

Spawner–Recruit Analyses and Escapement Goal Recommendation for Kenai River Late-Run Sockeye Salmon

by

James J. Hasbrouck

William D. Templin

Andrew R. Munro

Kathrine G. Howard

and

Toshihide Hamazaki

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Alaska Department of Fish and Game

Divisions of Sport Fish and Commercial Fisheries



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Weights and measures (metric)		General		Mathematics, statistics	
centimeter	cm	Alaska Administrative		<i>all standard mathematical</i>	
deciliter	dL	Code	AAC	<i>signs, symbols and abbreviations</i>	
gram	g	all commonly accepted abbreviations	e.g., Mr., Mrs., AM, PM, etc.	alternate hypothesis	H _A
hectare	ha			base of natural logarithm	e
kilogram	kg			catch per unit effort	CPUE
kilometer	km	all commonly accepted professional titles	e.g., Dr., Ph.D., R.N., etc.	coefficient of variation	CV
liter	L			common test statistics	(F, t, χ^2 , etc.)
meter	m	at	@	confidence interval	CI
milliliter	mL	compass directions:		correlation coefficient	
millimeter	mm	east	E	(multiple)	R
		north	N	correlation coefficient	
		south	S	(simple)	r
		west	W	covariance	cov
		copyright	©	degree (angular)	°
		corporate suffixes:		degrees of freedom	df
		Company	Co.	expected value	E
		Corporation	Corp.	greater than	>
		Incorporated	Inc.	greater than or equal to	≥
		Limited	Ltd.	harvest per unit effort	HPUE
		District of Columbia	D.C.	less than	<
		et alii (and others)	et al.	less than or equal to	≤
		et cetera (and so forth)	etc.	logarithm (natural)	ln
		exempli gratia		logarithm (base 10)	log
		(for example)	e.g.	logarithm (specify base)	log ₂ , etc.
		Federal Information		minute (angular)	'
day	d	Code	FIC	not significant	NS
degrees Celsius	°C	id est (that is)	i.e.	null hypothesis	H ₀
degrees Fahrenheit	°F	latitude or longitude	lat or long	percent	%
degrees kelvin	K	monetary symbols		probability	P
hour	h	(U.S.)	\$, ¢	probability of a type I error	
minute	min	months (tables and		(rejection of the null	
second	s	figures): first three		hypothesis when true)	α
		letters	Jan,...,Dec	probability of a type II error	
		registered trademark	®	(acceptance of the null	
		trademark	™	hypothesis when false)	β
		United States		second (angular)	"
		(adjective)	U.S.	standard deviation	SD
		United States of	USA	standard error	SE
		America (noun)	United States	variance	
		pH	Code	population	Var
hydrogen ion activity		U.S.C.	use two-letter	sample	var
(negative log of)			abbreviations		
parts per million	ppm	U.S. state	(e.g., AK, WA)		
parts per thousand	ppt, ‰				
volts	V				
watts	W				

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**SPAWNER-RECRUIT ANALYSES AND ESCAPEMENT GOAL
RECOMMENDATION FOR KENAI RIVER LATE-RUN
SOCKEYE SALMON**

by

James J. Hasbrouck
Alaska Department of Fish and Game, Division of Sport Fish, Anchorage

William D. Templin, Andrew R. Munro
Alaska Department of Fish and Game, Division of Commercial Fisheries, Anchorage

Kathrine G. Howard
Alaska Department of Fish and Game, Division of Sport Fish, Anchorage

and

Toshihide Hamazaki
Alaska Department of Fish and Game, Division of Commercial Fisheries, Anchorage

Alaska Department of Fish and Game
Division of Sport Fish, Research and Technical Services
333 Raspberry Road, Anchorage, Alaska, 99518-1565

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James J. Hasbrouck (retired)
Alaska Department of Fish and Game, Division of Sport Fish
333 Raspberry Road, Anchorage, AK 99518 USA

William D. Templin, Andrew R. Munro
Alaska Department of Fish and Game, Division of Commercial Fisheries,
333 Raspberry Road, Anchorage, AK, 99518 USA

Kathrine G. Howard
Alaska Department of Fish and Game, Division of Sport Fish,
333 Raspberry Rd, Anchorage AK 99518 USA

and

Toshihide Hamazaki
Alaska Department of Fish and Game, Division of Commercial Fisheries,
333 Raspberry Road, Anchorage. AK 99518 USA

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ABSTRACT

The current sustainable escapement goal (700,000–1,200,000) for Kenai River late-run sockeye salmon was established in 2011. For this escapement goal review, the escapement time series and production data were updated through 2018. The fit of 6 spawner–recruit models to data from brood years 1968–2012 and brood years 1979–2012 was examined. Although the classic Ricker model was determined the most appropriate to use given the data, all brood years were estimated to have replaced themselves, which compromised obtaining accurate and precise estimates of most model parameter estimates and biological reference points, including a scientifically defensible estimate of maximum sustained yield. Markov-type yield tables were constructed to evaluate yields at different levels of escapement. We recommend the sustainable escapement goal for Kenai River late-run sockeye salmon be revised to 750,000–1,300,000 fish because the analyses indicated escapements in this range will likely provide better yields.

Keywords: BEG, biological escapement goal, brood interaction, Kenai River, maximum sustained yield, MSY, recruits, recruits per spawner, Ricker model, SEG, sustainable escapement goal, sockeye salmon, *Oncorhynchus nerka*, spawner–recruit models

INTRODUCTION

The Kenai River is a glacially occluded river that drains approximately 5,200 km² of the western Kenai Peninsula and produces the largest of 4 major sockeye salmon (*Oncorhynchus nerka*) runs (Figure 1) in upper Cook Inlet (UCI); the other 3 are the Kaslof, Susitna, and Crescent Rivers. The Kenai River has 2 runs of sockeye salmon, an early run that enters the river from late May through early July and a late run that enters the river from late June through late August. From 1976 to 2008, estimated total UCI sockeye salmon runs ranged from 1,800,000 to 12,100,000, while estimated Kenai River late-run sockeye salmon runs ranged from 651,000 to 8,600,000 (Tobias and Willette 2013). Kenai River late-run sockeye salmon rear as juveniles in Hidden, Kenai, Skilak, and Russian Lakes, with most juvenile rearing assessment conducted in glacially turbid Kenai and Skilak Lakes (DeCino and Willette 2014). Radiotelemetry studies (Willette et al. 2012) indicated that 35–42% of late-run sockeye salmon spawned in the mainstem Kenai River between the Russian River confluence and Skilak Lake (Figure 1). Another 10–20% spawned in an approximately 16 km segment of the Kenai River immediately below Skilak Lake, while 11–21% spawned in upper tributaries of the watershed. The majority of early-run sockeye salmon, which number in the low hundred thousand, spawn in upper tributaries of the watershed.

Kenai River late-run sockeye salmon are harvested in mixed-stock gillnet fisheries in Cook Inlet, a personal use fishery at the river mouth, and inriver sport and federal subsistence fisheries. Management of these sockeye salmon fisheries is based upon achieving spawning escapements to achieve a specific escapement goal. The first escapement goal for Kenai River late-run sockeye salmon of 150,000 fish, established in 1968, was based on the belief that Russian River fish counted at a weir contributed on average 30% to the entire Kenai River escapement (Fried 1994). The escapement goal has been reviewed and increased several times since 1968 as the Alaska Department of Fish and Game (ADF&G, department) collected additional data on abundance and production of this stock.

The current sustainable escapement goal range of 700,000 to 1,200,000 was implemented by ADF&G in 2011 (Fair et al. 2010). The escapement goal was based on a brood-interaction simulation model in which returns per spawner were a function of spawner abundance in the brood year and the previous year (Carlson et al. 1999) using adult sonar data for brood years 1969–2005. The range approximately represented the escapement that on average will produce 90–100% of the model estimate of maximum sustained yield (MSY; Fair et al. 2010).

