	R_1992	91,625	13,604
22	u_95	0.700	0.046	50	R_1993	106,056	13,100
23	u_96	0.547	0.064	51	R_1994	97,157	15,396
24	u_97	0.501	0.062	52	R_1995	92,382	19,605
25	u_98	0.632	0.054	53	R_1996	66,177	14,668
26	u_99	0.672	0.047	54	α	10.762	1.422
27	s_3	1.000	0.074	55	β	5.19E-05	1.51E-05
28	s_4	1.000	0.171	56	γ	0.068	0.013

RSS(CommCatch)	22,550
RSS(Aerial)	5,619
RSS(S-R)	3,245
Total RSS	31,414

Table 6. The residual sum of squares, population parameter estimates and standard errors from approach II.

Parameter	Description	Estimate	SE	Parameter	Description	Estimate	SE
1	p_3,80	0.003	7.89E-05	29	R_1972	28,425	5,526
2	p_4,80	0.061	0.008	30	R_1973	28,425	5,526
3	p_5,80	0.497	0.016	31	R_1974	24,298	7,862
4	p_6,80	0.417	0.015	32	R_1975	25,884	5,662
5	p_7,80	0.021	0.005	33	R_1976	42,109	6,831
6	p_8,80	0.001	0.000	34	R_1977	68,141	8,391
7	u_80	0.607	0.078	35	R_1978	89,567	10,169
8	u_81	0.702	0.055	36	R_1979	60,122	7,966
9	u_82	0.710	0.050	37	R_1980	50,347	6,852
10	u_83	0.843	0.018	38	R_1981	80,797	8,130
11	u_84	0.613	0.046	39	R_1982	46,984	6,518
12	u_85	0.850	0.015	40	R_1983	53,442	6,934
13	u_86	0.517	0.052	41	R_1984	47,530	6,737
14	u_87	0.721	0.045	42	R_1985	42,759	6,547
15	u_88	0.735	0.044	43	R_1986	78,379	8,847
16	u_89	0.565	0.057	44	R_1987	33,640	5,928
17	u_90	0.621	0.054	45	R_1988	78,316	7,958
18	u_91	0.734	0.045	46	R_1989	72,124	8,103
19	u_92	0.831	0.031	47	R_1990	94,949	8,898
20	u_93	0.737	0.042	48	R_1991	84,455	8,764
21	u_94	0.742	0.037	49	R_1992	87,131	8,681
22	u_95	0.850	0.018	50	R_1993	102,870	9,567
23	u_96	0.708	0.038	51	R_1994	96,800	11,346
24	u_97	0.714	0.038	52	R_1995	94,859	14,112
25	u_98	0.833	0.021	53	R_1996	67,399	6,031
26	u_99	0.850	0.014	54	α	11.325	1.184
27	s_3	1.000	0.006	55	β	5.58E-05	9.98E-06
28	s_4	1.000	0.014	56	γ	0.082	0.012

RSS(TotalCatch)	20,593
RSS(Aerial)	3,059
RSS(S-R)	2,740
Total RSS	26,392

Table 7. The residual sum of squares, population parameter estimates and standard errors from approach III.

Parameter	Description	Estimate	SE	Parameter	Description	Estimate	SE
1	p_3,80	0.002	7.38E-05	34	μ_r,3,87	0.060	0.015
2	p_4,80	0.062	0.017	35	μ_r,3,88	0.035	0.015
3	p_5,80	0.466	0.018	36	μ_r,3,89	0.033	0.014
4	p_6,80	0.446	0.018	37	μ_r,3,90	0.045	0.017
5	p_7,80	0.022	0.005	38	μ_r,3,91	0.068	0.019
6	p_8,80	0.001	0.000	39	μ_r,3,92	0.070	0.016
7	μ_c,3,80	0.335	0.082	40	μ_r,3,93	0.134	0.024
8	μ_c,3,81	0.572	0.074	41	μ_r,3,94	0.078	0.009
9	μ_c,3,82	0.645	0.060	42	μ_r,3,95	0.082	0.008
10	μ_c,3,83	0.700	0.030	43	μ_r,3,96	0.063	0.015
11	μ_c,3,84	0.524	0.061	44	μ_r,3,97	0.091	0.008
12	μ_c,3,85	0.700	0.029	45	μ_r,3,98	0.085	0.018
13	μ_c,3,86	0.436	0.060	46	μ_r,3,99	0.070	0.016
14	μ_c,3,87	0.545	0.053	47	μ_s,3,80	0.141	0.035
15	μ_c,3,88	0.586	0.058	48	μ_s,3,81	0.069	0.021
16	μ_c,3,89	0.467	0.067	49	μ_s,3,82	0.033	0.012
17	μ_c,3,90	0.474	0.062	50	μ_s,3,83	0.091	0.019
18	μ_c,3,91	0.565	0.059	51	μ_s,3,84	0.031	0.010
19	μ_c,3,92	0.674	0.053	52	μ_s,3,85	0.072	0.020
20	μ_c,3,93	0.519	0.061	53	μ_s,3,86	0.029	0.010
21	μ_c,3,94	0.586	0.054	54	μ_s,3,87	0.099	0.023
22	μ_c,3,95	0.700	0.037	55	μ_s,3,88	0.095	0.023
23	μ_c,3,96	0.578	0.055	56	μ_s,3,89	0.045	0.015
24	μ_c,3,97	0.532	0.055	57	μ_s,3,90	0.080	0.021
25	μ_c,3,98	0.662	0.043	58	μ_s,3,91	0.087	0.019
26	μ_c,3,99	0.688	0.034	59	μ_s,3,92	0.080	0.023
27	μ_r,3,80	0.097	0.027	60	μ_s,3,93	0.073	0.022
28	μ_r,3,81	0.049	0.016	61	μ_s,3,94	0.066	0.019
29	μ_r,3,82	0.021	0.008	62	μ_s,3,95	0.077	0.019
30	μ_r,3,83	0.039	0.010	63	μ_s,3,96	0.049	0.014
31	μ_r,3,84	0.038	0.010	64	μ_s,3,97	0.076	0.018
32	μ_r,3,85	0.071	0.019	65	μ_s,3,98	0.077	0.019
33	μ_r,3,86	0.035	0.010	66	μ_s,3,99	0.090	0.018

-continued-

Table 7 continued.

Parameter	Description	Estimate	SE
67	s_c,3	1.000	0.033
68	s_c,4	0.883	0.173
69	s_r,3	0.079	0.006
70	s_r,4	1.000	0.236
71	s_s,3	0.873	0.050
72	s_s,4	1.000	0.199
73	R_1972	30,253	10,180
74	R_1973	30,253	10,180
75	R_1974	30,253	10,180
76	R_1975	24,891	7,475
77	R_1976	43,347	8,559
78	R_1977	70,706	9,778
79	R_1978	94,029	13,195
80	R_1979	61,712	10,170
81	R_1980	55,475	9,267
82	R_1981	84,461	11,924
83	R_1982	46,269	7,744
84	R_1983	55,690	9,406
85	R_1984	48,142	8,802
86	R_1985	43,614	8,545
87	R_1986	81,124	10,040
88	R_1987	31,317	6,826
89	R_1988	81,845	10,103
90	R_1989	71,907	9,429
91	R_1990	95,813	10,813
92	R_1991	86,927	10,965
93	R_1992	88,390	10,636
94	R_1993	100,625	10,511
95	R_1994	101,924	12,294
96	R_1995	96,082	15,740
97	R_1996	67,041	7,343
98	α	11.07	0.179
99	β	5.37E-05	8.76E-06
100	γ	0.074	0.011

RSS(CommCatch)	21,057.82
RSS(CatchAgeRec)	2,026.45
RSS(CatchAgeSub)	3,409.98
RSS(RecCatch)	692.81
RSS(SubCatch)	875.50
RSS(Aerial)	3,460.08
RSS(S-R)	3,030.92
Total RSS	34,553.55

Table 8. The residual sum of squares, population parameter estimates and standard errors from approach IV.

Parameter	Description	Estimate	SE	Parameter	Description	Estimate	SE
1	p_3,80	0.003	6.77E-03	34	R_1979	68,694	9,106
2	p_4,80	0.060	0.026	35	R_1980	62,509	9,954
3	p_7,80	0.021	4.97E-04	36	R_1981	92,458	13,366
4	p_8,80	0.001	1.18E-10	37	R_1982	58,809	9,175
5	u_80	0.503	0.105	38	R_1983	68,079	11,287
6	u_81	0.617	0.099	39	R_1984	53,578	10,264
7	u_82	0.630	0.083	40	R_1985	48,508	7,645
8	u_83	0.778	0.060	41	R_1986	85,300	9,285
9	u_84	0.509	0.090	42	R_1987	38,558	6,898
10	u_85	0.850	0.057	43	R_1988	88,660	10,813
11	u_86	0.453	0.092	44	R_1989	78,246	8,833
12	u_87	0.584	0.089	45	R_1990	103,027	10,639
13	u_88	0.647	0.083	46	R_1991	96,166	12,237
14	u_89	0.489	0.095	47	R_1992	101,150	11,168
15	u_90	0.516	0.097	48	R_1993	114,667	10,428
16	u_91	0.655	0.077	49	R_1994	101,610	13,011
17	u_92	0.764	0.070	50	R_1995	104,096	13,315
18	u_93	0.649	0.086	51	R_1996	74,400	9,493
19	u_94	0.660	0.079	52	α	9.580	0.258
20	u_95	0.831	0.050	53	β	3.89E-05	2.13E-05
21	u_96	0.615	0.081	54	γ	0.054	3.14E-02
22	u_97	0.629	0.079	55	p_5,1975	0.393	0.057
23	u_98	0.771	0.057	56	p_5,1976	0.369	0.047
24	u_99	0.800	0.054	57	p_5,1977	0.625	0.038
25	s_3	1.000	0.141	58	p_5,1978	0.464	0.039
26	s_4	1.000	0.205	59	p_5,1979	0.482	0.048
27	R_1972	31,370	6,200	60	p_5,1980	0.277	0.048
28	R_1973	31,370	6,200	61	p_5,1981	0.608	0.035
29	R_1974	28,611	6,808	62	p_5,1982	0.352	0.042
30	R_1975	31,370	6,068	63	p_5,1983	0.245	0.037
31	R_1976	47,953	7,507	64	p_5,1984	0.418	0.043
32	R_1977	76,661	9,462	65	p_5,1985	0.396	0.049
33	R_1978	103,241	13,425	66	p_5,1986	0.440	0.033

-continued-

Table 8 continued.

Parameter	Description	Estimate	SE	Parameter	Description	Estimate	SE
67	p 5,1987	0.421	0.052	71	p 5,1991	0.601	0.035
68	p 5,1988	0.442	0.035	72	p 5,1992	0.638	0.035
69	p 5,1989	0.489	0.040	73	p 5,1993	0.631	0.031
70	p 5,1990	0.509	0.037	74	p 5,1994	0.531	0.086

RSS(Total Catch)	8,127
RSS(Aerial)	442
RSS(S-R)	2,546
Total RSS	11,115

age classes. An explanation for the selectivity differences may be there is too many parameters to estimate with not enough information.

Even though parameter estimates are relatively similar for each approach, the RSS's are not. The RSS(CommCatch) for approaches I and III represents the commercial catch, whereas the RSS(TotalCatch) in approaches II and IV correspond to the catch from all three fisheries. Therefore, the RSS's from approaches I and III are analogous, but the RSS(TotalCatch), which includes RSS(CommCatch), RSS(Rec), and RSS(Sub), from approach III is naturally much greater than approaches II and IV. Approach IV returns the smallest RSS for the catch, and both auxiliary data sources. The RSS(S-R)'s are comparable among approaches.