ADF&G reviews escapement goals corresponding to the Alaska Board of Fisheries (BOF, board) triennial cycle for considering area regulatory proposals. This report documents a review of the escapement goal for Kenai River late-run sockeye salmon. The review was based on the *Policy for the Management of Sustainable Salmon Fisheries* (SSFP; 5 AAC 39.222) and the *Policy for Statewide Salmon Escapement Goals* (EGP; 5 AAC 39.223). The BOF adopted these policies into regulation during winter 2000–2001 to ensure that the state’s salmon stocks are conserved, managed, and developed using the sustained yield principle. Three important terms defined in the SSFP follow:

Biological Escapement Goal (BEG): means the escapement that provides the greatest potential for maximum sustained yield; BEG will be the primary management objective for the escapement unless an optimal escapement or inriver run goal has been adopted; BEG will be developed from the best available biological information, and should be scientifically defensible on the basis of available biological information; BEG will be determined by the department and will be expressed as a range based on factors such as salmon stock productivity and data uncertainty; the department will seek to maintain evenly distributed salmon escapements within the bounds of a BEG;

Maximum Sustained Yield (MSY): means the greatest average annual yield from a salmon stock; in practice, MSY is achieved when a level of escapement is maintained within a specific range on an annual basis, regardless of annual run strength; the achievement of MSY requires a high degree of management precision and scientific information regarding the relationship between salmon escapement and subsequent return; the concept of MSY should be interpreted in a broad ecosystem context to take into account species interactions, environmental changes, an array of ecosystem goods and services, and scientific uncertainty; and

Sustainable Escapement Goal (SEG): means a level of escapement, indicated by an index or an escapement estimate, that is known to provide for sustained yield over a 5 to 10 year period, used in situations where a BEG cannot be estimated or managed for; the SEG is the primary management objective for the escapement, unless an optimal escapement or inriver run goal has been adopted by the board; the SEG will be developed from the best available biological information; and should be scientifically defensible on the basis of that information; the SEG will be determined by the department and will take into account data uncertainty and be stated as either a “SEG range” or “lower bound SEG”; the department will seek to maintain escapements within the bounds of the SEG range or above the level of a lower bound SEG.

METHODS

STOCK ASSESSMENT DATA

The following description of Kenai River late-run sockeye salmon stock assessment data is largely from Clark et al. (2007a), updated to summarize new or modifications to existing assessment projects since 2005. The Kenai River late-run sockeye salmon escapement goal is based on reconstructions of the total return by brood year and the estimated number of wild sockeye salmon spawning within the watershed. Reconstructions combine information on escapement and

stock-specific harvest by age. Various data sources have been used to construct brood tables for Kenai River late-run sockeye salmon beginning with brood year 1968 (Tarbox et al. 1983), but the most consistent and least biased methods have been applied since brood year 1979 (Tobias and Willette 2013). Unaccounted uncertainty remains for these reconstructions, particularly related to changes in escapement assessment methodology over time and challenges in apportioning harvest by stocks and age.

Escapement

The number of wild sockeye salmon spawning within the watershed has been estimated from the total sonar counts of sockeye salmon escapement minus (1) the number of sockeye salmon harvested in inriver fisheries upstream of the sonar and (2) the number of hatchery-origin sockeye salmon enumerated at a weir on Hidden Creek (Tobias and Willette 2013). The number of sockeye salmon harvested in sport fisheries upstream of the Kenai River sonar site has been estimated annually using statewide harvest surveys (SWHS; Jennings et al. 2015) and creel surveys conducted during the fishery (King 1995, 1997). The inriver federal subsistence fishery began in 2007 with average annual harvest of less than 500 fish (Begich et al. 2017). Prior to 1999, the number of hatchery-origin sockeye salmon passing the weir on Hidden Creek was estimated from the ratio of hatchery to wild smolt by brood year (Tobias and Willette 2013). After 1999, the number of hatchery-origin sockeye salmon passing this weir was estimated from recovery of otolith thermal-marked salmon; however, for UCI escapement goal reviews since 2017 (Erickson et al. 2017), the number of hatchery-produced sockeye salmon passing the Hidden Creek weir was not subtracted from the sockeye salmon sonar count because hatchery-produced Hidden Lake fish were not enumerated in the commercial, sport, or personal use harvests, and their contribution to Kenai River sockeye salmon sonar estimates were very small (1981–2014 average 1.5%).

Since 1968, sonars operated on the Kenai River at river mile 19.2 during July and early August each year were used to estimate numbers of sockeye salmon migrating into the Kenai River (Glick and Willette 2018). Sonar technology has been used because high glacial turbidity precludes visual enumeration of migrating salmon in this river. The use of sonar to estimate the inriver salmon migration began on the Kenai River in 1968 with the use of multiple transducer systems (MTS), transducers arrayed linearly in up-looking positions (Namtvedt et al. 1978). Side-looking Bendix sonar units proved more practical and were implemented on both banks of the Kenai River starting in 1978. MTS and Bendix sonar performances were compared, and it was determined that MTS salmon passage estimates were likely biased low relative to Bendix-based estimates; discrepancies between sonar estimates were not fully rectified (Namtvedt et al. 1978).

Dual-frequency identification sonar (DIDSON; Belcher et al. 2001, 2002) was used for the first time to estimate salmon migration on the south bank of the Kenai River in 2007 and on the north bank in 2008. Between 2004 and 2007, a study compared sockeye salmon abundance estimates using the historical Bendix sonar and the more modern DIDSON sonar on the Kenai River (Maxwell et al. 2011). In addition, mark–recapture estimates of sockeye salmon abundance in 2006–2008 indicated DIDSON estimates gave relatively unbiased estimates of abundance during the 3 years of the study (Willette et al. 2012). Based on this information, historical daily Bendix sonar abundance estimates were converted to DIDSON units (Fair et al. 2010). Fish wheel catches have historically been used to apportion sonar counts to species when the fraction of other species in catches exceeded 5%. This typically occurred only in early August during even-numbered years

when pink salmon *O. gorbuscha* were abundant. Fish wheel catches of sockeye salmon were also used to collect age data of the inriver run.

Stock-Specific Harvest

A variety of sockeye salmon stocks are harvested in mixed-stock commercial fisheries in UCI (Marston and Frothingham 2019). Commercial harvests were compiled from ADF&G fish ticket information. From 1969 to 2004, a weighted age composition apportionment model was used to estimate stock-specific harvests of sockeye salmon by age in commercial gillnet fisheries (Tobias and Willette 2013). This method assumed age-specific harvest rates were equal among stocks in the gillnet fisheries (Bernard 1983) and was dependent upon accurate, precise escapement and age composition estimates for all contributing stocks. Prior to 1979, in addition to sonar used on the Kenai River mentioned earlier, upstream oriented sonar arrays were also used to estimate escapement on the Kasilof River, and peak ground survey counts on 23 streams were used to index escapements in the Susitna drainage. In addition, age sample collection in commercial harvests and escapements prior to 1979 was sporadic and limited (Waltemyer 1997). Beginning in 1979, side-looking sonars were used to enumerate sockeye salmon to assess escapement and fishwheels were used to collect scale samples for age data on all major sockeye-producing river systems in UCI (Glick and Willette 2018). Sampling efforts were modified so age-composition of sockeye salmon commercial harvests were estimated annually using a stratified systematic sampling design (Tobias et al. 2013). A minimum sample ($n = 403$) of readable scales has been used to estimate the age composition of sockeye salmon in each stratum within 5% of the true proportion 90% of the time (Thompson 1987).

The precision of the weighted age composition apportionment harvest estimates is questionable and the estimates are undoubtedly biased. Most fish included in recruitment estimates for Kenai River late-run sockeye salmon come from these catch allocation estimates because there are more fish in the commercial harvest than in the escapement. However, it is unknown if the bias is substantial, varies across years, or if the historical recruit estimates are unsound. Since 2005, the primary means for estimating stock-specific sockeye salmon commercial harvests has been the use of genetic markers (Barclay 2017, 2019). Incorporating genetic-based stock-specific harvests into the brood table assumes the age composition of stock-specific harvests was the same as stock-specific escapements (i.e., no age-dependent gear selectivity). The weighted age composition apportionment model was used to estimate stock-specific commercial harvests by age for sockeye salmon runs in 2018 rather than genetic stock identification because the estimates based on genetics were unavailable when analyses reported here were done. To assess 2018 escapement as part of the apportionment model, we used DIDSON estimates for Kenai River and Kasilof River sockeye salmon, and expanded sockeye salmon weir counts at Judd, Chelatna, and Larson Lakes based on a relationship between weir counts at these lakes and mark–recapture estimates of Susitna River sockeye salmon escapement (Erickson et al. 2017).

Sockeye salmon harvested in the Kenai River downstream of the sonar site were included to estimate total annual runs and brood year returns by age. The number of sockeye salmon harvested in sport fisheries downstream of the Kenai River sonar site has been estimated annually using statewide harvest surveys (SWHS; Jennings et al. 2015) and creel surveys conducted during the fishery (King 1995, 1997). Harvests in the personal use fishery at the mouth of the Kenai River were estimated from fishery permit data (Dunker 2018; A. St. Saviour, Sport Fish Biologist, ADF&G, Palmer, personal communication). Age data from sockeye salmon captured in the fishwheels at the sonar site were used to estimate age composition of these inriver harvests.

SPAWNER-RECRUIT MODELS

Consistent with methods used previously (Clark et al. 2007a, Erickson et al. 2017), 2 sets of analyses were conducted to examine the fit of 6 spawner–recruit models to the Kenai River late-run sockeye salmon data (Appendix A1), with recruits being returning adults. In the first set, the 6 models were fit to the data from brood years 1968–2012 because data from 1968–1978 brood years were used in earlier spawner–recruit analyses for this system (Clark et al. 2007a; Erickson et al. 2017). In the second set, the 6 models were fit to data from brood years 1979–2012 because more consistent methods were used to estimate salmon escapements and stock-specific harvests in commercial fisheries during this period (Clark et al. 2007a). The models examined were classic Ricker, autoregressive Ricker, Beverton-Holt, Deriso-Schnute, and additive and multiplicative brood interaction Ricker.