Brood-year returns and their resultant CV's are displayed in Figure 6. The pattern of estimates is identical across approaches. An increase or decrease in the brood-year returns for one approach is reflected in the returns of the other three. However, the brood-year returns from approach IV are slightly larger. Confidence intervals surrounding approaches I and III are more pronounced than approaches II and IV, but CV's across approaches follow a similar pattern. The large confidence interval for approach III in 1995, despite little change in the CV, resulted from extreme bootstrap values of the brood-year return that occurred in some replications. CV's range from 8-40% with the largest values being 40.7, 33.0, 33.6, and 25.6%, for approaches I, II, III, and IV, respectively. One explanation for increasing CV's in the earliest years is because brood-year return estimates are smaller, which is a common phenomenon for CV's

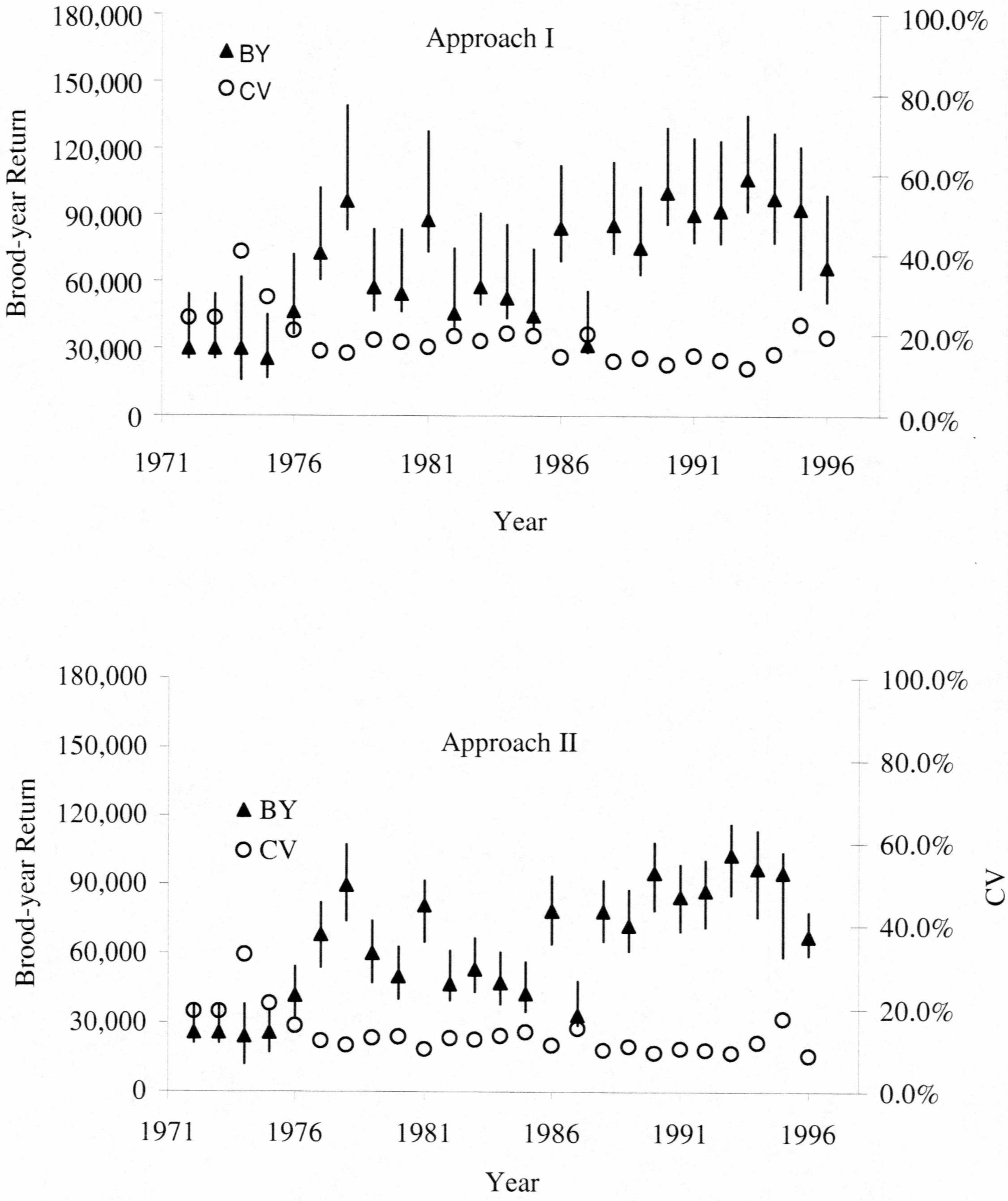
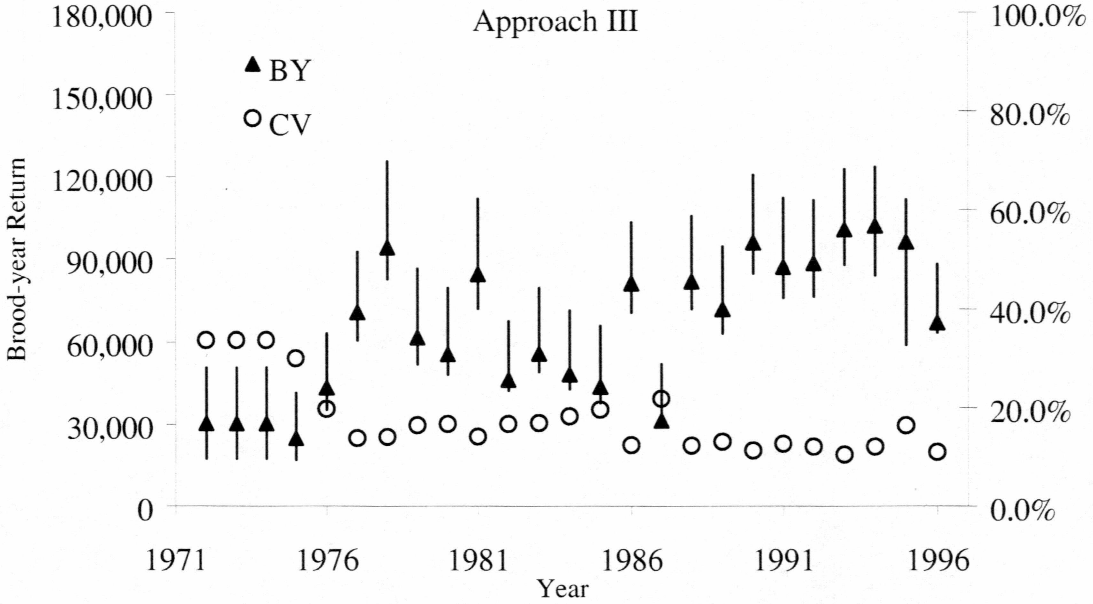


Figure 6. Brood-year return estimates and coefficients of variation, (a) approach I, (b) approach II, (c) approach III, (d) approach IV.



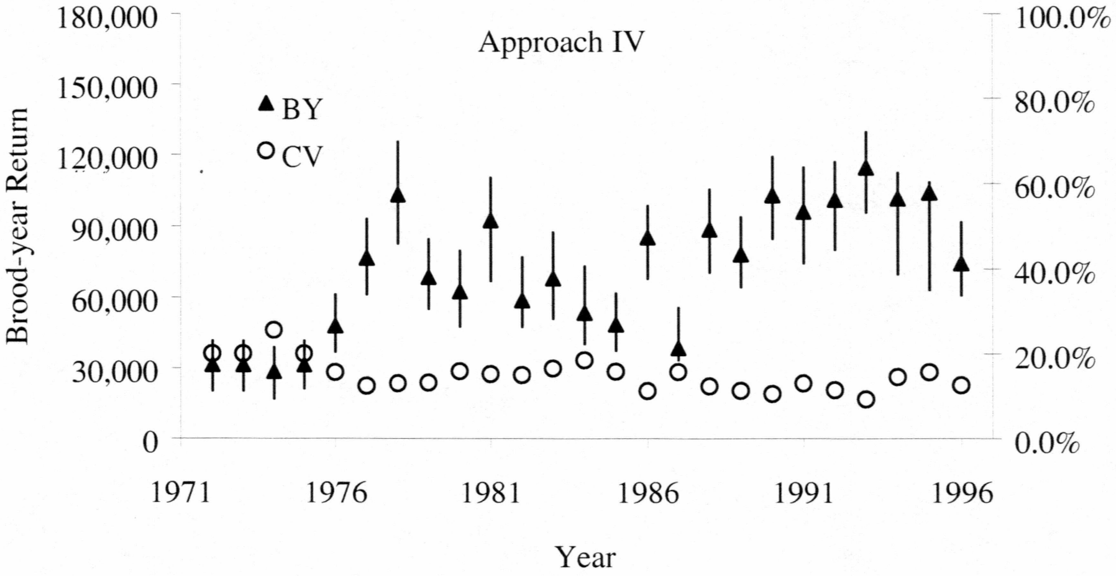


Figure 6, continued.

(Williams and Quinn 1997). Another possibility could be the minimal amount of information available to support these estimates.

The observed aerial index and the resultant estimated index are found in Figure 7. The proportion counted through aerial surveys was estimated at 6.7, 8.1, 7.4, and 5.4% for approaches I, II, III, and IV, respectively. The same pattern is found throughout each approach. Large aerial counts result in an under-estimate and low counts result in an over-estimate. With the exception of 1985 and 1986 in approach I and 1985, 1986, and 1995 in approach II and 1985-1987, 1992 and 1995 in approach III, every observed value was encompassed by the estimate's confidence intervals, indicating a reasonable fit to the index.

Total catch and commercial catch estimates for approaches II and IV, and I and III, respectively, are in located in Figures 8 and 9. Observed trends in the catch are reflected in all four approaches. Approach II's and approach IV's estimates are greater than approaches I and III, because they represent total catch instead of commercial catch. With the exception of 1982, 1986, and 1987 in approach I, all of the observed catches fall within the estimated confidence intervals. Furthermore, with the exception of 1980, the CV's from each approach are relatively small, ranging from 7-21%. The recreational and subsistence catch estimates from approach III and corresponding observed values are found in Figure 10. The model was able to reliably estimate the catches in years without catch-age data. With the exception of 1985 and 1986 in the recreational fishery and 1985 and 1986 in the subsistence fishery all observed values are within the estimated confidence intervals. The observed recreational and subsistence catches from years with

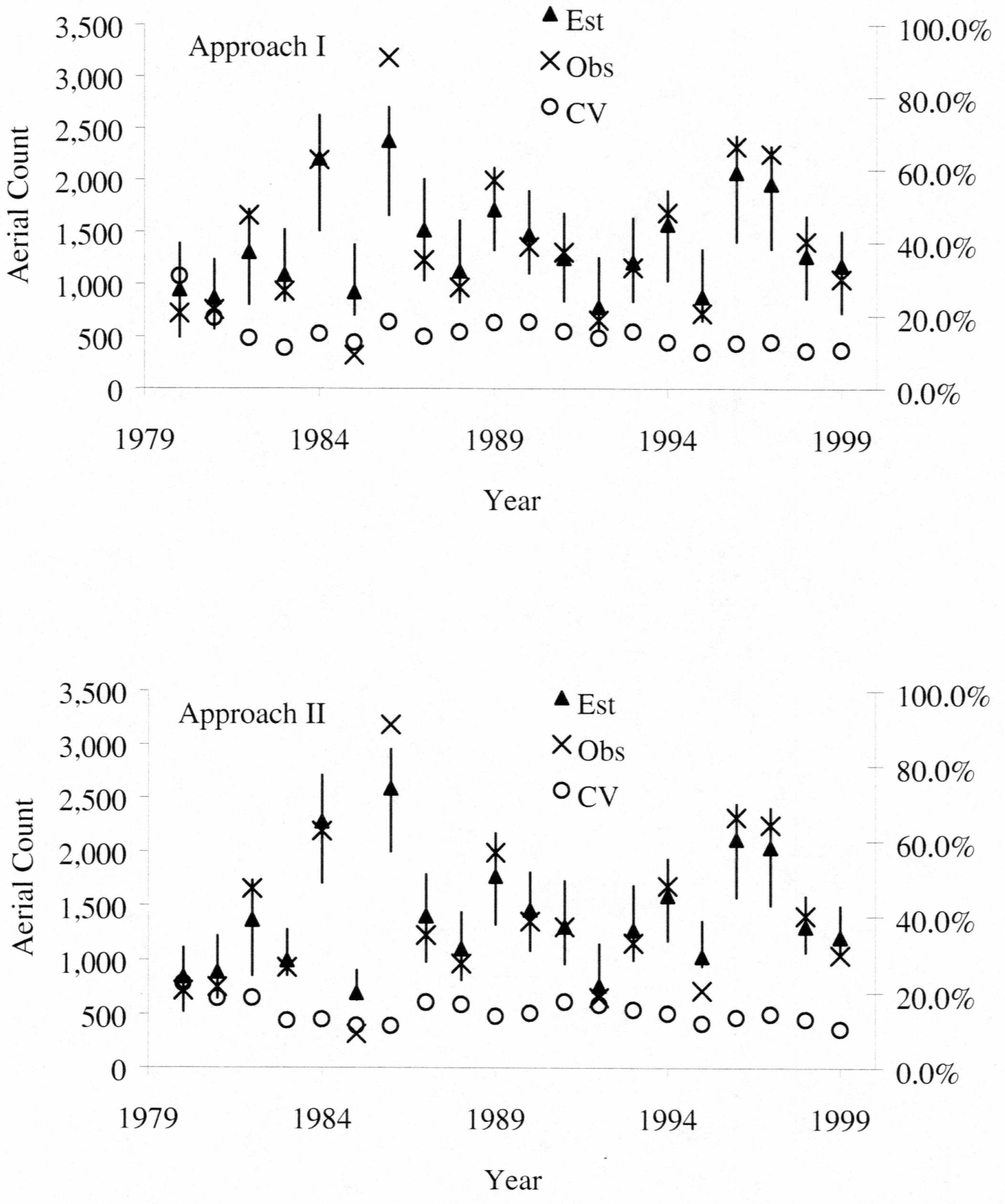
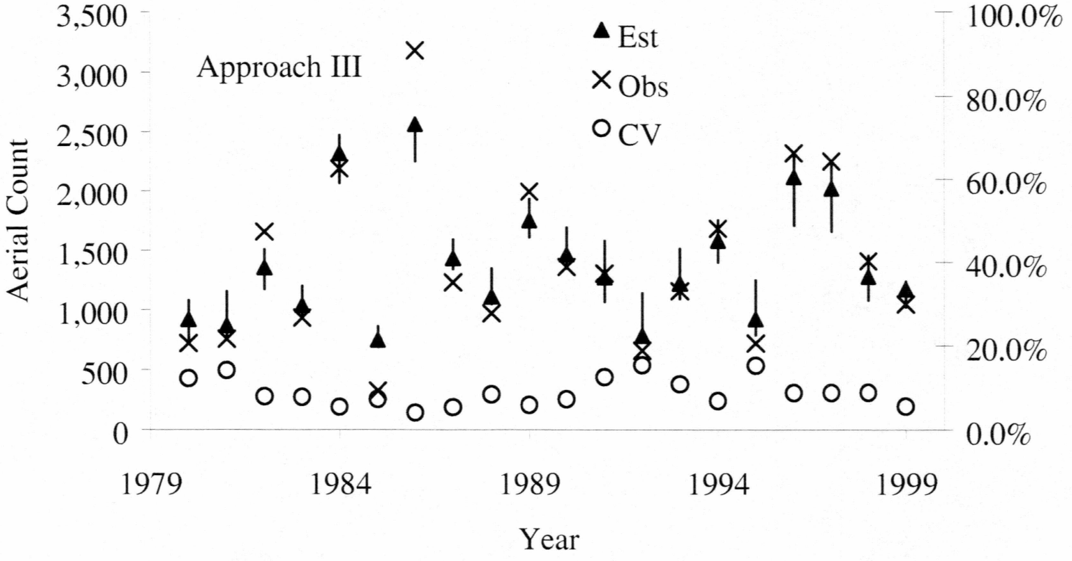


Figure 7. Observed and estimated aerial index and coefficients of variation, (a) approach I, (b) approach II, (c) approach III, (d) approach IV.