The classic Ricker model provides for compensation at high stock size (Ricker 1954, 1975; Hilborn and Walters 1992; Quinn and Deriso 1999):

$$R_t = \alpha S_t \exp[-\beta S_t] \exp(\varepsilon_t), \quad (1)$$

where R_t is number of recruits, S_t is number of spawners (i.e., escapement), α is a density-independent parameter, β is a density-dependent parameter, ε is a lognormal process error with a mean of zero and a constant variance σ^2 , and t indicates the brood year. The Ricker model assumes over-compensative density-dependent effects. This results in a biological reference point termed carrying capacity, or spawning equilibrium (S_{EQ}), where number of recruits produced from the escapement equals the number of spawners in that escapement, with continual decline in recruits and no future yields as escapements increase beyond the carrying capacity.

To account for potential time-varying productivity, which manifests as serially correlated model residuals, an autoregressive error term with a lag of 1 year (AR(1)) was included as (Noakes et al. 1987):

$$R_t = \alpha S_t \exp[-\beta S_t] \exp(\varphi \omega_{t-1} + \varepsilon_t), \quad (2)$$

where φ is a lag-1 autoregressive parameter ($-1 \leq \varphi \leq 1$) and ω_{t-1} is a residual of the previous year. The autoregressive Ricker model assumes process errors are not independent, but serially dependent on the escapement from the previous brood year.

For this escapement goal review, we also fit a Beverton-Holt model to the data set using the methods of Quinn and Deriso (1999):

$$R_t = \frac{\alpha S_t}{1 + \beta S_t} \exp(\varepsilon_t), \quad (3)$$

which assumes compensative density-dependence. This would produce near constant recruits when the number of spawners exceeds S_{EQ} .

The Deriso-Schnute model (Deriso 1980; Schnute 1985) is an intermediate between the Ricker and Beverton-Holt models:

$$R_t = \alpha S_t (1 - \beta \gamma S_t)^{\frac{1}{\gamma}} \exp(\varepsilon_t), \quad (4)$$

where γ is a parameter ($-1 \leq \gamma \leq 0$). When $\gamma = 0$ the model corresponds to the Ricker model and $\gamma = -1$ corresponds to the Beverton-Holt model.

Several authors have examined density-dependent models that include interaction terms between brood-year spawners and prior year spawners with lags from 1–3 years (Ward and Larkin 1964; Larkin 1971; Collie and Walters 1987; Welch and Noakes 1990). However, Myers et al. (1997) examined data from 34 sockeye salmon stocks and found no evidence for brood interactions at lags exceeding 1 year. The Kenai River late-run sockeye salmon data were modified to a Ricker model used by many of these investigators with only a 1-year lag in a brood interaction additive model:

$$R_t = \alpha S_t \exp[-\beta_1 S_t - \beta_2 S_{t-1}] \exp(\varepsilon_t), \quad (5)$$

and a statistical interaction multiplicative model:

$$R_t = \alpha S_t \exp[-\beta S_t S_{t-1}] \exp(\varepsilon_t), \quad (6)$$

where S_{t-1} is number of spawners from the previous year. Both models assume density dependent effects occur not only due to individuals (i.e., eggs, fish) produced from the spawning escapement in brood year t (S_t) but also from the escapement the previous year (S_{t-1}). Sockeye salmon typically spend 1 to 2 years in freshwater habitats (e.g., nursery lakes) before migrating to the ocean. The effects of competition among juvenile fish on recruitment could be additive (additive model) or multiplicative (multiplicative model). Since 1999, the multiplicative brood interaction Ricker model has been selected for setting the escapement goal of Kenai River late-run sockeye salmon because it was thought to best describe the spawner–recruit relationship for this stock (Carlson 1999; Erickson et al. 2017).

MODEL FITTING, EVALUATION AND SELECTION

All the above models were fitted using Bayesian Markov Chain Monte Carlo (MCMC) methods using the modeling software JAGS (Lunn et al. 2013; Appendix B1). First, the models were converted to log-linear form and S_t divided by 10 to the fifth power (i.e., $S_t = S_t \times 10^{-5}$). Furthermore, for Deriso-Schnute model, parameter γ was converted to a positive term ($\gamma' = -\gamma$).

These conversions make all model estimated parameters within the range of 0 to 10, which produces better and more efficient parameter estimation. For all models, priors were set to uniform distribution of $\ln(\alpha) \sim \text{unif}(0,10)$, $\beta \sim \text{unif}(-10,10)$, $\varphi \sim \text{unif}(-1,1)$, $\gamma' \sim \text{unif}(0,1)$. Initial value for each of the model parameters were randomly selected.

Spawner–Recruit Model	Linearized form
Classic Ricker	$\ln(R_t) = \ln(\alpha) + \ln(S_t) - \beta s_t$
Autoregressive Ricker	$\ln(R_t) = \ln(\alpha) + \ln(S_t) - \beta s_t + \varphi \omega_{t-1}$
Beverton-Holt	$\ln(R_t) = \ln(\alpha) + \ln(S_t) - \ln(1 + \beta s_t)$
Deriso-Schnute	$\ln(R_t) = \ln(\alpha) + \ln(S_t) - \frac{I}{\gamma'} \ln(1 + \beta \gamma' s_t)$
Additive brood interaction Ricker	$\ln(R_t) = \ln(\alpha) + \ln(S_t) - \beta_1 s_t - \beta_2 s_{t-1}$
Multiplicative brood interaction Ricker	$\ln(R_t) = \ln(\alpha) + \ln(S_t) - \beta s_t \cdot s_{t-1}$

Each model was run for 100,000 iterations, of which the first 20,000 were discarded (i.e., burn-in). MCMC samples were drawn from the joint posterior probability distribution of all unknowns in each model. For results presented here, every 10th sample from a single Markov chain was written to disk. Diagnostic tools within R (R Development Core Team 2016), including trace plots and the Gelman-Rubin statistic (Gelman and Rubin 1992), were used to assess mixing and convergence. No major problems of convergence of the models were encountered. Interval estimates were constructed from the percentiles of the posterior distribution.

For selection of the best model relative to the other models considered, Deviance Information Criterion (DIC) was calculated. DIC is a Bayesian equivalent of Akaike's Information Criterion (AIC). For comparison of 2 models, the exponential of half the difference between the DICs of the 2 models corresponds to a likelihood ratio (i.e., likelihood ratio $\approx \exp((\text{DIC}_0 - \text{DIC}_1)/2)$ (Lunn et al. 2013). A difference of less than 5 in DIC among models does not provide definitive support of one model over another being considered (Carlin and Louis 2009).

REFERENCE POINTS AND OPTIMAL YIELD PROFILE

For each model and brood year dataset, biological reference points were estimated from corresponding model parameter estimates. Spawning abundance providing maximum sustained yield S_{MSY} was approximated by (Hilborn 1985):

$$S_{MSY} \cong \frac{\ln(a)}{\beta} (0.5 - 0.07 \ln(a)). \quad (7)$$

Sustained yield at a specified level of S was obtained by subtracting spawning escapement from recruitment:

$$Y_S = R - S = S e^{\ln(a) - \beta S} - S. \quad (8)$$

Other relevant quantities include harvest rate leading to maximum sustained yield (MSY), approximated by (Hilborn 1985):

$$U_{MSY} \cong \ln(a) (0.5 - 0.07 \ln(a)), \quad (9)$$

escapement leading to maximum production:

$$S_{MAX} = \frac{1}{\beta}. \quad (10)$$

and equilibrium spawning abundance, where recruitment exactly replaces spawners:

$$S_{EQ} = \frac{\ln(a)}{\beta}. \quad (11)$$

The probability that a given spawning escapement S would produce average yields exceeding X% (e.g., 90%) of MSY was obtained by calculating Y_S at incremental values of S for each MCMC sample, then comparing Y_S with X% of the value of MSY for that sample. The proportion P_Y of samples in which Y_S exceeded X% of MSY is an estimate of the desired probability, and the plot of P_Y versus S is termed an optimal yield probability profile (Fleischman et al. 2013).

YIELD ANALYSIS

Markov yield tables (Hilborn and Walters 1992) were developed previously to further evaluate yields at different ranges of escapement (Clark et al. 2007a; Erickson et al. 2017). In this review, we also developed a Markov yield table for Kenai River late-run sockeye salmon. We constructed

the yield table by partitioning the data into overlapping ranges of escapement and determined the mean, median, minimum, and maximum yield of each range.