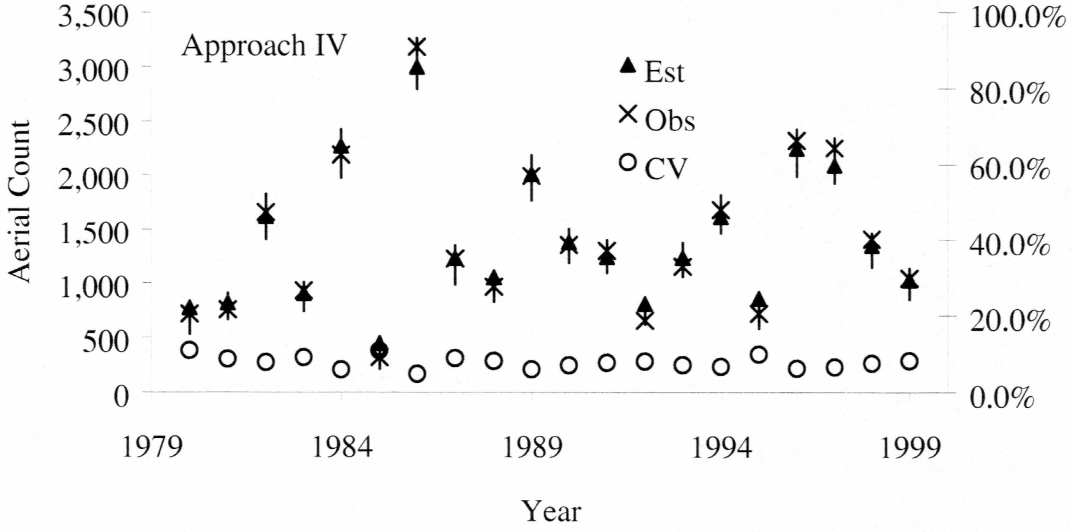
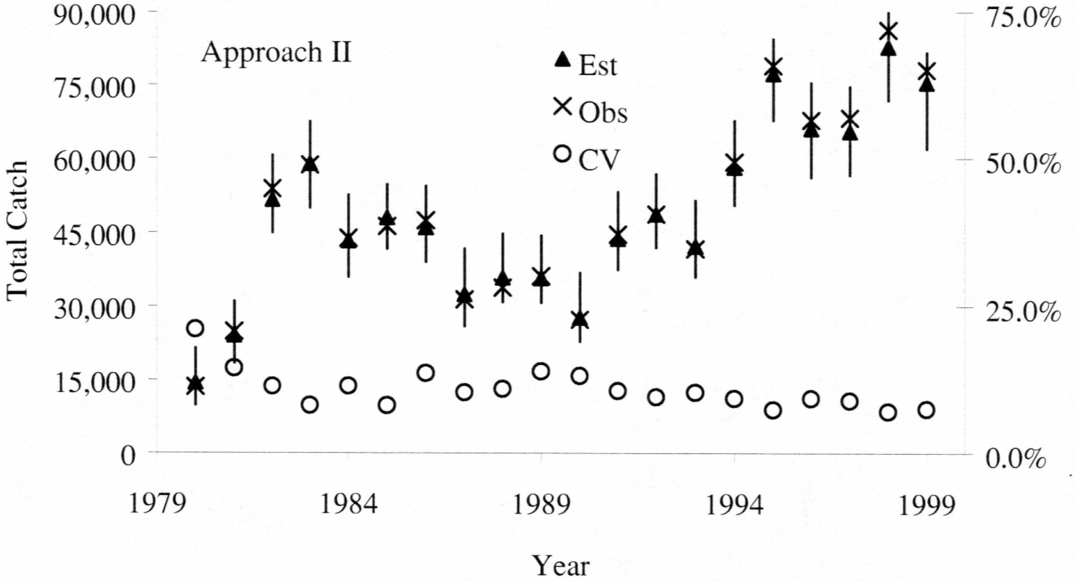


Figure 7, continued.



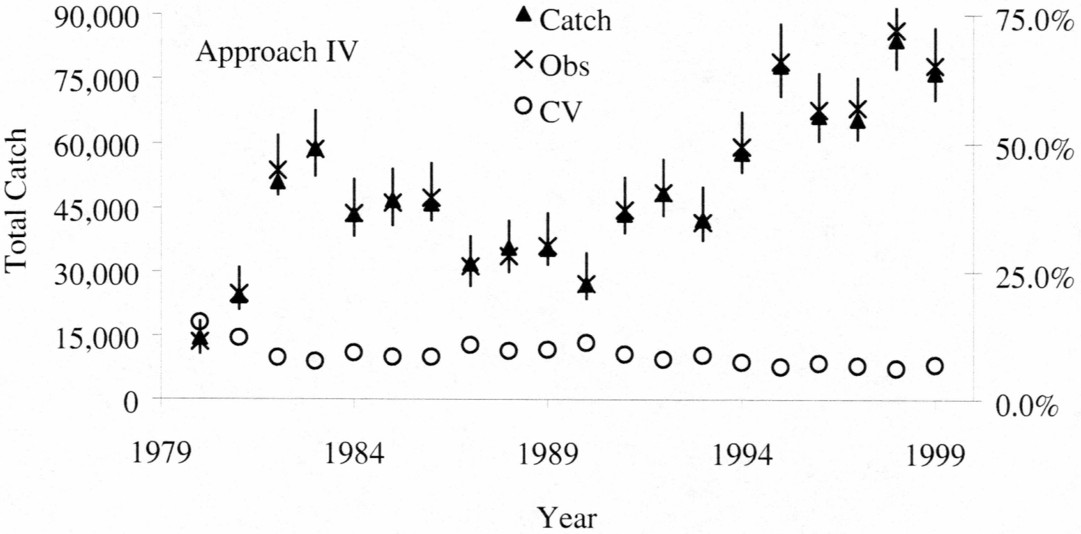


Figure 8. Observed and estimated total catch for approaches II and IV.

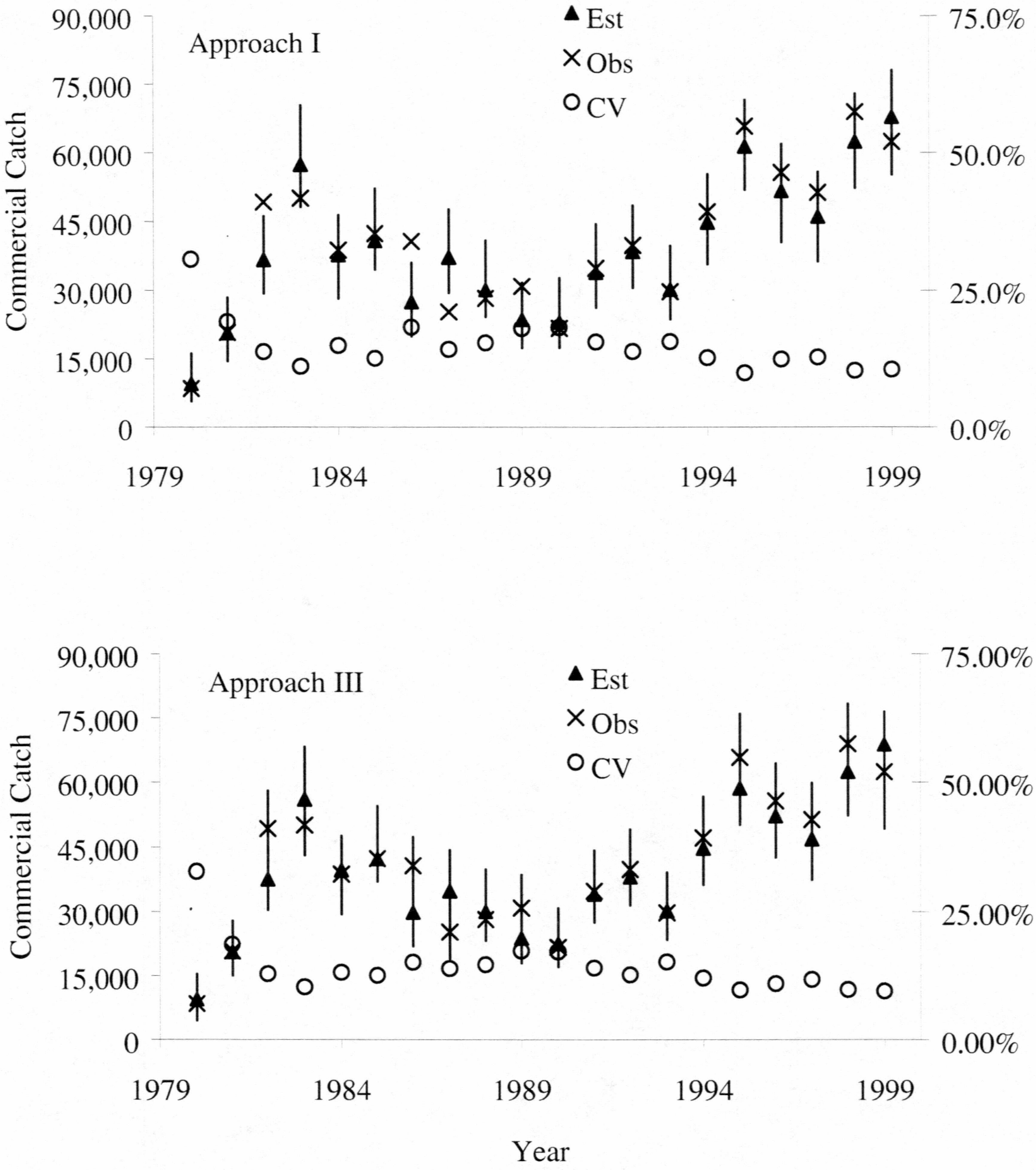
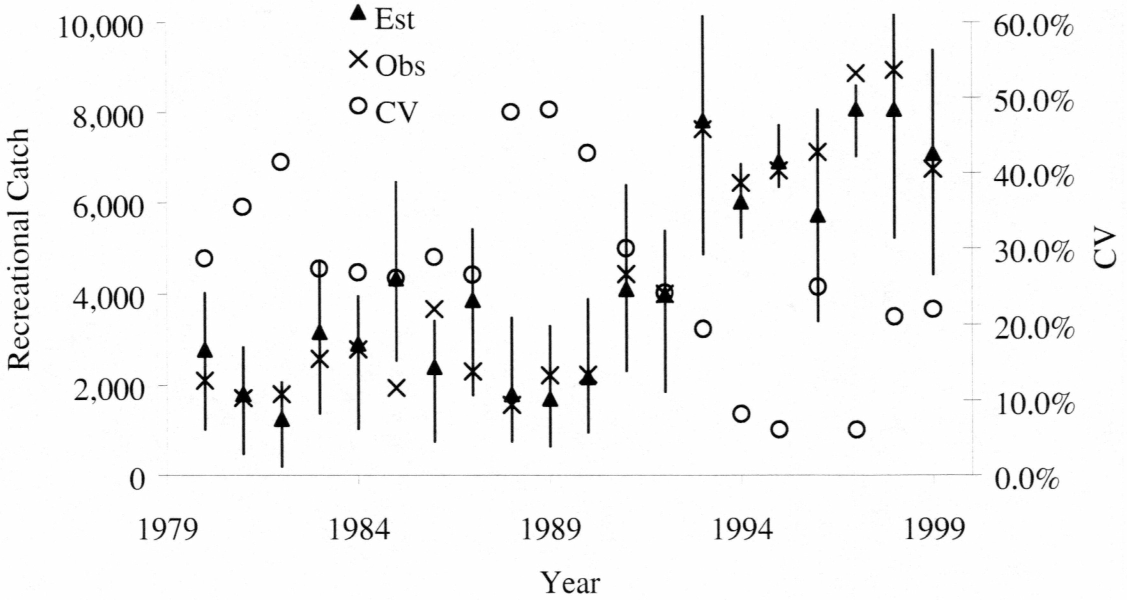


Figure 9. Observed and estimated commercial catch from approaches I and III.



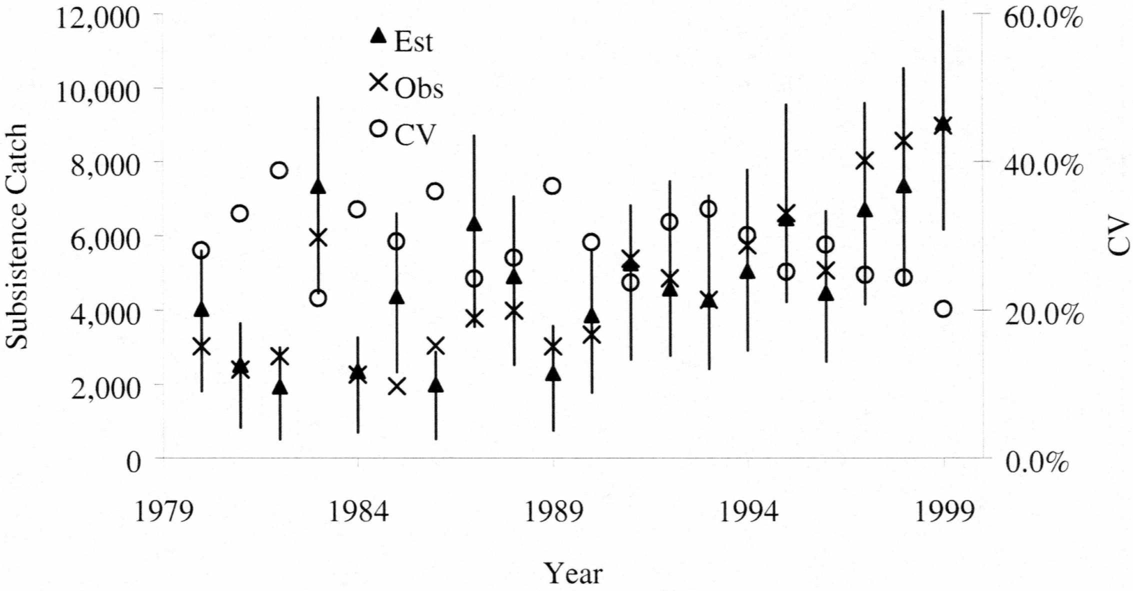


Figure 10. Observed and estimated recreational and subsistence catches for approach III. The top graph is the recreational catch and the bottom graph is the subsistence catch.

catch-age information available (1988-1991, 1996, and 1999 for recreational and 1992-1999 for subsistence) are also within estimated confidence intervals. However, all of the estimates are imprecise and the CV's are much larger compared to those from the commercial fishery. This is expected because the recreational and subsistence sample sizes are small.

Resulting total return and escapement estimates from the catch–age model, including CV's, are shown in Tables 9-12. Recall that the sum of catch and escapement equals the total return. The return estimates are nearly identical among approaches, and so are the escapement estimates. Approach IV results in the largest estimates of total return and escapement. However, approaches I, II, and III are only slightly less, with approach II being the smallest. The CV's from approaches I, III and IV are also analogous, with approach IV having larger CV's for the escapement estimates and comparable CV's for the return estimates.

Choosing the Best Model

Each of the approaches produced estimates that provided a good fit to the catch and escapement data (Figures 7-10). Moreover, estimated confidence intervals of all four approaches encompass the majority of observed values.

An analysis of residuals determined that the model's fit to the catch and aerial index produced no apparent pattern in residuals for all four approaches (Figure 11). In contrast, the spawner-recruit residuals (Figure 11) display a positive relationship in the

Table 9. Total return and escapement estimates from approach I.

Year	Total Return	CV	Escapement	CV
1980	28,591	22.9%	13,964	39.4%
1981	37,571	16.3%	12,809	35.6%
1982	60,440	13.5%	19,224	33.8%
1983	81,874	12.0%	16,033	33.4%
1984	75,235	12.8%	32,487	25.6%
1985	58,263	14.0%	13,582	37.6%
1986	69,203	13.6%	35,039	24.4%
1987	65,625	14.4%	22,368	34.9%
1988	52,258	14.7%	16,593	36.2%
1989	54,095	14.6%	25,263	28.2%
1990	50,343	14.8%	21,754	30.5%
1991	62,129	11.9%	18,430	33.1%
1992	58,753	12.4%	11,506	37.9%
1993	59,897	11.5%	17,858	31.3%
1994	80,095	10.4%	23,170	29.3%
1995	87,521	10.0%	12,948	35.2%
1996	94,305	10.6%	30,526	27.8%
1997	91,836	10.9%	28,894	29.0%
1998	98,538	9.3%	18,734	34.1%
1999	100,812	9.6%	17,370	32.7%

Table 10. Total return and escapement estimates from approach II.

Year	Total Return	CV	Escapement	CV
1980	26,341	14.2%	10,357	22.4%
1981	36,689	10.2%	10,923	18.5%
1982	57,642	8.1%	16,716	18.6%
1983	77,655	7.6%	12,177	12.6%
1984	72,004	7.4%	27,871	13.0%
1985	57,118	7.8%	8,568	11.3%
1986	65,536	7.1%	31,660	11.2%
1987	61,549	7.3%	17,172	17.5%
1988	50,936	7.9%	13,515	16.9%
1989	49,816	7.8%	21,669	13.9%
1990	47,125	8.1%	17,883	14.6%
1991	60,130	7.8%	16,000	17.6%
1992	55,327	8.0%	9,345	16.8%
1993	59,344	7.4%	15,619	15.6%
1994	75,324	6.7%	19,459	14.5%
1995	84,363	6.7%	12,654	11.9%
1996	88,778	6.4%	25,892	13.5%
1997	87,158	6.4%	24,963	14.4%
1998	95,521	6.3%	15,993	13.0%
1999	98,904	7.1%	14,836	10.4%

Table 11. Total return and escapement estimates from approach III.

Year	Total Return	CV	Escapement	CV
1980	28,632	16.2%	12,340	28.5%
1981	36,585	13.5%	11,636	32.2%
1982	58,865	10.3%	18,168	26.4%
1983	80,338	9.8%	13,914	26.8%
1984	75,970	10.4%	31,123	24.4%
1985	60,931	11.6%	10,000	26.8%
1986	68,594	11.0%	34,410	22.1%
1987	64,133	10.9%	19,201	26.2%
1988	51,638	11.4%	14,897	29.2%
1989	51,275	12.1%	23,483	25.6%
1990	48,228	12.4%	19,631	26.5%
1991	60,509	10.0%	17,088	28.7%
1992	57,060	10.3%	10,470	35.3%
1993	58,633	10.1%	16,361	30.3%
1994	76,959	8.8%	21,241	25.3%
1995	84,197	8.6%	12,347	31.8%
1996	90,666	8.5%	28,424	25.2%
1997	88,670	8.6%	27,133	25.0%
1998	94,925	7.7%	17,162	26.6%
1999	100,608	7.6%	15,739	22.3%

Table 12. Total return and escapement estimates from approach IV.

Year	Total Return	CV	Escapement	CV
1980	28,760	18.0%	14,283	35.9%
1981	39,387	14.9%	15,084	35.6%
1982	80,955	13.3%	29,956	34.1%
1983	75,445	9.5%	16,757	35.1%
1984	85,417	16.6%	41,962	33.3%
1985	55,024	8.9%	8,254	35.0%
1986	101,386	17.0%	55,424	32.7%
1987	54,668	14.7%	22,744	34.0%
1988	55,132	13.3%	19,434	35.2%
1989	72,526	17.2%	37,080	34.1%
1990	52,583	16.3%	25,466	33.9%
1991	66,483	12.5%	22,956	33.5%
1992	63,358	10.7%	14,933	34.7%
1993	65,107	13.7%	22,827	35.7%
1994	87,560	12.1%	29,813	34.0%
1995	93,745	8.4%	15,841	34.0%
1996	107,771	12.8%	41,484	32.8%
1997	104,141	12.0%	38,642	32.3%
1998	108,938	9.2%	24,952	33.1%
1999	95,269	8.9%	19,019	33.5%

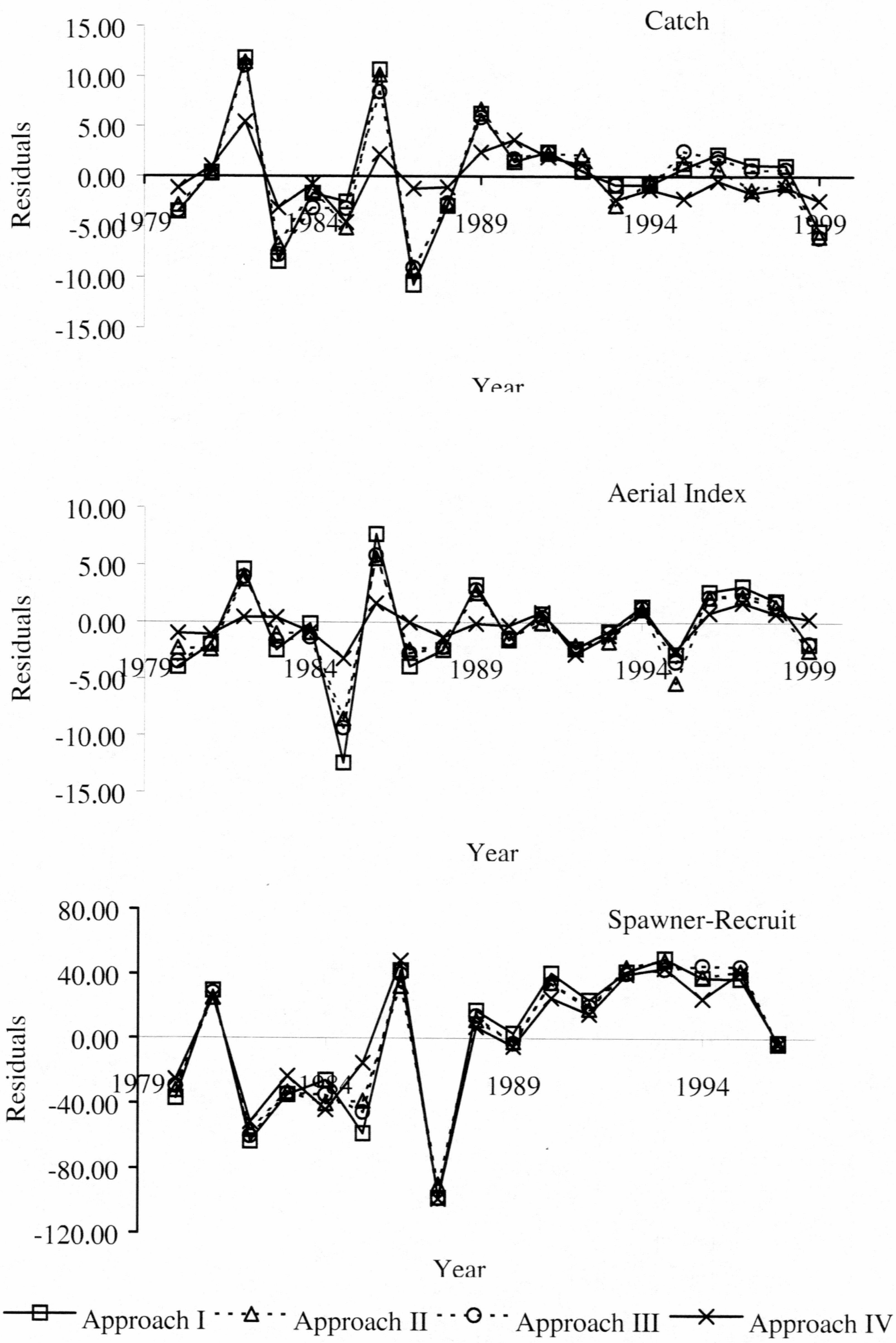


Figure 11. Catch, aerial index, and spawner-recruit residuals.

most recent years since 1988 in all four approaches, and the magnitude of the residuals is the same.

The parameter uncertainties in the brood-year return, catch, and escapement index estimates are displayed in Figure 12. All four approaches display the same pattern of uncertainty and show a substantial increase in the RMSE surrounding brood year 1995. The RMSE's from approach I are generally larger than those from approaches II, III, and IV. Approach IV's RMSE's from the catch and aerial index are smaller than the remaining approaches, particularly in the most recent years. In contrast, the uncertainty associated with brood year returns from approach II is slightly less than approach IV.

The estimates of recruits versus estimated spawners from the four approaches are shown in Figure 13, along with the Ricker spawner-recruit fits and replacement line. The patterns for all four approaches are similar, although approach IV shows the largest contrast in escapement estimates. For all four approaches, the estimates are above the replacement line.

After the fit to the Ricker spawner-recruit curve was determined, biological reference points such as peak spawning abundance, S_p, the subsequent number of recruits, R_p, and MSC were calculated where $(R_p, S_p) = (\alpha/\beta e, 1/\beta)$ (Table 13). For approaches I, II, and III, the recruitment peak is approximately 75,000 and the corresponding number of spawners is roughly 18,000 (Table 13). Approach IV's peak recruitment and spawning abundance are much larger, approximately 88,000 and 25,000, respectively.