ESCAPEMENT GOAL REVIEW PROCESS

An interdivisional escapement goal review team convened to review the available data, discuss analyses and results, and make an escapement goal recommendation. Appropriate data and models were systematically evaluated for further consideration in escapement goal development. Models were not considered viable for escapement goal development if parameter estimates included zero or model structure was problematic.

The escapement goal recommended in this report is the product of several collaborative meetings of the review team and other ADF&G staff. The final recommendation was achieved by consensus of review team members from both fisheries divisions.

RESULTS

ABUNDANCE, ESCAPEMENT AND HARVEST RATES

Escapement and total return data have previously been reported for brood years since 1968 (Clark et al. 2007a; Cunningham 2019). From 1968 to 2018, estimated escapements of Kenai River late-run sockeye salmon have ranged from approximately 73,000 to 2,026,000 fish (Figure 2, Appendix A1). There has been a general trend of increasing escapements through time, in part from increase in the escapement goal. Adult returns, or recruits, from the 1968–2012 escapements have also been previously reported and varied greatly from a low of nearly 431,000 from the 1969 brood year to a high of almost 10,400,000 from the 1987 brood year (Figure 2, Appendix A1). The largest run and escapement occurred in 1987, and the largest return was from the 1987 brood year. Total run since 1975 has varied greatly, from just under 500,000 in 1975 to nearly 9,400,000 in 1987 (Figure 2). Based on these estimates, Kenai River late-run sockeye salmon averaged 4.4 return-per-spawner, with return-per-spawner greater than 10.0 for the 1982, 1983, and 2000 brood years (Figure 2). Observed brood year harvest rate of Kenai River late-run sockeye salmon is relatively high (Figure 3, Appendix A1), averaging 0.70 for the 1968–2012 brood years. Harvest rate was 0.80 or greater in 12 years during this time series. This high harvest rate is somewhat expected because these fish are targeted by several fisheries in UCI.

EVALUATION OF SPAWNER–RECRUIT MODELS

Based on statistical model selection criteria, none of the 6 models examined clearly best fit the spawner–recruit data from 1979–2012 (Table 1). All 6 models have similar DIC values (Table 1) and give similar fits to the spawner–recruit curve (Figure 4). For completeness, models were also evaluated with the inclusion of early (1968–1978) spawner and recruit data as reported in previous analyses. Results of fit for the 6 models were similar for the 1968–2012 as for the 1979–2012 spawner–recruit data (Table 1, Figure 4).

Although the multiplicative brood interaction Ricker model had the lowest DIC, the difference in DIC values among the models was less than 5. As stated earlier, a difference in DIC less than 5 among models is minimal and does not indicate a preferred model. In addition, the multiplicative brood interaction Ricker is inappropriate for revising the escapement goal (previously discussed in Clark et al. 2007a) because the model: (1) structure and taking the square root of the product of 2 successive escapements are flawed; and (2) predicts maximum yield would occur only when

very high escapements one year (little fishing opportunity) are followed by very low escapements the following year in an alternating pattern, a management strategy not in the best interests to the economy of Alaska. Beverton-Holt and Deriso-Schnute models are not generally used to analyze salmon stock production but were included here as these models were examined in previous escapement goal reviews. Parameter estimates of autoregressive Ricker and additive brood interaction Ricker models included zero, indicating these models would likely not be appropriate to provide an accurate estimate of maximum sustained yield. This result indicates the added complexity of these 2 models provides no benefit over the classic Ricker and there is no evidence for autocorrelation or brood interaction in the data. There were also no apparent trends in recruitment residuals from the classic Ricker model, further indicating no correlation in recruitment among brood years (Figure 5). Consequently, the classic Ricker model, which is generally used in salmon escapement goal analysis, was deemed most appropriate for examining production of Kenai River late-run sockeye salmon.

For brood years 1979–2012, the estimate of S_{MSY} from the classic Ricker model was 1,212,000 fish and escapements in the range of 774,000 and 1,735,000 fish produce 90% of MSY (Table 1). These results are consistent with those reported previously (Clark et al. 2007a; Erickson et al. 2017; Cunningham 2019). The harvest rate leading to MSY (UMSY) estimated from the model is 0.69 (Figure 3).

Potential biases introduced using the 1968–1978 brood years did not result in very different estimates of $\ln(\alpha)$ (Table 1, Figure 6). The classic Ricker model using data from brood years 1968–2012 resulted in an estimate of S_{MSY} of 1,284,000 sockeye salmon and escapements in the range of 819,000 and 1,821,000 fish produce 90% of MSY. The classic Ricker model fits of the 2 data sets show similar patterns during the ascending portion of the spawner–recruit curve (Figure 6), although the descending portion of the curve and estimates of S_{EQ} (Figure 6) and yield (Figure 7) differ slightly.

YIELD ANALYSIS

Estimates of mean and median yield based on a yield table analysis differ little among various escapement ranges relative to the estimated minimum and maximum potential yields from the classic Ricker model using data from 1979–2012 brood years (Table 2). Median yields were slightly larger for escapement ranges with at least 750,000 sockeye salmon. Both mean and median yields decreased for escapement ranges when the upper bound was greater than 1,300,000.

The optimal yield profiles look similar for the 2 data sets (Figure 8). The plots of both data sets indicate a fair degree of uncertainty because of the relatively wide range of escapement that produce a certain probability of 90%, 85%, and 80% of MSY. The peak of the profiles was also lower for the 1979–2012 brood years than the 1968–2012 brood years.

DISCUSSION

The current SEG (700,000–1,200,000) for Kenai River late-run sockeye salmon was established in 2011. Note historical escapements have been below the current goal ~30% of the time and above the current goal ~30% of the time; by default, the upper bound of the goal has been explored without increasing it. Most of the low escapements occurred in the 1970s and 1980s when the escapement goal was much lower.

This review updated the escapement time series and incorporated production data through 2018. This review then evaluated the accuracy and precision of source data used in escapement goal development and examined the fit of 6 spawner–recruit models to data from brood years 1968–2012 and 1979–2012. Reconstruction of early year data was problematic and estimates of escapement and/or return for years prior to 1979 are likely not reliable for multiple reasons. As previously mentioned, significant differences in sonar estimation methodology occurred prior to and post 1979. Although a directed study allowed for the conversion of Bendix (1979–2007) and DIDSON estimations (2008–2018), it is unclear how MTS sonar units (1968–1978) were treated in these previously reported estimates. No comparable study to develop a conversion between MTS and Bendix sonar units was conducted. It is also unclear how harvest and total run were estimated for deriving return estimates by brood year prior to 1975. Additionally, it is likely that harvest and total run estimates (and consequently brood year return estimates) may not be accurate prior to 1979 because (1) the weighted age composition apportionment model requires accurate, precise escapement estimates for all contributing stocks to accurately and precisely apportion harvest to stock, (2) historical assessment programs did not accurately assess all escapements, (3) harvest estimates are the largest component of the run, and (4) scale collections of the harvests and escapements were sporadic and limited. Similar observations were noted by Clark et al. (2007a). Therefore, the following results and escapement goal review were based on the 1979–2012 brood year data. In the future, we recommend not using spawner and recruit estimates prior to 1979, or the multiplicative brood interaction Ricker model for previously stated reasons.

We recommend the Kenai River late-run sockeye salmon SEG be revised to 750,000 to 1,300,000 fish. Often spawner–recruit-based SEGs are recommended as some range around the estimate of S_{MSY} . The lower bound of the recommended SEG was rounded from the lower bound estimate of escapements that produce 90% of MSY (774,000 fish). The yield table indicated that, for the escapement ranges examined, yields were generally greater at a lower bound of 750,000 than 700,000 or 800,000 fish at a given level of the upper escapement bound. The recommended upper bound represents a compromise among differing pieces of information. The recommended upper bound allows the point estimate of S_{MSY} (1,212,000) to be included in the SEG range but recognizes uncertainty in the right-hand side of the spawner–recruit curve (Figure 4). There is concern the modeled upper bound estimate of escapements that produce 90% of MSY (1,735,000 fish) could be too high for an appropriate escapement goal given this uncertainty. Results from the classic Ricker model and Markov yield table using 1979–2012 brood year data indicate escapements of 750,000 to 1,300,000 sockeye salmon produce sustained yields like those of the current goal but are more likely to include spawner abundances that contain S_{MSY} . This escapement goal range is precautionary regarding recognized limitations in available stock productivity information and avoids potential risks of adversely impacting available yield. The results indicate the current Kenai River late-run sockeye salmon SEG could be less likely to maximize yields. It is recognized, however, that a wide range of escapements appear sustainable for this stock and available data does not provide enough information to clearly discern a best estimate of S_{MSY} . Finally, previous analyses found estimate of U_{MSY} was less than the observed average harvest rate, indicating the current SEG could be increased somewhat (Clark et al. 2009); increasing the SEG slightly may result in a slight reduction in harvest rate to better align average observed harvest rate with U_{MSY} .