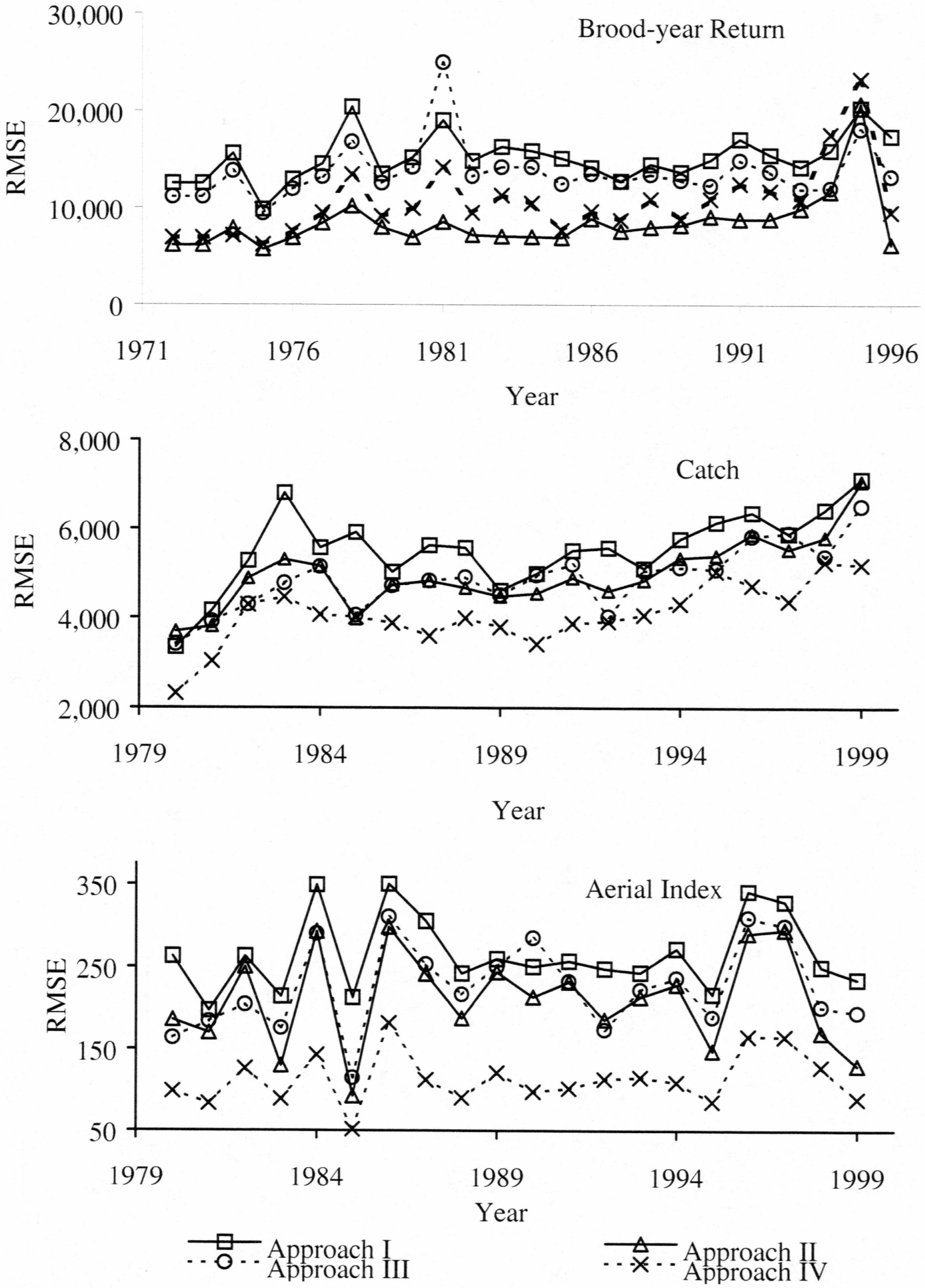


Figure 12. Root mean square error from brood-year return, catch, and aerial index estimates.

The MSC and its related exploitation rate were determined from the Ricker spawner-recruit relationship (Table 13). The estimates from approaches I, II, and III are similar but the estimates from approach IV produce a moderately higher optimal escapement under less exploitation. The major difference is in the estimates from approaches II and IV. Even though each approach utilized the same data sources, approach II results in the largest exploitation at the lowest optimal escapement level, whereas approach IV has the lowest exploitation at the highest optimal escapement level. The increase in (R_p, S_p), MSC, and optimal escapement are likely the result of the time-varying return proportions used in approach IV.

Table 13. Estimates of the peak recruitment and spawning (S_p, R_p), maximum sustained catch (C_m) and the associated level of escapement (S_m), recruitment (R_m), and exploitation (μ_m).

	R_p	S_p	R_m	S_m	C_m	μ_m
Approach I	76,312	19,274	74,460	15,311	59,149	0.794
Approach II	74,667	17,920	73,011	14,388	58,623	0.803
Approach III	75,741	18,606	73,991	14,868	59,123	0.799
Approach IV	87,492	25,687	84,722	19,711	65,012	0.767

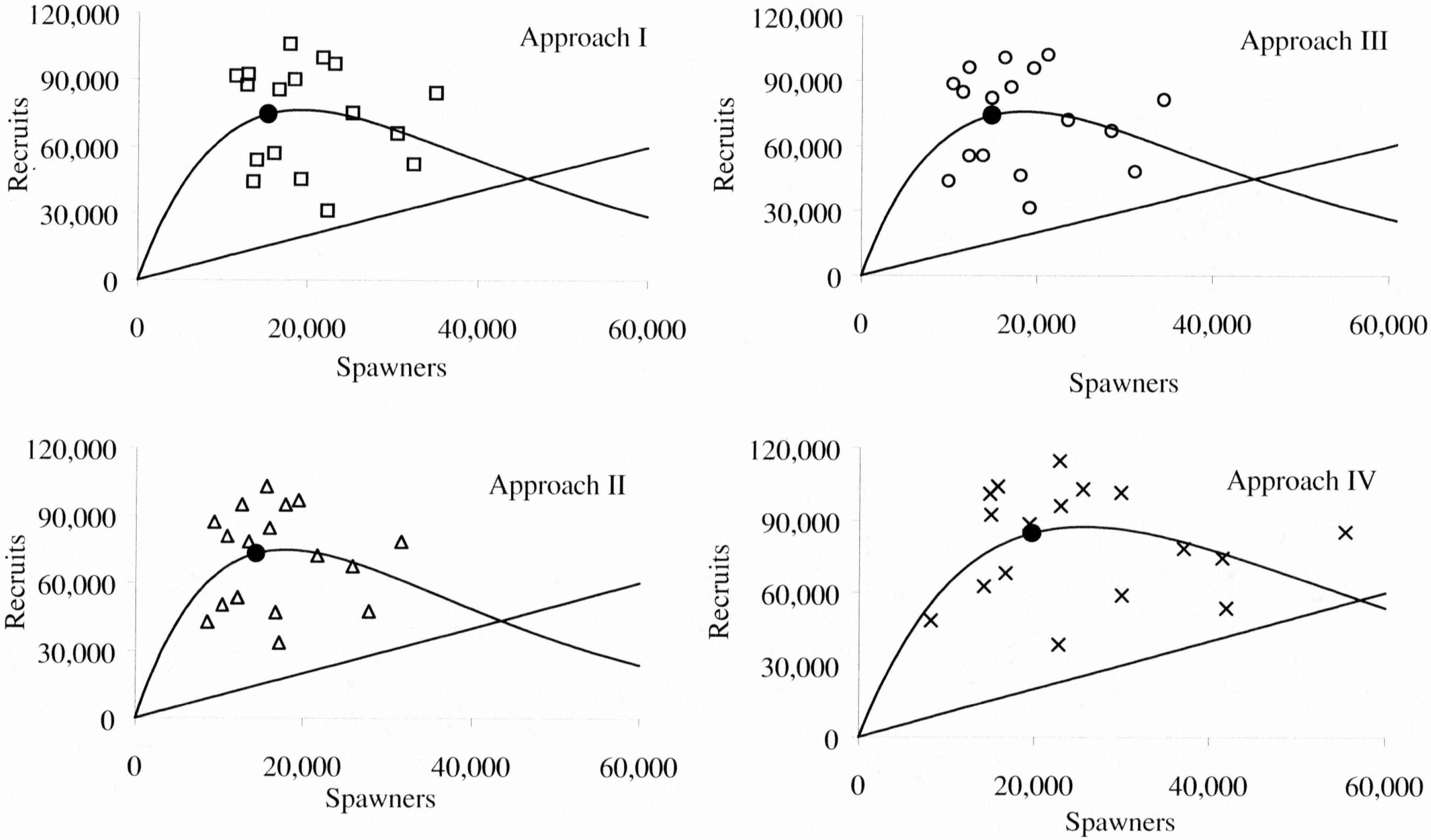


Figure 13. The model's fit to the Ricker spawner-recruit relationship. The large circles indicate optimal spawning and recruitment (S_m, R_m).

The last criterion used to choose the most appropriate approach deals with robust and plausible parameter estimates. Once a weighting scheme is chosen, population parameter estimates are similar across approaches (Tables 5-8); within an approach a range of λ values produces analogous results. Based on the efficiency of the commercial fleet, historical catches, sonar counts, and the characteristics of large chinook salmon populations in Alaska, I believe each approach produces plausible parameter estimates.

The pairwise comparisons between the MSE's are located in Table 14. A significant result indicates the approach with a lower MSE has a better fit to that individual data source. Approach IV's MSE for the catch and aerial data components are smaller than the MSE's from the constant proportion models. In addition, the MSE's for the catch and aerial information from approaches II and III are smaller than the corresponding MSE's from approach I; however, the MSE's from approaches II and III are not significantly different from one another. In contrast, there was no significant difference in the spawner-recruit information across all four approaches, which is expected because the spawner-recruit relationship is internal to the model.

In the end, approach IV provides the most accurate fit to the catch-age information, with the most precision and least bias. However, of the constant proportion models, approach II performs slightly better than approaches I and III (Table 15). Summary statistics from all four approaches can be found in Table 15. These summary statistics show that all four approaches provided consistent estimates, but certain approaches did better than others for estimating specific types of parameters.

Table 14. Catch-age model comparisons, based on Lehmann's test for equality of mean squared errors. MSE's are on top and correlations (*r*) are below.

	MSE			
	Approach1	Approach II	Approach III	Approach IV
Catch	187.92	171.61	167.74	67.72
Aerial Index	280.96	152.96	163.65	22.08
Spawner-Recruit	190.87	161.15	171.73	149.79

Pairwise Tests

Catch Lehmann Correlations

	Approach I	Approach II	Approach III
Approach II	0.20^{*}		
Approach III	0.23^{*}	0.04	
Approach IV	0.54^{**}	0.51^{**}	0.52^{**}

Aerial Index

	Approach I	Approach II	Approach III
Approach II	0.65^{**}		
Approach III	0.81^{**}	-0.18	
Approach IV	0.85^{**}	0.81^{**}	0.81^{**}

Spawner-Recruit

	Approach I	Approach II	Approach III
Approach II	0.43		
Approach III	0.24	-0.43	
Approach IV	0.33	0.15	0.32

* Significant at the 95% confidence level, $p < 0.05$.

** Significant at the 99% confidence level, $p<0.01$

Critical *r*-values at $\alpha = 0.05$ equal 0.18, 0.44, and 0.48 for catch, aerial index, and spawner-recruit, respectively.

Table 15. Summary statistics from all four approaches.

	Approach I	Approach II	Approach III	Approach IV
Unweighted RSS				
Commercial Catch	22,550	NA	21,058	NA
Total Catch	NA	20,593	NA	8,127
Aerial Index	5,619	3,059	3,460	442
Spawner-Recruit	32,448	27,396	30,309	25,465
Brood Year Return				
Average	65,844	62,987	64,884	71,564
CV	19.0%	14.0%	16.3%	15.0%
Total Return				
Average	68,369	65,363	66,871	74,683
CV	13.0%	7.8%	10.5%	13.0%
Exploitation Rate				
Average	0.56	0.72	0.57	0.65
CV	14.5%	5.8%	10.0%	12.4%
Commercial Catch				
Average	39,001	NA	39,078	NA
CV	15.0%	NA	14.9%	NA
Total Catch				
Average	NA	48,199	NA	48,849
CV	NA	10.8%	NA	8.8%
Aerial Index				
Average	1,385	1,402	1,395	1,398
CV	19.3%	14.9%	8.8%	7.8%
Escapement				
Average	20,428	17,164	18,738	25,846
CV	32.5%	14.9%	27.3%	34.1%

Even though the variation surrounding approach IV's escapement estimates is more than the others, the pairwise comparison tests coupled with the previous criteria suggest approach IV produces more accurate point estimates. The overall fit to the catch and aerial index data is much better than the other approaches (Table 15), residual patterns in the catch are not apparent, parameter uncertainty is low, and all estimates are plausible. In addition, the increases in biological reference points such as peak spawners and optimal escapement compared to the other approaches are more in-line with the current perceptions of the fishery's managers. Moreover, estimates of the spawning abundance reflect the mark-recapture estimate (16,386) determined by ADF&G in 1999 (Evenson and Wuttig 2000).

Sensitivity Analysis: Approach IV

The previous sensitivity analysis on approach IV revealed a λ_I of 0.3 and a λ_F of 0.2 lessened the pattern in residuals, improved the fit to the catch-age data, and induced some variation around the model's exact fit to the aerial index. Furthermore, the peak number of spawners and optimal escapement increase dramatically to roughly 35,000 and 25,000, respectively.

Because I chose approach IV as the best descriptive model, the previous sensitivity analysis prompted me to conduct a separate sensitivity analysis comparing the influence of alternative weighting scenarios. The scenarios chosen were: (1) a λ_I of 1.0 and λ_F of 0.1, (2) a λ_I of 1.0 and λ_F of 0.2, (3) a λ_I of 0.5 and λ_F of 0.1, and (4) a λ_I of 0.3 and λ_F of 0.2. Furthermore, for comparison purposes between the two best approaches, Approach II (scenario 5) was also run at a λ_I of 0.3 and λ_F of 0.2. Bootstrap procedures were not run on the approach II scenario because this weighting scheme produces obvious patterns in the residuals, consequently there are no CV's reported in the summary table.

The results from this sensitivity analysis are found in Figure 14 and Table 16. The effects of changing the aerial and spawner-recruit influence on the estimated catch are small. In contrast, there is a substantial effect on the estimates of the aerial escapement index. A λ_I of 0.3 induces excessive deviation around the aerial escapement index — e.g., scenario 4 results in a smoothing of extreme aerial counts in later years and consistently over-estimates the index in recent years (Figure 14). A λ_I of 0.5 induces the amount of deviation around the aerial index that one might expect. A λ_I of 1.0 induces very little deviation around the aerial index. Nevertheless, the appropriate weighting really depends on the ratio of variances of the commercial catch and the aerial index, but this ratio is not known. The sensitivity scenarios generally have larger CV's than the base case, as a result of applying less weight to the auxiliary information sources

Pairwise comparison tests between scenario 3 and the constant proportion models illustrate the process of inducing variation into the aerial index (Table 17). The unweighted MSE's were used for a fair comparison among the models with different weighting scenarios. Test results on the MSE's from the catch, the aerial index, and the spawner-recruit relationship are the same as before. However, the decrease in λ_I from 1.0 to 0.5 lessened the pattern in the aerial index residuals and decreased the correlations (r)

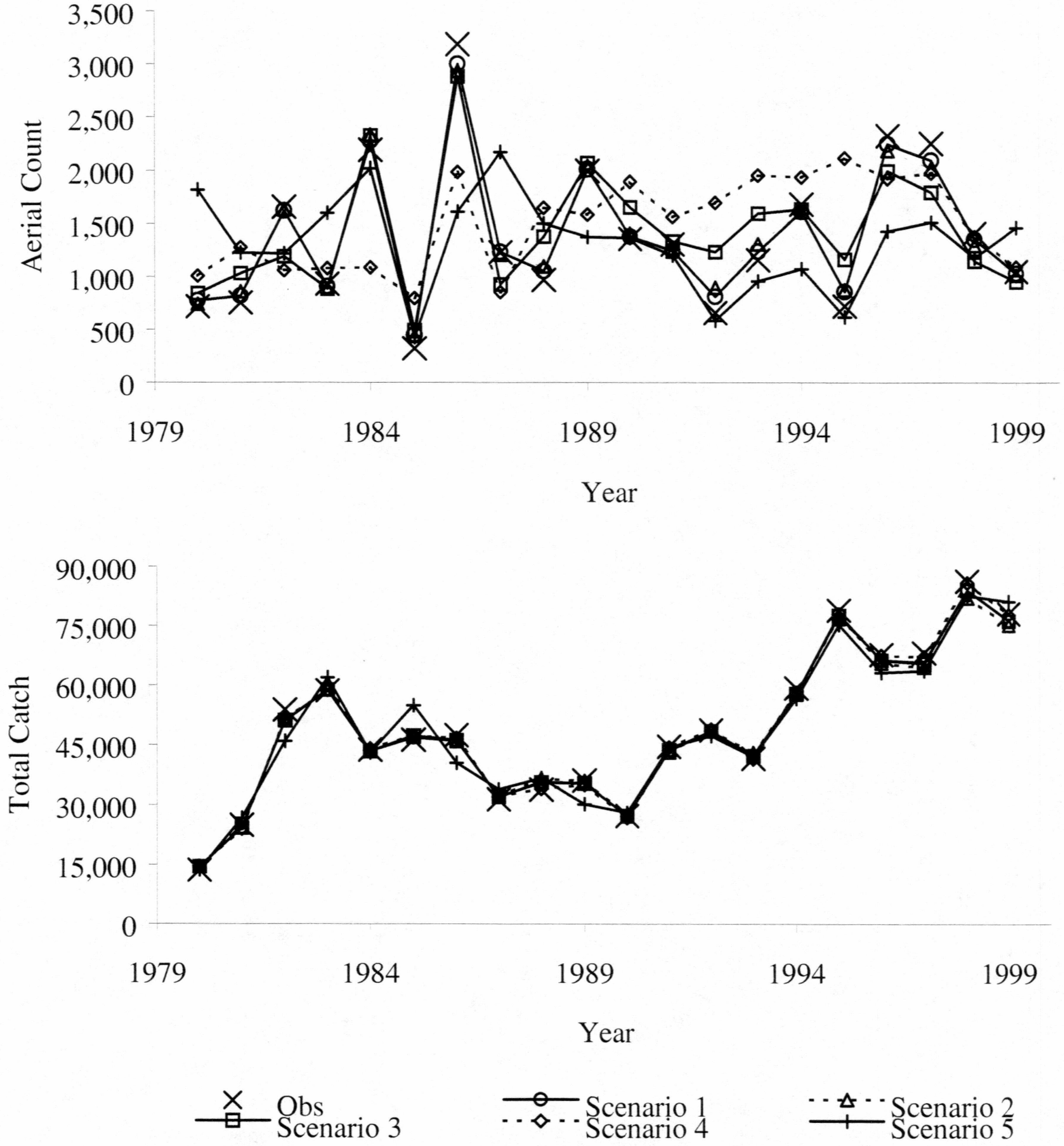


Figure 14. Observed and estimated aerial index (top graph) and catch (bottom graph) from approach IV's sensitivity analysis. Scenario1: $\lambda_I = 1.0$ and $\lambda_F = 0.1$. Scenario 2: $\lambda_I = 1.0$ and $\lambda_F = 0.2$. Scenario 3: $\lambda_I = 0.5$ and $\lambda_F = 0.2$. Scenario 4: $\lambda_I = 0.1$ and $\lambda_F = 0.2$. Scenario 5: $\lambda_I = 0.3$ and $\lambda_F = 0.2$.

Table 16. Summary statistics from approach IV's sensitivity analysis.

	Scenario 1	Scenario 2	Scenario 3	Scenario 4	Scenario 5
λ_I	1.00	1.00	0.50	0.30	0.30
λ_F	0.10	0.20	0.10	0.20	0.20
Unweighted RSS					
Total Catch	8,127	8,927	7,945	8,402	15,411
Aerial Index	442	729	1,010	1,349	19,544
Spawner-Recruit	25,465	17,905	23,371	11,698	8,630
Brood Year Return					
Average	71,564	71,519	70,344	70,497	78,265
CV	15.0%	15.4%	17.1%	18.9%	NA
Total Return					
Average	74,683	75,229	73,266	73,352	78,483
CV	13.0%	14.2%	16.3%	18.3%	NA
Exploitation Rate					
Average	0.65	0.64	0.66	0.65	0.61
CV	12.4%	13.3%	14.9%	17.1%	NA
Total Catch					
Average	48,849	48,698	48,872	48,849	48,560
CV	8.8%	9.2%	9.1%	9.1%	NA
Aerial Index					
Average	1,398	1,399	1,425	1,494	1,317
CV	7.8%	10.0%	15.4%	20.0%	NA
Escapement					
Average	25,846	25,861	24,355	24,502	29,923
CV	34.1%	33.3%	38.6%	43.7%	NA

Table 17. Pairwise comparison tests between the constant proportion models and approach IV's sensitivity analysis. The weighting scenario on approach IV equals a λ_I of 0.5 and λ_F of 0.1. The constant proportion models are weighted with a λ_I of 1.0 and λ_F of 0.1.

Catch

	Approach I	Approach II	Approach III
Approach IV			
r	0.55	0.52	0.53
p-value	< 0.001*	< 0.001*	< 0.001*
r-critical[a]	0.18	0.18	0.18

Aerial Index

	Approach I	Approach II	Approach III
Approach IV			
r	0.68	0.53	0.55
p-value	0.001*	0.02*	0.01*
r-critical[a]	0.44	0.44	0.44

Spawner-Recruit

	Approach I	Approach II	Approach III
Approach IV			
r	0.44	0.37	0.46
p-value	0.07	0.19	0.06
r-critical[a]	0.48	0.48	0.48

[a] reject H_o if $r > r$-critical.

* significant at the 95% confidence level.

among approaches. Interestingly enough, the exact opposite was seen in the spawner-recruit residuals.

These results imply that approach IV with a λ_I of 0.5 and λ_F of 0.1 may be the best weighting scenario. However, a pairwise comparison test between scenarios 1 and 3 revealed no significant difference between the catch MSE's ($r = -0.17$ with $p = 0.07$). Differences between the aerial index and spawner-recruit MSE's were expected due to the decrease in λ_I and its association with the Ricker spawner-recruit relationship. Further work is needed to explore the optimal weightings of the model, but for the purposes of this thesis, the full results are given for the original weighting scenario.

Forecasting Future Returns

The forecasts derived from the reduced model (catch-age data through 1998) and the full model (catch-age data through 1999) are found in Figure 15. ADF&G estimated the 1999 escapement after commercial fishing at 32,090 (Evenson and Wuttig 2000). Adding this to the catch from the remaining fisheries and accounting for escapement produces a total return of approximately 100,000. The 2000 escapement estimate, after commercial fishing, is approximately 39,000 (Klaus Wuttig 1300 College Road Fairbanks, Alaska 99701). Providing for the remaining catch and escapement produces a total return of approximately 80,000. Predicted returns from the catch-age model are similar to these estimates (Figure 15), which implies that the model's ability to predict total returns is relatively robust.

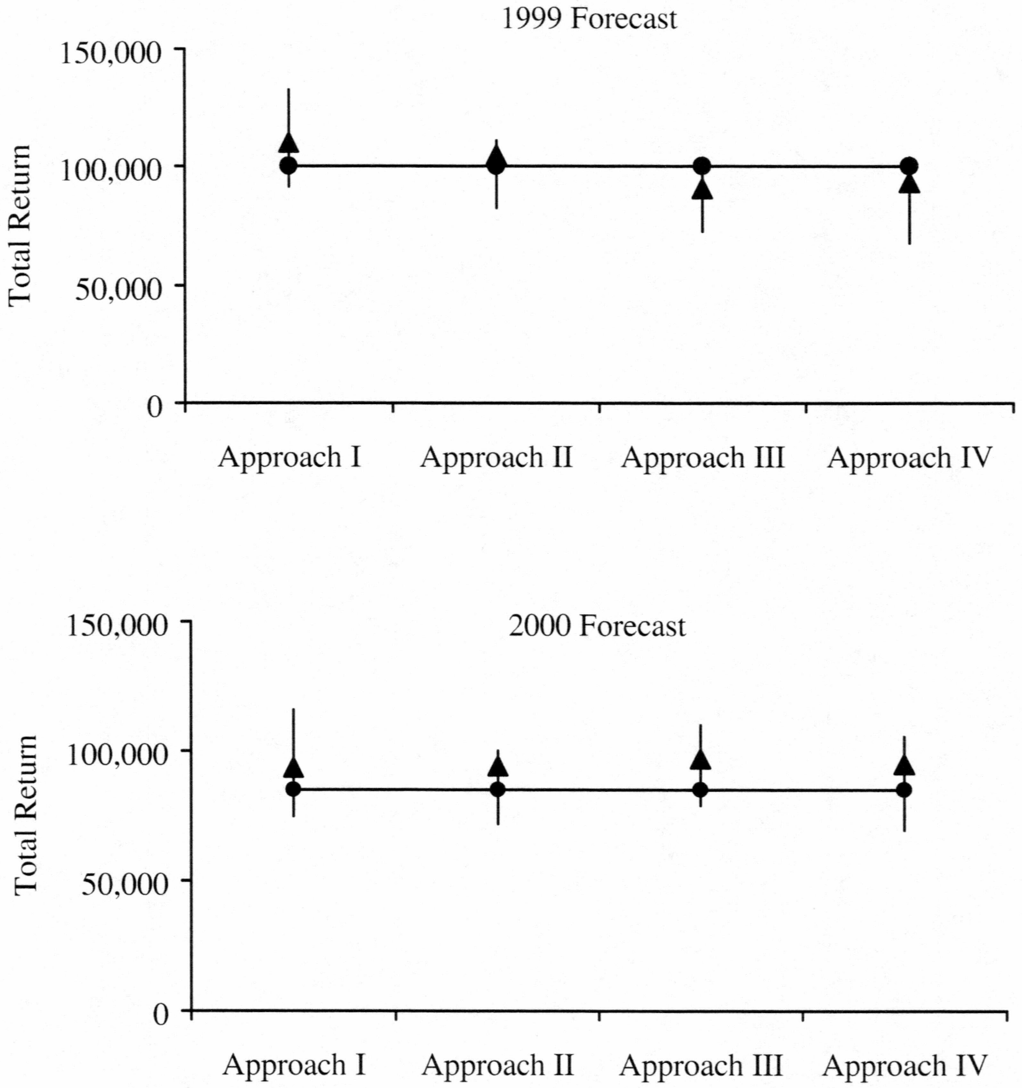


Figure 15. Forecasts of the total return from the reduced (data from 1980-1998) and full (data from 1980-1999) model. The top graph contains the 1999 forecast and the bottom graph contains the 2000 forecast. The line indicates ADF&G's estimates of the total return

DISCUSSION

I successfully developed an age-structured assessment model of Copper River chinook salmon escapement by year. The model's four approaches employed information about catch and escapement to estimate the total return. Of the four approaches utilized to obtain these estimates I believe approach IV, the time-varying approach, is the best based on the model selection criteria previously described.

Run Reconstruction

The results from the run reconstruction point to its primitive nature. Brood-year returns are incomplete for many years and all estimates of returns are based on a constant exploitation rate, which rarely, if ever, exists. Moreover, its inability to provide complete brood-year return estimates makes it impossible to predict future returns. Run reconstruction does provide reliable starting values for the catch-age analysis. It may also offer a frame of reference for any model that estimates brood-year returns.