Fisheries with a history of high harvest rates (>50% harvested annually) tend to have recruit data clustered on the left-hand side of the spawner–recruit plot. In these situations there is good

information to estimate the intrinsic rate of increase ($\ln(\alpha)$) but little knowledge to estimate (or get precise estimates of) β , MSY, S_{MSY} , or S_{EQ} (Clark et al. 2007b, 2009). This was the case with Kenai River late-run sockeye salmon (Clark et al. 2007a–b; Cunningham 2019). Because the time series of data does not contain large escapements that fail to replace themselves, there was insufficient information in the data to understand the potential for overcompensation. In this situation, the classic Ricker spawner–recruit analysis gives a precise estimate of $\ln(\alpha)$, but the estimate of β may be imprecise. Thus, estimates of S_{MSY} and S_{EQ} are imprecise and the estimates remain potentially sensitive to additional data.

Clark et al. (2007a) also pointed out the lack of information associated with large escapements as a serious technical issue with analysis of spawner–recruit data for the Kenai River late-run sockeye salmon. When no escapements fail to replace themselves, ability to estimate the production curve for a stock against background environmental “noise” is problematic because little of the curve has been observed. This serious technical concern coupled with the spawner–recruit data precision and bias issues mentioned earlier in this report can lead to technical misinformation and problems if ignored. Such problems include spurious results, poor model fits, great uncertainty in estimated parameters, and nonsensical consequences when models are chosen based simply on statistical fit without informative large escapements. Although we fit models to the spawner–recruit data, we acknowledge the results assume the data were collected without error, which is clearly not the case. We also realize the lack of information from large escapements means much of the analysis is speculative concerning maximum sustained yield escapement levels. Further, we fully realize that the precision and bias issues inherent in this spawner–recruit data set means that alternate data sets could be developed, and if similarly analyzed, could lead to different inferences concerning an appropriate escapement goal.

Recently there has been discussion about harvest of UCI sockeye salmon stocks in areas other than UCI (e.g., Kodiak and southern Alaska Peninsula). These harvests were not included in the analyses presented here. Inclusion of outside-of-area harvests is a substantial and complex topic with potential to unnecessarily complicate, and may not add greatly to, the analyses. For example, the problem of not having any escapements that failed to replace themselves would persist. Inclusion of outside-of-area harvests will make UCI stocks appear more productive than currently believed, so not including them here should not raise potential conservation-based arguments in the analysis or results.

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TABLES

Table 1.—Parameter and reference point estimates in thousands of fish (95% credible intervals in parentheses) from 6 spawner–recruit models fit to Kenai River late-run sockeye salmon data.

Parameter	Ricker	Autoregressive	Beverton-Holt	Deriso-Schnute	Brood Interaction	
					Additive	Multiplicative
1979–2012						
$\ln(\alpha)$	1.860 (1.395–2.351)	1.751 (1.103–2.343)	2.892 (1.792–3.635)	2.571 (1.600–3.793)	2.085 (1.591–2.641)	1.705 (1.390–2.030)
β	0.057 (0.016–0.099)	0.045 (0.003–0.097)	0.417 (0.071–0.957)	0.226 (0.037–0.935)		0.038 (0.016–0.061)
β_1					0.042 (0.006–0.088)	
β_2					–0.037 (–0.080–0.005)	
ϕ		0.156 (–0.105–0.756)				
γ				0.813 (0.134–0.992)		
σ_w	0.542 (0.431–0.707)	0.534 (0.423–0.712)	0.532 (0.423–0.693)	0.536 (0.424–0.705)	0.521 (0.411–0.687)	0.510 (0.406–0.672)
S_{MSY}	1212 (784–3629)	1464 (801–>12,000)	778 (511–2100)	820 (378–2406)	930 (634–1864)	980 (800–1468)
$S_{90\%MSY}$	774 – 1735	885 – 2071	395 – 1527	445 – 1443	589 – 1334	695 – 1278
U_{MSY}	0.69 (0.57–0.79)	0.67 (0.48–0.79)	0.76 (0.59–0.84)	0.76 (0.58–0.89)	0.74 (0.62–0.84)	0.74 (0.66–0.80)
S_{MAX}	1758 (1006–6306)	2238 (1031–>12,000)	>12,000 (>12,000–>12,000)	2358 (585–>12,000)	1257 (767–2951)	1141 (902–1786)
S_{EQ}	3274 (2291–8971)	3870 (2317–>12,000)	4157 (3233–7405)	3676 (2524–7449)	2623 (1980–4832)	2109 (1779–3052)
DIC	1079.6	1081.1	1077.7	1079.5	1078.8	1076.3
1968–2012						
$\ln(\alpha)$	1.798 (1.497–2.098)	1.701 (1.278–2.046)	2.004 (1.593–2.557)	1.906 (1.543–2.364)	1.868 (1.559–2.181)	1.655 (1.441–1.873)
β	0.052 (0.023–0.082)	0.043 (0.007–0.077)	0.118 (0.038–0.304)	0.080 (0.028–0.199)		0.004 (0.002–0.005)
β_1					0.038 (0.005–0.076)	
β_2					–0.023 (–0.059–0.015)	
ϕ		0.108 (–0.089–0.568)				
γ				0.656 (0.050–0.987)		
σ_w	0.496 (0.407–0.622)	0.493 (0.401–0.620)	0.495 (0.407–0.630)	0.493 (0.405–0.623)	0.490 (0.400–0.618)	0.482 (0.394–0.609)
S_{MSY}	1284 (885–2627)	1521 (934–8359)	1458 (842–3296)	1359 (842–3003)	1126 (791–2097)	1010 (840–1411)
$S_{90\%MSY}$	819 – 1821	966 – 2174	828 – 2377	809 – 2069	720 – 1604	714 – 1319
U_{MSY}	0.68 (0.60–0.74)	0.65 (0.54–0.73)	0.63 (0.55–0.72)	0.65 (0.57–0.74)	0.69 (0.61–0.76)	0.73 (0.67–0.77)
S_{MAX}	1908 (1212–4333)	2344 (1296–>12,000)	>12,000 (>12,000–>12,000)	3702 (1410–>12,000)	1630 (1055–3375)	1188 (965–1706)
S_{EQ}	3420 (2473–6669)	3979 (2582–>12,000)	5460 (3715–10,769)	4516 (2827–9196)	3045 (2254–5392)	2160 (1826–2951)
DIC	1399.2	1400.3	1399.9	1399.1	1399.5	1396.8

Table 2.—Markov yield table with mean, median, minimum and maximum for Kenai River late-run sockeye salmon constructed in various escapement range intervals (in thousands) using data from brood years 1979–2012.

Escapement range	n ^a	Yield			
		Mean	Median	Min	Max
700–1200	15	3,233,341	2,671,592	692,086	8,832,028
700–1300	19	2,968,862	2,671,592	277,212	8,832,028
700–1400	21	2,876,765	2,587,086	277,212	8,832,028
700–1500	22	2,769,527	2,544,591	277,212	8,832,028
700–1800	24	2,734,403	2,544,591	277,212	8,832,028
750–1200	12	3,429,989	2,774,213	692,086	8,832,028
750–1300	16	3,066,758	2,774,213	277,212	8,832,028
750–1400	18	2,948,435	2,544,591	277,212	8,832,028
750–1500	19	2,820,492	2,502,096	277,212	8,832,028
750–1800	21	2,775,496	2,502,096	277,212	8,832,028
800–1200	8	2,724,714	2,774,213	692,086	4,805,786
800–1300	12	2,475,498	2,774,213	277,212	4,805,786
800–1400	14	2,407,833	2,544,591	277,212	4,805,786
800–1500	15	2,281,813	2,502,096	277,212	4,805,786
800–1800	17	2,289,603	2,502,096	277,212	4,805,786
<600	5	1,982,586	1,928,799	947,229	3,412,812
<700	7	2,618,897	2,014,160	947,229	6,361,435
<750	10	2,567,253	2,036,037	947,229	6,361,435
<800	14	3,216,763	2,036,037	713,077	8,832,028
>1200	12	2,584,730	2,346,393	277,212	8,344,970
>1300	8	2,888,562	2,346,393	517,521	8,344,970
>1500	5	3,717,458	3,114,190	1,546,053	8,344,970
>1800	3	4,630,407	3,114,190	2,432,060	8,344,970

^a Number of years of escapement estimates within range.