Data Weighting and Sensitivity Analysis

Since the commercial catch-age matrix is the most reliable data source, explaining the auxiliary data or recreational and subsistence fisheries without regard to the commercial catch would be inappropriate. The idea was to bring in information about escapement and recreational and subsistence fisheries without taking away from the commercial catch-age fit. Therefore, a weighting scenario was chosen that resulted in robust parameter estimates that followed the trends in the catch and aerial index while conveying plausible brood-year returns that exhibited a Ricker spawner-recruit relationship.

The sensitivity analysis to changes in the data weightings λ_I and $\lambda_{Comm} = 1.0$, $\lambda_F = 0.1$, $\lambda_{CatchAgeRec}$, and $\lambda_{CatchAgeSub} = 0.9$, and $\lambda_{RecCatch}$, and $\lambda_{SubCatch} = 0.7$ revealed that brood-year, catch, and escapement index estimates are robust to large changes in λ's. In addition, the range that provides a thorough explanation of the data without patterns in the residuals is fairly small. Increasing the influence of any λ forces the estimates to comply with observed values, which in turn increases the commercial catch RSS. Decreasing λ_I values in the constant proportion models (approaches I, II, and III) diminished the model's ability to describe the aerial index data.

In contrast, a decrease in approach IV's λ_I (from 1.0 to 0.5) improved the fit to the catch data and relaxed the precise fit to the aerial index (Table 16). The sensitivity analysis and comparison test revealed two weighting scenarios equally described the catch information (Figure 14 and Table 17). The central question is whether or not choosing the scenario with a lower λ_I is warranted just because the alternative scenario fits the aerial index too well. Further investigation into the ratio of the variances of the catch and aerial index data sources would help decipher the most appropriate weighting scenario. However, based on the comparison test and the small differences in CV's, I believe both scenarios will result in accurate parameter estimates of the population. Nevertheless, in other salmon systems I recommend utilizing approach IV to describe various data sources, then a sensitivity analysis can be performed to ensure each auxiliary source is weighted accordingly. This allows managers to see how their perceptions of the auxiliary data sources will influence the model's parameter estimates.

Retrospective Analysis

Parma (1993) concluded that retrospective patterns arise with the addition of updated catch-age and auxiliary information into catch-age models. One reason for this pattern may be that abundance estimates for the early years in a data series are inclined to converge to stable values whereas estimates for the most recent years can differ considerably (Pope 1972). Another reason for this pattern stems from the modeling of a salmon population returning over several years. For example, data through 1999 does not contain complete information on the total return from brood-years 1992-1996. Therefore, the total brood-year returns in recent years are estimated with limited information and by relying on the model's assumptions.

The absence of strong deviations in the retrospective patterns of the brood-year returns (Figure 5) suggests that there are no serious model misspecifications present. Similar brood-year return patterns across approaches and the fact that each set of retrospective data falls directly on top of their related data sets supports this finding. Furthermore, the expected deviations in the most recent brood-years are also similar across approaches.

Final Estimation

The estimated population parameters from the catch-age model provide useful information about the Copper River chinook salmon population. The majority of the total return is comprised of salmon aged 5 and 6. Furthermore, the continuing large returns coupled with substantial exploitation rates suggest that the population is fairly resistant to the effects of fishing. However, the spawner-recruit analysis (Table 13) suggests that the fishery is at or near MSC, and a substantial increase in the overall exploitation could force escapement to fall below ADF&G's biological escapement goal (BEG) of 28,000 to 56,000 chinook salmon. Still, it appears as though the Copper River chinook salmon can tolerate exploitation rates greater than 40% and still produce large returns.

The connection between brood-year returns and the catch-age equations resulting from them plays a fundamental role in the model's capacity to produce results that explain the data. With the exception of brood-year 1974, the CV's are fairly small. When a population parameter is the foundation from which the estimated abundance, catch, and escapement is derived, estimates of this parameter must exhibit a minimal amount of bias without sacrificing precision. Although each approach yields brood-year estimates that produce credible results, the least amount of error surrounds approaches II and IV (Figure 12).

Another vital aspect of catch-age analysis is the incorporation of auxiliary data. The consequences of estimating abundance without some sort of auxiliary information is an unreliable estimate from which nothing about the population can be inferred. In the case of the escapement index, the estimates were precise except for years 1985, 1986, and

1995. The CV's are larger than the brood-year returns but with few exceptions are generally less than 20%. This level of variation appears to be acceptable when one is utilizing the data source as a model constraint. The reason for the poor fit to years 1985, 1986, and 1995 stems from either the aerial count or survey quality. The lowest count on the Gulkana River was in 1985, the highest count in 1986, and the poorest survey in 1995. Therefore, even though the model was unable to accommodate the extreme aerial counts, it paid little attention to the count with the lowest weight.

In any case, it was surprising to find that a relative index of escapement led to a precise estimate of the absolute spawning abundance in approach II (Table 10). In fact the fit is so good that the model is likely over-parameterized. In other words, the extremely close fit is because of the strong influence from λ_I and the large number of parameters being utilized to describe the data. Weighting the aerial index at one means the uncertainty around the index is equivalent to that found in the catch-age compositions. Since the aerial index covers a relatively small area and is thus only a sample of the true spawning abundance, I suspect that the variability (and potential bias) in the aerial index is larger than in the catch-age data. However, the weight chosen decreased the patterns in the residuals and still allowed the model to describe the catch-age information. In addition, the sheer number of descriptive parameters may enable this model to fit almost any aerial index. Nevertheless, studies that identify an absolute estimate of escapement or provide a more representative index of the entire escapement would help validate the catch-age model.

The foundation of this age-structured model centers on minimizing the residuals between the observed and estimated catch-age compositions. The model's fit to the commercial catch is exemplary; nearly all of the observed values fall within the bounds of their corresponding estimates and the CV's are relatively small, especially approaches II and IV— with the majority of their CV's less than 20%.

In 1982 and 1986 the model under-estimated the catch (Figures 8 and 9). The total return in these years was small relative to the total catch, and the model's exploitation rate wasn't sufficient enough to provide for the catch. However, if the model were to increase the exploitation rate any further, the possibility of negative escapement values could take place. Since the model was constrained to produce positive parameter estimates, the increase in exploitation could not occur. In this case, the brood-years that comprise the returns in question may be under-estimated, forcing the model to take a large proportion of the return. In other words, a larger return and the same exploitation rate would increase the catch without diminishing the escapement.

The only observed values greater than the upper limits of the confidence intervals are in 1987. The observed catch is fairly small so one would expect a relatively small exploitation rate. However, the estimated exploitation fractions are substantial (0.57, 0.72, 0.55, and 0.58 for approaches I, II, III and IV, respectively), which resulted in an over-estimate of the catch. One explanation may be autocorrelated catch data. The observed pooled and commercial catch data are significantly autocorrelated: first order autocorrelations equal 0.67 with $p < 0.001$ and 0.76 with $p < 0.001$, respectively so a large catch tends to be followed by another large catch. In non-linear least squares estimation, a degree of autocorrelation is expected among the estimates, as long as it's not significant. In this case, the catch data is autocorrelated and because the model fits the data well, the subsequent catch estimates are too.

The recreational and subsistence catch-age data, coupled with commercial information, completes the foundation for approach III. Again, all of the observed values fall within the estimated confidence intervals; however, the small sample sizes increased the variability of these catch-age and total catch estimates (Figure 10). I believe a substantial increase in the number of salmon sampled from these fisheries would allow the model to describe these fisheries with less variation and most certainly improve the stratified approach's population estimates. However, the costs accrued to collect these samples should be weighed against the benefits of obtaining a larger sample size.

The estimates of escapement derived from the catch-age model are a crucial part of forecasting returns because the escapement from recent years is required to estimate recent brood-years. A reliable estimate of the spawning abundance would allow managers to project the return under a variety of spawner-recruit relationships and exploitation scenarios. A mark-recapture experiment in 1999 estimated the escapement after commercial fishing to be 32,090 (Evenson and Wuttig 2000). When the catch from the remaining fisheries is accounted for, the estimated escapement after all fisheries is 16,386. The escapement estimates from 1999 from all four approaches (14,836-19,019) are comparable to the 1999 mark-recapture estimate (Tables 9-12). Estimates of escapement from 1980-1998 are similar among the four approaches, suggesting robust parameter estimates. Even though the CV's surrounding approach IV (time-varying) are large, the comparison tests suggest it returns more accurate parameter estimates (Table 14). In contrast, the large CV's and comparison tests associated with approach I (commercial) diminishes my confidence in the ability of this approach to predict future returns. The escapement estimates from the remaining approaches, on the other hand, have reasonable CV's and appear to be unaffected by the possible compounding error caused by the hierarchical structure of the catch-age formulas.

This model produced robust and plausible estimates of escapement in relation to the historical catch and aerial index data. Estimates were simple to obtain compared to extensive mark-recapture experiments and cost-demanding weirs. In addition, the relatively small CV's from approach II suggest that measurement errors in the age-composition that produced the estimates of escapement were accounted for in the model. The larger CV's from approach I are a result of the limited catch-age information, whereas approach IV's large CV's likely stem from the relaxation of the constant proportion returning. The ability of this catch-age model to estimate escapement in an accurate, relatively precise, and cost-effective (minimal field work and computer time) manner is an advantage for fisheries managers because decisions regarding salmon fisheries are complicated and often based on unreliable measures of spawning abundance and budget constraints.

The close connection between the catch-age model formulae enabled me to estimate the total return from information about the observed catch and the escapement index. The return estimates follow the same pattern as the escapement, which is to be expected considering their connection to each other. Approaches I and IV have the largest CV's and the CV's for the other two are nearly identical (Tables 9-12). Thus, the only major difference between the return and escapement estimates across approaches is the decrease in the CV's.

Escapement CV's from approaches I and IV were large, but the CV's from the return estimates are relatively small (Tables 9 and 12). This is surprising because escapement is the return minus the catch. Relatively small CV's around the catch and return estimates should provide precise estimates of escapement, as in approach II. This precision may be a consequence of assuming that return proportions at age are constant over time. The large escapement CV's from approach I may have occurred because the return estimates are internal to the model; whereas the escapement estimates are determined after the recreational and subsistence catches are subtracted from the number of fish remaining after commercial fishing. In contrast, return estimates from approaches III and IV are internal and may be more susceptible to estimated changes in the return proportions, which subsequently affect estimates of escapement. Again, the comparison tests suggest that approach IV provides the best fit to the catch and aerial index data. Given that the escapement equals the return minus the catch, I am confident in approach IV's ability to provide more accurate, albeit less precise estimates of escapement and total return.

The return CV's from approaches II, III, and IV are smaller than those from approach I. The small CV's imply precise return estimates representative of the observed data. This stems from the fact that all of the catch-age information was utilized to determine the return and escapement estimates instead of just the commercial data.

Choosing the Best Model

The ability of the model to describe the catch and escapement index is evident in that each approach's estimates encompass nearly all of the observed values (Figures 7-10). The lack of a pattern in the catch and escapement index residuals implies a good overall fit to the catch-age model (Figure 11).

In contrast, a positive trend is seen in the spawner-recruit residuals (Figure 11). This result is a consequence of the weighting assigned to the spawner-recruit relationship. Since the spawner-recruit residuals equal the model's brood-year return minus a predicted Ricker brood-year return, increasing the spawner-recruit weight sufficiently would completely eliminate the difference between the two estimates. The Ricker relationship is internal to the model; therefore, the amount of variation explained can be improved by increasing the influence, λ_F, on the spawner-recruit RSS. This was not done to a large degree because very little is known about the Copper River chinook's spawner-recruit relationship. By design, the Ricker relationship was utilized mainly to provide a constraint for the model's brood-year returns without forcing the model to strictly follow the relationship.

Model uncertainty is often used to determine the value of a particular assessment model. In my case the RMSE was used to provide a measure of model uncertainty. All four approaches displayed similar patterns of RMSE around parameter estimates; however, the RMSE's from approach II and IV are less than approaches I and III.

Combining catch-age information from all three fisheries seems to improve upon model estimates.

One explanation for the smaller RMSE values from approaches II and IV is the addition of catch-age information from the recreational and subsistence fisheries without having to estimate more parameters. In other words, approach I lacks the ability to account for measurement error in the recreational and subsistence catch. Even though the approach III compensates for this lack of information, the addition of separate selectivity and exploitation parameters greatly increases the complexity of the model.

Because the ADF&G manages the Copper River chinook salmon through BEG's, a spawner-recruit relationship that describes the number of recruits per spawner is beneficial. The true relationship is a stochastic phenomenon, which means one can only describe a spawner-recruit curve, not predict it (Hilborn and Walters 1992, p. 255). A thorough description allows managers to estimate the level of escapement required to produce the MSC, which is mandated by the Alaska state constitution. Furthermore, managers could forecast returns with increased confidence, in turn allowing them to set larger catch quotas in years with large returns without jeopardizing the escapement goal and future returns.

Therefore, even though the lack of fit can be explained by the amount of influence placed on the spawner-recruit relationship, the central question is whether or not to derive optimal escapement from this relationship. Estimates of optimal escapement are 15,311, 14,388, 14,868, and 19,711 for approaches I, II, III, and IV, respectively. A combination of factors can influence a model's estimate of optimal escapement: (1) time-series bias;

(2) measurement errors in escapement; (3) lack of contrast in spawning abundance; and (4) stock structure.