FIGURES

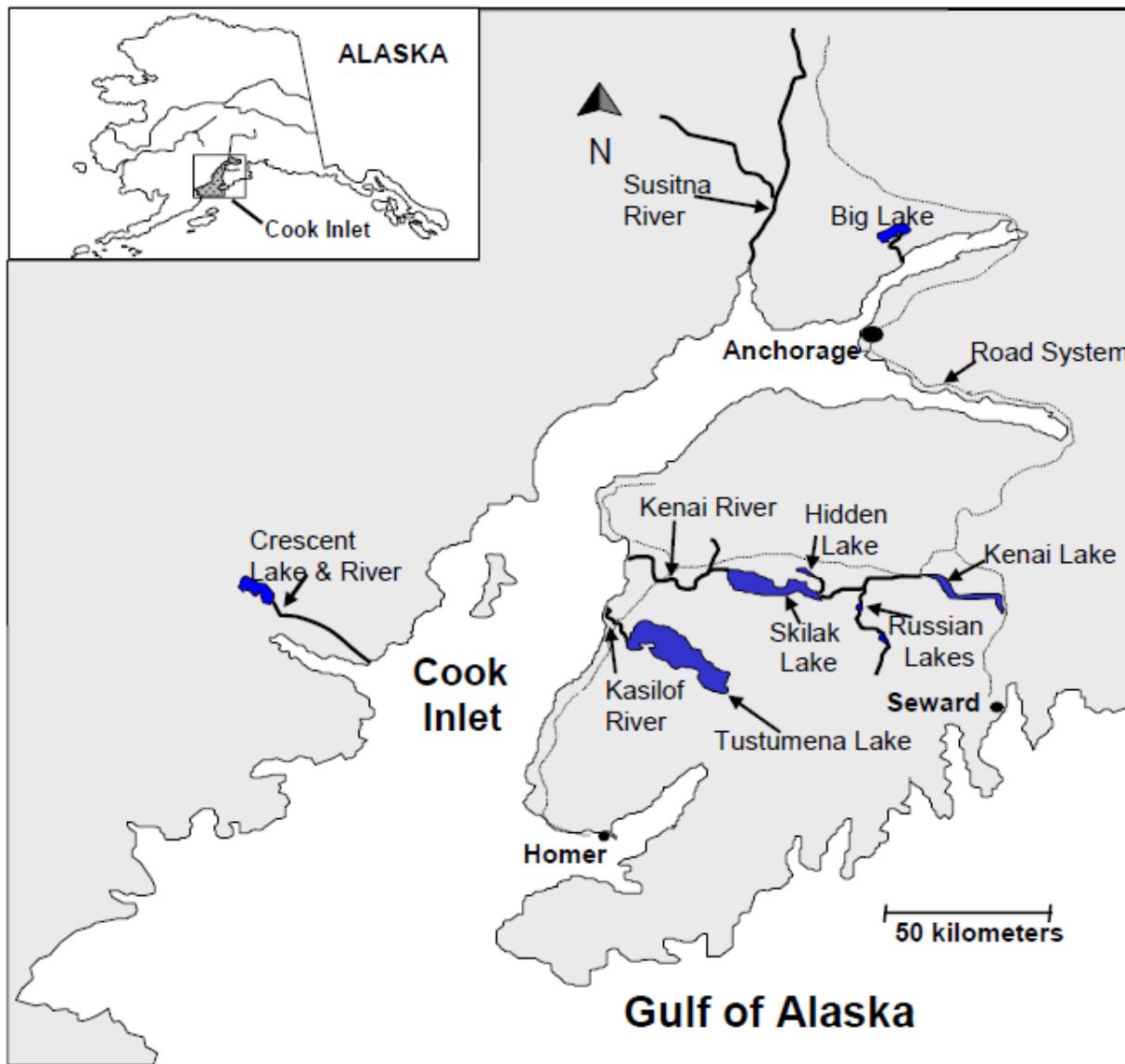


Figure 1.—Locations of the Kenai River and 3 other major sockeye salmon producing watersheds (Crescent, Susitna, and Kasilof rivers) in the upper Cook Inlet region.

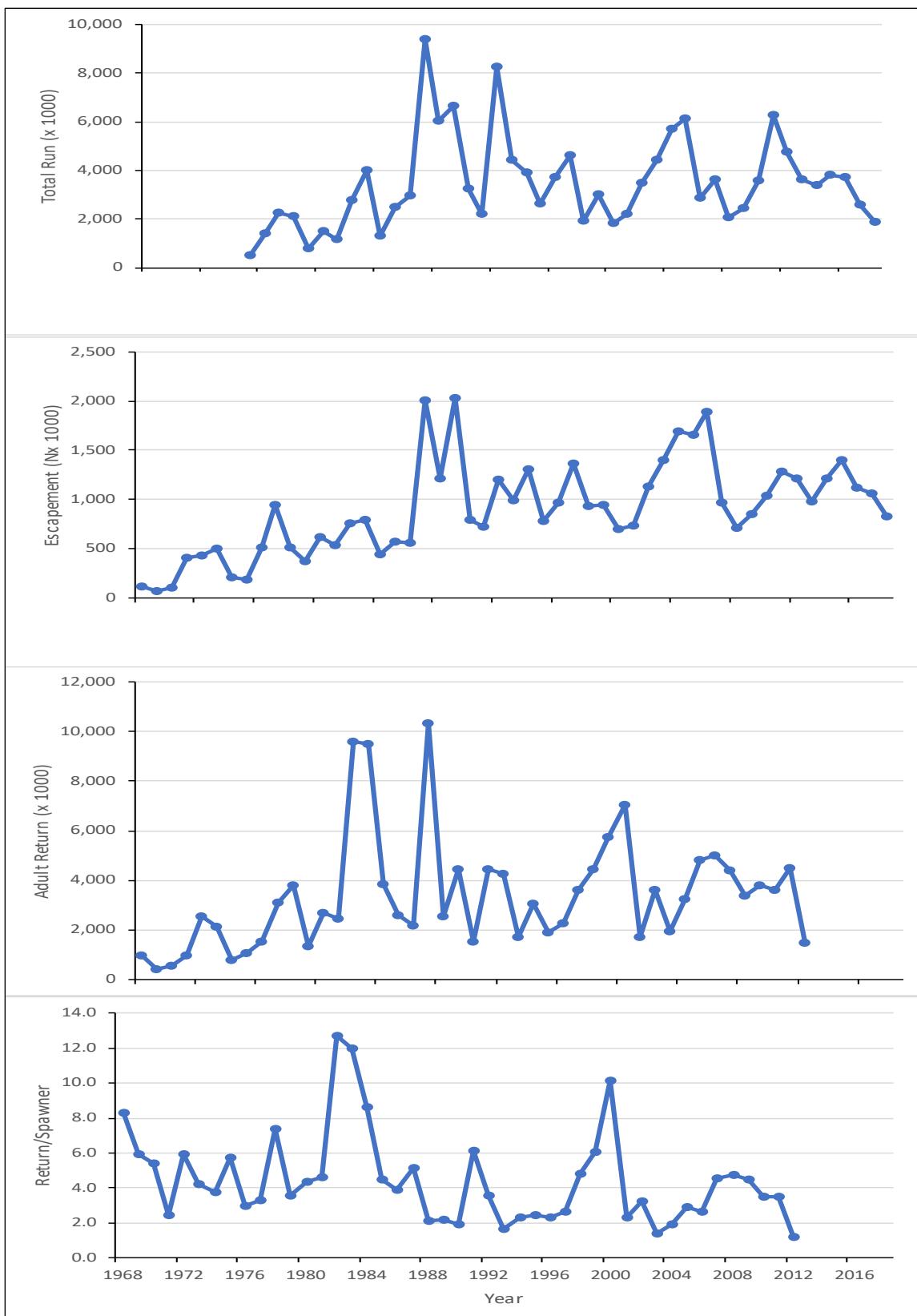


Figure 2.—Estimated total run, escapement, adult return (recruitment) and return per spawner of Kenai River late-run sockeye salmon from 1968–2018.

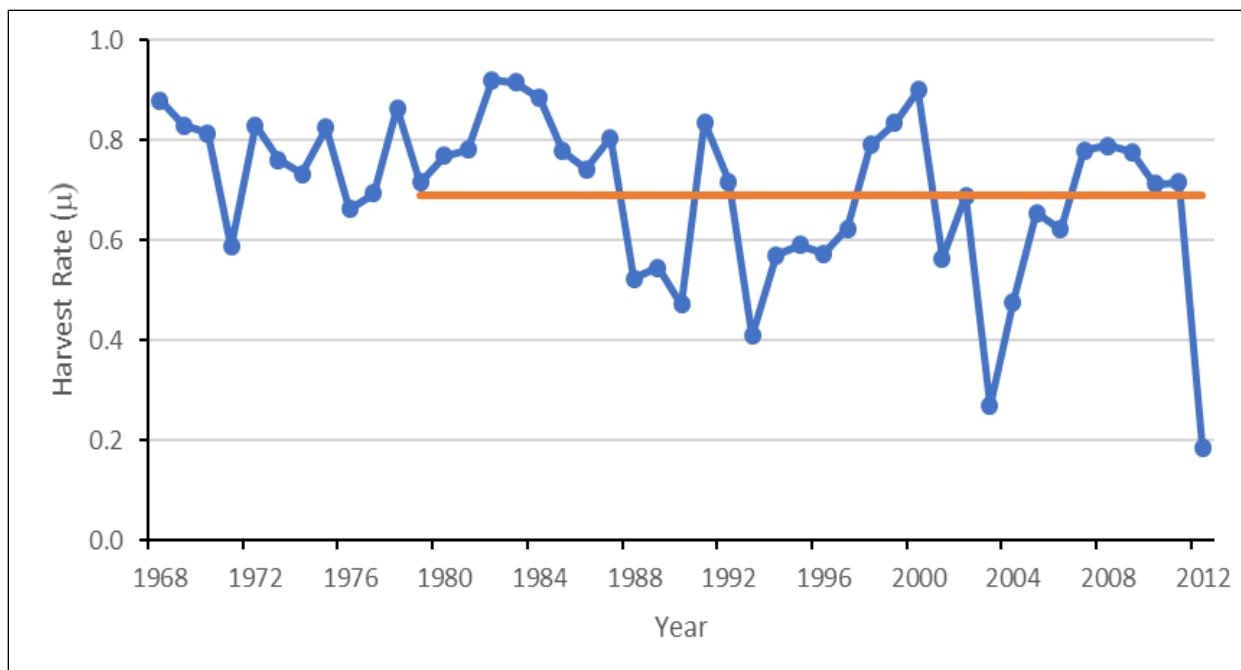


Figure 3.—Brood year harvest rate of Kenai River late-run sockeye salmon. Solid horizontal line is the harvest rate at MSY (U_{MSY}) estimated from classic Ricker model using spawner–recruit data from 1979–2012.

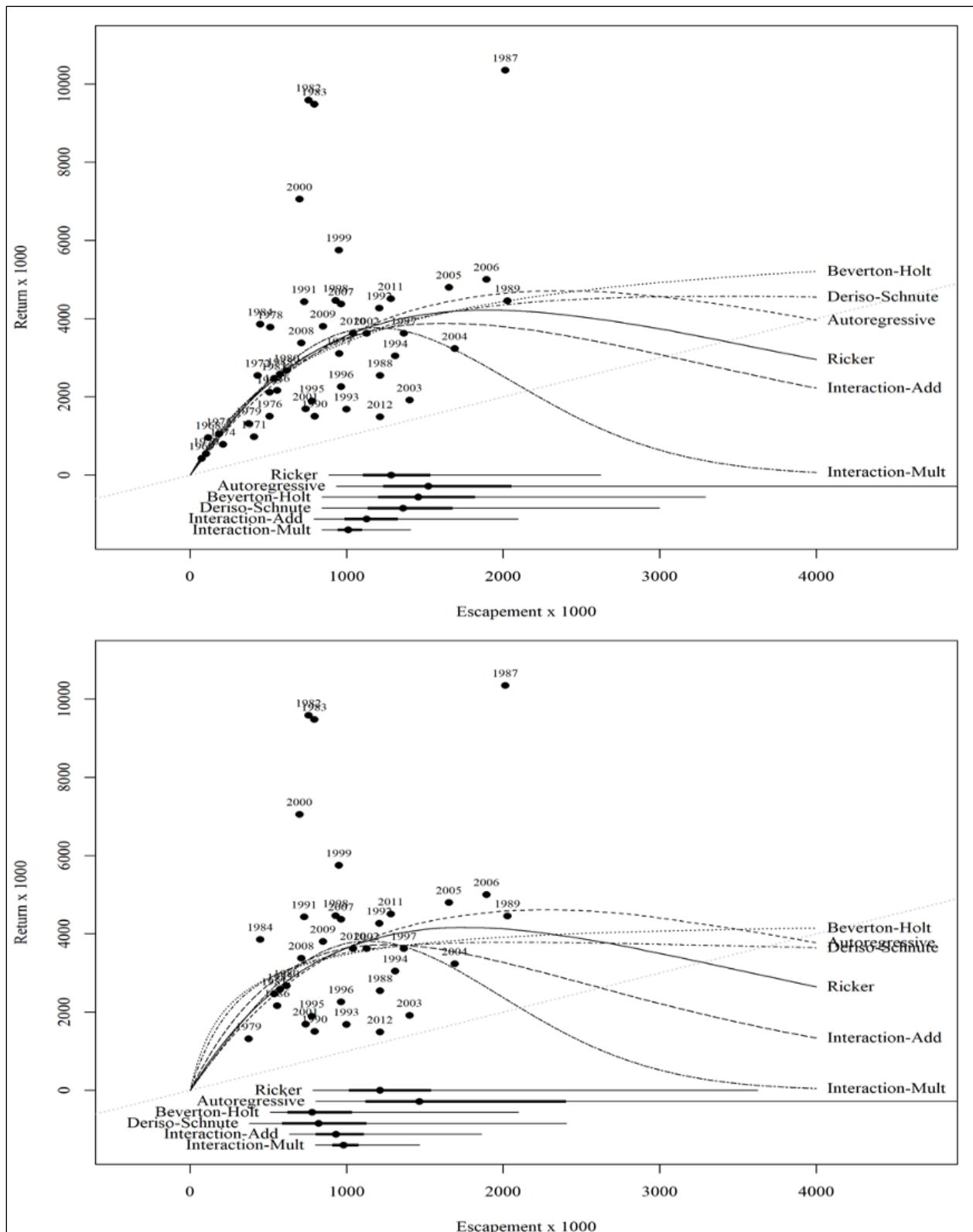


Figure 4.—Model fits to Kenai River late-run sockeye salmon spawner-recruit data for brood years 1968–2012 (top panel) and 1979–2012 (bottom panel). Horizontal lines at bottom of each panel show point estimate of SMSY and credibility intervals.

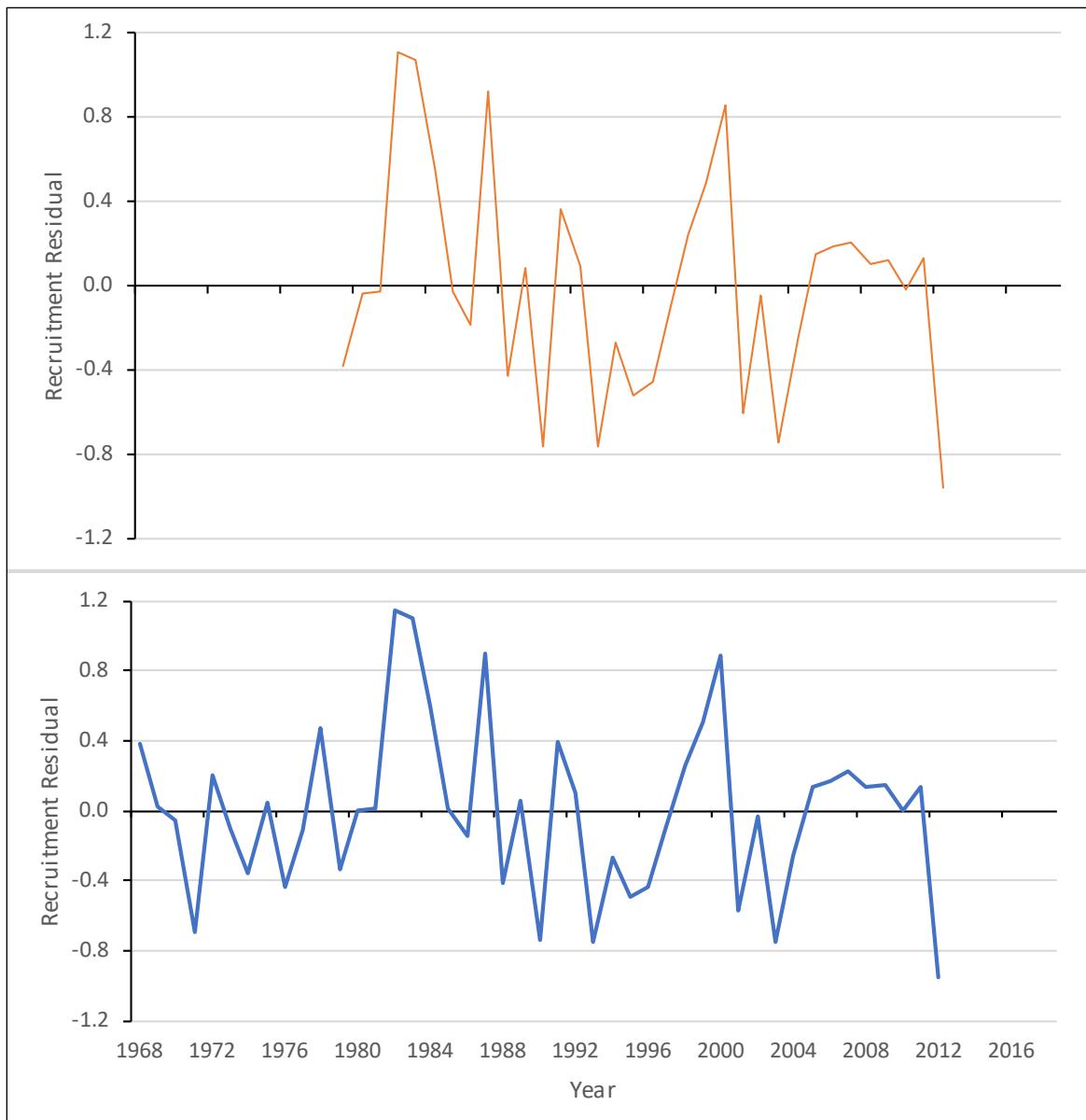


Figure 5.—Recruitment (productivity) residuals from the classic Ricker model fit to Kenai River late-run sockeye salmon spawner–recruit data from 1979–2012 (top panel) and 1968–2012 (bottom panel).