Hilborn and Starr (1984) found that even in the absence of measurement errors, Ricker spawner-recruitment parameters still exhibit a bias. This bias, known as time-series bias, stems from the fact that the independent variable, spawning abundance, is not independent of the process errors around the mean spawner-recruitment relationship. Positive process errors lead to large escapements later in time, and negative errors lead to low escapements. In other words, one's estimate of average recruitment would be biased upward for low spawning abundances and downward for high spawning abundances. Furthermore, Hilborn and Walters (1992, p. 291) believe this bias is at its worst when there is no contrast between the estimates of escapement for each year — when instead of being proportional on average to spawning abundance, recruitment will appear to be independent of the number of spawners. Optimum escapement subsequently will be under-estimated.

Obtaining reliable measures of escapement and subsequent recruitment is arguably the most challenging problem an assessment biologist endures. Walters and Ludwig (1981) verified a true linear spawner-recruit curve could be altered with the addition of relatively small measurement errors. Hilborn and Walters (1992, p. 288) demonstrated how these measurement errors increase the spread of spawner-recruit observations, which in turn causes the slope of the spawner-recruit relationship to appear smaller, and possibly independent of one another.

Studies on Alaska salmon populations suggest the productivity parameter, α, lies between the values of 3.0 and 9.0 (Quinn and Eggers 2001). Research on large chinook salmon systems, such as the Stikine and Taku rivers, determined α to be 2.6 and 10.2, respectively (Bernard et al. 2000; McPherson et al. 2000). I believe measurement errors may have been partially responsible for the appearance of independence in Figure 13, which could occur if the model over-estimated the slope (α) at low levels of escapement. This would explain the relatively large productivity parameters (10.7, 11.3, 11.1, and 9.3 for approaches I, II, III, and IV, respectively), which allow the model to produce large recruitments even when spawning abundance is low. However, compared to the Taku River, which has a larger population than the Stikine and is more comparable to the Copper, the α is within reason.

Another possibility for the large productivity parameters may be a result of the regime shift in the mid-1970's. Evidence has shown that during this time there was a significant change in the physical and biological conditions of the Northeast Pacific Ocean (Graham 1994). Adkison et al. (1996) suggest that a shift from low to high productivity in eight out of the nine sockeye salmon stocks from Bristol Bay, Alaska are related to climate-driven changes in oceanographic processes. Unfortunately, it is difficult to detect major changes in salmon production as they occur, and it's almost impossible to forecast them because there is a lack of understanding about the complex oceanographic processes that influence salmon survival (Peterman et al. 2000). Therefore, it's entirely possible the recruitment estimates in later years are higher because of this shift in the oceanographic environment. In which case, the optimal escapement at the current time may be higher than the level returned by the entire time series.

In general, spawner-recruit assessments follow the assumption of stationarity — that the particular spawner-recruit relationship chosen doesn't vary over time. Obviously, this is not true; however, understanding the causes of nonstationarity will ensure a thorough spawner-recruit analysis. Factors 3 and 4 from above are components of nonstationarity.

Hilborn and Walters (1992, p. 288) believe the amount of bias caused by measurement errors depends on the magnitude of the errors and the amount of contrast in the escapement. To understand the influence spawners have on recruitment, a wide range of escapement levels needs to be employed. Furthermore, the levels need to encompass extreme low and high values to overcome the effects of the time-series bias explained earlier. They believe spawning abundances that fluctuate no more than 2-4 times will cause severe biases. In my model, the plots of recruits versus spawners imply relatively good contrast, especially in approach IV. The CV's surrounding the escapement estimates from approach II are the lowest of the constant proportion models, which suggests the magnitude of the measurement errors is small. In contrast, the CV's from approaches I and IV are relatively high, which suggests measurement errors may be influencing escapement estimates. I believe the CV's are higher for approach I, because the recreational and subsistence catch has no effect on the model's structure. The increase in approach III's CV's is from estimating more population parameters. In approach IV the same information is used as approach II, so measurement error is probably not the cause. I believe the increase in CV's stem from relaxing the constant proportion assumption. Therefore, the increased model complexity going from approach II to IV provided more accuracy with less precision.

The concept of stock structure is found throughout population dynamics. In this case, the Copper River chinook salmon population is made up of a number of different stocks that are spatially and temporally divided during spawning. This division produces relatively isolated populations with their own distinct spawner-recruit curve (Hilborn and Walters 1992, p. 293). Hilborn (1985) found that when a spawner-recruit curve represents a population made up of different stocks, a period of over-fishing would decrease the abundance and contribution of less productive stocks, thereby making the remaining stock appear more productive but of smaller size.

Radio-telemetry studies on the Copper River have shown a difference in the in-river run-timing of chinook salmon stocks (Evenson and Wuttig 2000). Up-river stocks are the first to arrive on their spawning grounds, whereas lower river stocks arrive last. If this run-timing holds true at the mouth of the Copper River, where fish are vulnerable to the commercial fishery, then certain stocks that arrive earlier may be subject to less exploitation because the fishery has yet to open. Stocks that arrive later will be subjected to a higher rate of exploitation because the fishery is open. Furthermore, even if the early stocks arrive when the fishery is open, the catch per unit effort (CPUE) typically starts out low, reaches a peak then tapers off, implying differential exploitation. Currently, ADF&G is relying on a coded wire-tagging project to determine whether or not there is significant differential pressure on stock components. I believe stock structure coupled with high exploitation rates may be imparting the illusion that relatively small escapements will provide for large brood-year returns. This is evident in the comparatively large productivity parameters (α) returned by the model.

The model estimates of total brood-year returns were consistently above the Ricker replacement line (Figure 13). This could be the result of managing the fishery to provide for the MSC. The point (R_m, S_m) at which MSC occurs refers to the escapement level S_m, also known as optimal escapement, that produces the largest sustained catch. This point on the Ricker curve is always above the replacement line; therefore, because the fishery is managed for the MSC, model estimates of brood returns should reflect this management strategy. Another explanation may be high productivity in the last few years due to the regime shift or overestimation of recruitment and/or spawning stock, such as underestimating the proportion, γ, due to the uncertainties in the aerial index.

In the end, consideration of the previous factors leads me to believe the optimal escapement and its resultant MSC can be derived from the model. The time-series bias that may cause a model to under-estimate optimal escapement is not augmented by the lack of contrast in spawning abundance. Although stock structure is important to consider, there is no substantial evidence that it pertains to this population. Furthermore, the minimal effects of measurement error suggest that drawing accurate optimal escapement and subsequent exploitation rates from this analysis is reasonable.

ADF&G's main concern is to provide for the MSC, but the uncertainty surrounding their estimate of optimal escapement forces them to manage for the minimum probability of making a mistake. The current BEG is from 28,000 to 56,000 chinook salmon. This range was derived from an optimal escapement of 35,000, which replaced the previous goal of 17,500 because ADF&G believes such a goal is unable to sustain the level of harvest experienced over the past 22 years. They determined this by setting up a what-if scenario with different escapement goals at the current population level (Matt Evenson, ADF&G, 1300 College Road Fairbanks, AK 99701, personal communication). Based on factors such as time-series bias, measurement errors, and nonstationarity, I believe ADF&G was correct in setting a more precautionary approach to the escapement goal by establishing a range of 28,000 to 56,000 chinook salmon.

Many different approaches, including the methods used in this analysis, have produced optimal escapement goals at similar exploitation levels that parallel the previous goal of 17,500 (Matt Evenson, personal communication). However, when compared to another large chinook salmon system such as the Stikine River, each approach exhibits a higher estimated return per spawner at optimal escapement (Bernard et al. 2000).

ADF&G may be under-estimating the Copper River chinook salmon's productivity. While my estimates of the number of recruits per spawner at optimal escapement (4.9, 5.1, 5.0, and 4.3 for approaches I, II, III, and IV, respectively) are larger than the Stikine River (1.7), they are nearly identical to the estimates determined in the Taku River (4.6) (McPherson et al. 2000). Furthermore, I utilized a variety of different approaches that suggest recruit per spawner estimates are robust. The conservative nature of ADF&G managers may have led them to abandon methods that produce large average recruits per spawner, because other comparable populations do not share this characteristic.

In the end, my model's optimal escapement range ($\approx$ 16,000 to 32,000) overlaps the independent range (28,000 to 56,000) produced by ADF&G. Unfortunately, there are always uncertainties surrounding the estimates of optimal escapement. I believe the true optimal escapement lies between the point estimates of ADF&G's conservative approach (35,000) and this catch-age model's more liberal approach ($\approx$ 20,000). However, similar estimates across all four approaches justifies treating the model's estimates of optimal escapement as a lower bound of ADF&G's conservative BEG. This should account for any time-series bias and stock structure influence, while providing a minimum escapement threshold based on information about the population.

The majority of researchers and mangers believe robust and plausible estimates are important when describing a model's utility. Based on my results, population parameter estimates are robust across and within approaches. This implies the model has the ability to describe a variety of different data sources under dissimilar methods. However, there is a relatively small range of λ values that produce similar results without residual patterns or substantial bias. Overall, each approach is insensitive to rational changes in the weighting scenario and consequently produces analogous results.

An explanation for this may be that the assembled catch-age and auxiliary time series cover an ample amount of time under a variety of different harvest strategies, policies, and environmental conditions, enabling the model to decipher the fluctuations in the total catch and the escapement index. Another possibility stems from the underlying root normal distribution used to accommodate measurement errors in the catch and escapement. Either this distribution handles the influence of measurement error, or there is very little measurement error to begin with. The very nature of aging scales and the variation between individual salmon scales leads me to believe the root normal distribution is an appropriate distribution for handling errors in salmon catch-age and escapement information.

Even though the plausibility of model estimates is an important criterion when selecting the best approach, it should never take the place of what the data is articulating. In other words, if the model's output seems implausible, one cannot disregard the results based on this alone. In this analysis the plausibility was in a sense pre-determined during the sensitivity analysis. Plausible brood-year returns were a criterion for the most appropriate weighting scenario. Since the brood-year returns provide the basis for which all of the remaining catch-age equations are derived, plausible brood returns will produce plausible parameter estimates. The model's ability to reflect the historical catch leads me to believe the model generates plausible brood-year return estimates along with catch, escapement, and population parameters.

The pairwise comparison tests indicate that the smallest amount of error surrounds approach IV's catch and escapement index (Table 14). I believe this a direct effect of approach IV's ability to estimate varying brood year proportions of the dominant age classes. The increase in the number of parameters used to optimize the objective function was warranted because the MSE associated with the catch and escapement index components from approach IV are significantly smaller than approaches II and III. I believe this stems from salmon life history characteristics; studies have suggested that life history characteristics such as length and age at maturity display significant variation between and within stocks (Hankin et al. 1993; Pyper et al. 1999). In contrast, with existing recreational and subsistence catch-age data, increasing the parameter string even further to estimate separate gear selectivities and exploitation rates for each fishery (Approach III) did not improve the model's ability to describe the data.

Forecasting Future Returns

Forecasts are used by managers in a variety of ways such as to evaluate trends in the population and to set the limits on catch. This catch-age model appears able to predict future returns (Figure 15). Estimates are analogous across all four approaches and based on the magnitude of the commercial catch are within reason. Furthermore, they coincided with the mark-recapture experiments conducted by ADF&G in 1999 and 2000. The calculations involved are straightforward, cost-effective, and can be accomplished in a relatively short period of time. However, variability in the spawner-recruit relationship and imperfect information will always place uncertainty on the forecasting process.

Fishery managers have to make decisions about important fisheries in the presence of imprecise information. They typically want to know whether or not a model is optimistic or conservative. Approach IV could be deemed optimistic compared to the other approaches because it consistently produces larger estimates of the total return. If the total return were to fall short of the predicted forecast than the escapement goal would be compromised. The conservative approach may be to just accept the uncertainties surrounding the most descriptive model. In other words, use the model as a reference and set harvest guidelines at a lower level than the model suggests to ensure the biological escapement goal will be met.

Based on the results, I think it's surprising that catch-age models are rarely used to assess and manage salmon populations. Other than Kope's (1987) work in California, this is the only catch-age model, which I'm aware of, that attempts to illustrate the complex population processes of an exploited chinook salmon population. This model will assist managers in making decisions about the Copper River chinook salmon, because it incorporates a variety of information sources, accounts for uncertainty, and provides an estimate of optimal escapement and its corresponding exploitation level. Furthermore, the lack of apparent patterns in the catch residuals plus the ability to track trends in the catch and escapement index indicates the model has a good fit to the data.

CONCLUSIONS

Even though catch-age models are rarely used in salmon fisheries management, development of this model allowed me to:

1. establish an integrated age-structured assessment model of Copper River chinook salmon that reliably estimates the total return and escapement;
2. determine that combined catch-age information from all three fisheries will provide a robust model approach;
3. decide that brood-year proportions, at least for dominant age-classes, should be estimated annually;
4. examine the effects of various weighting scenarios, which are influenced by perceptions of the data sources, on the model's parameter estimates;
5. accurately forecast the total return; and,
6. provide managers with a method to derive optimal escapement and its associated MSC and level of exploitation.

Future studies need to stress the importance of: (1) collecting catch-age information from all three fisheries to ensure a thorough account of the catch-age composition, (2) incorporating new forms of auxiliary data, such as the ongoing mark-recapture experiments and the proportion caught in the subsistence dipnet fishery applied to the total sonar count, to be used for model validation and/or a superior index of escapement, and (3) running simulation studies where spawning abundance is deliberately controlled at experimental levels of escapement will elucidate how severe any biases might be. Greater application of this model should lead to improvements in the management of other salmon systems by integrating a variety of information sources into their decision making process.

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