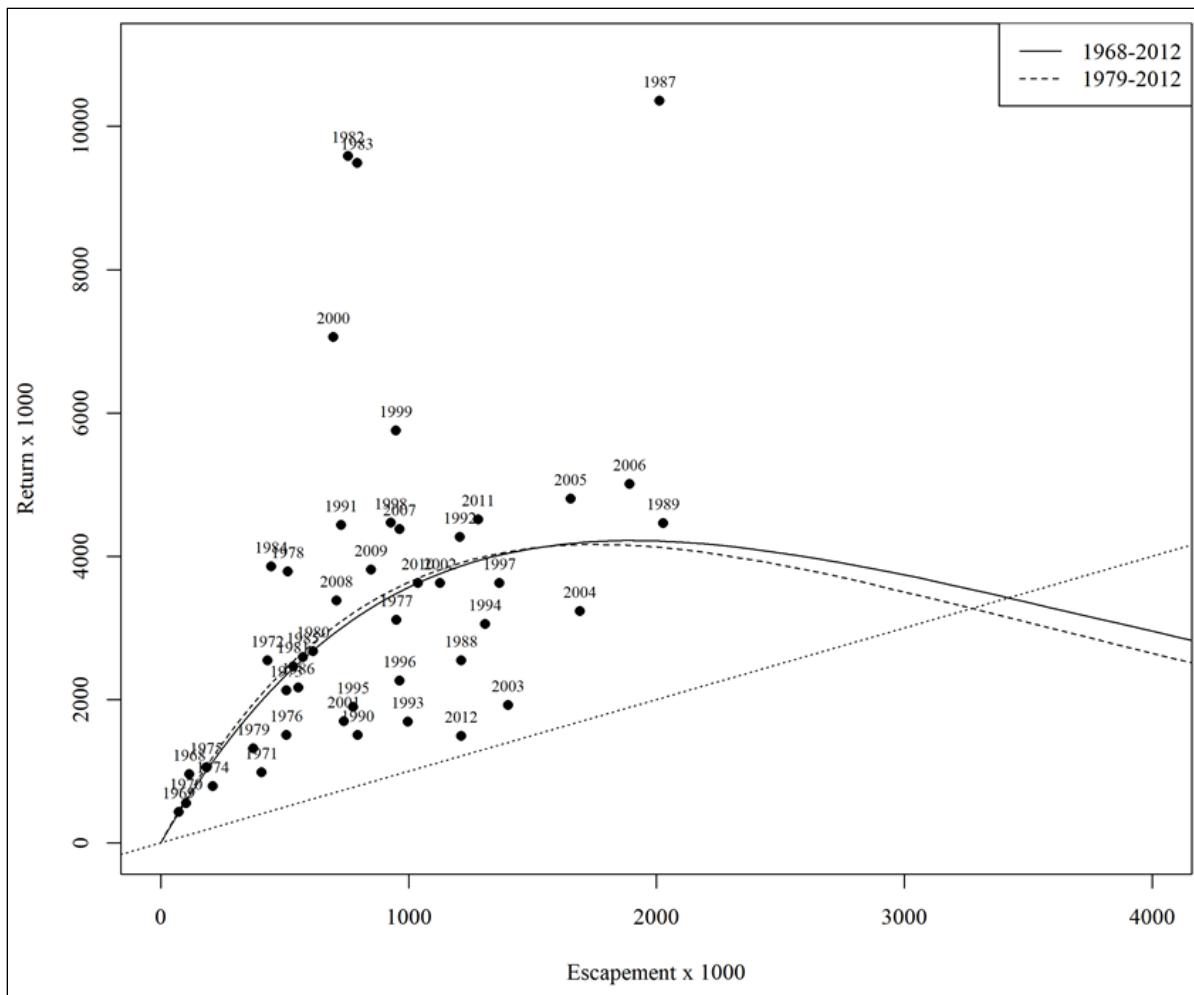


Figure 6.—Classic Ricker model fit to Kenai River late-run sockeye salmon spawner-recruit data from 1968–2012 (solid line) and 1979–2012 (dashed line).

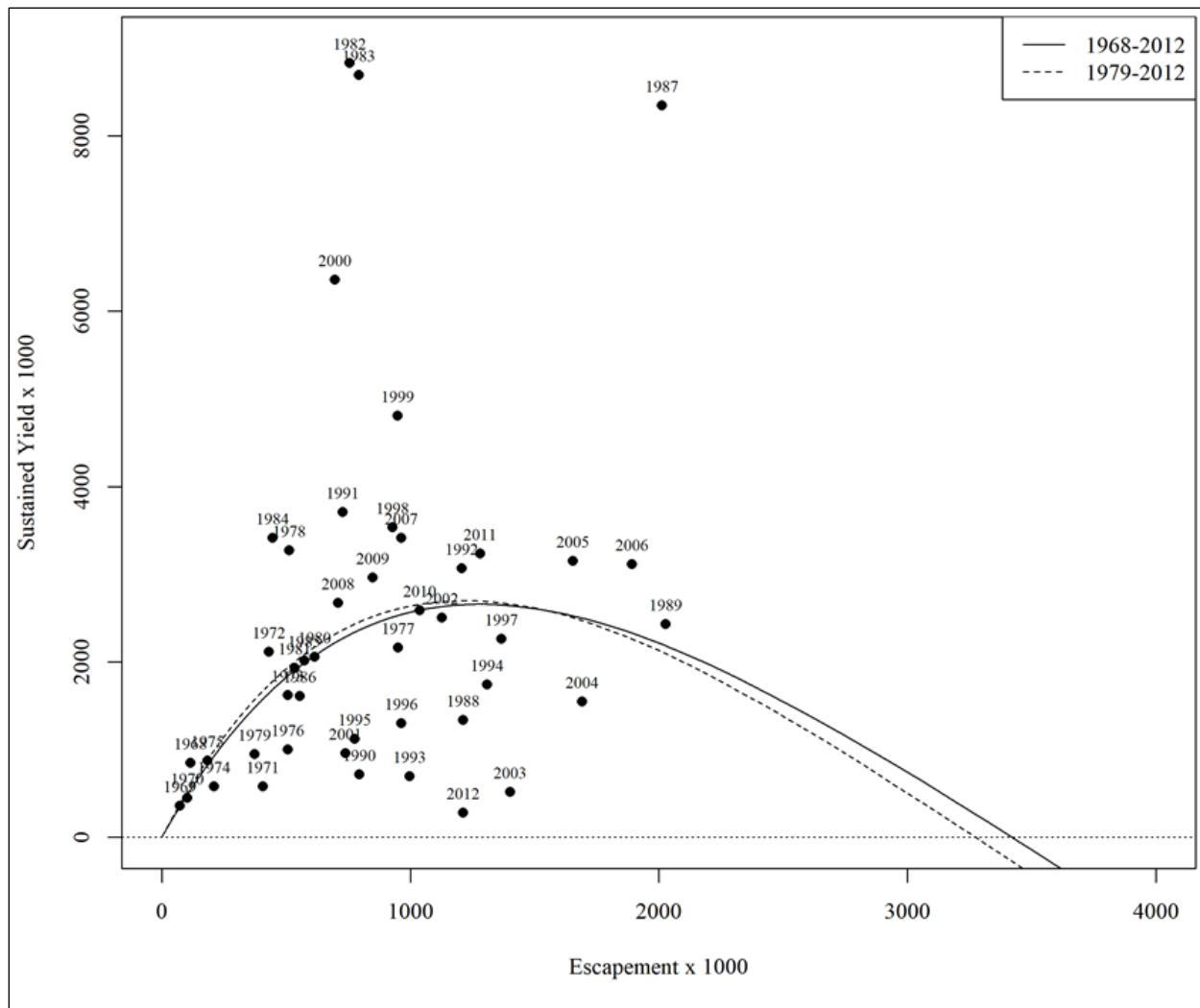


Figure 7.—Yield estimates from a classic Ricker model fit to Kenai River late-run sockeye salmon spawner–recruit data from 1968–2012 (solid line) and 1979–2012 (dashed line).

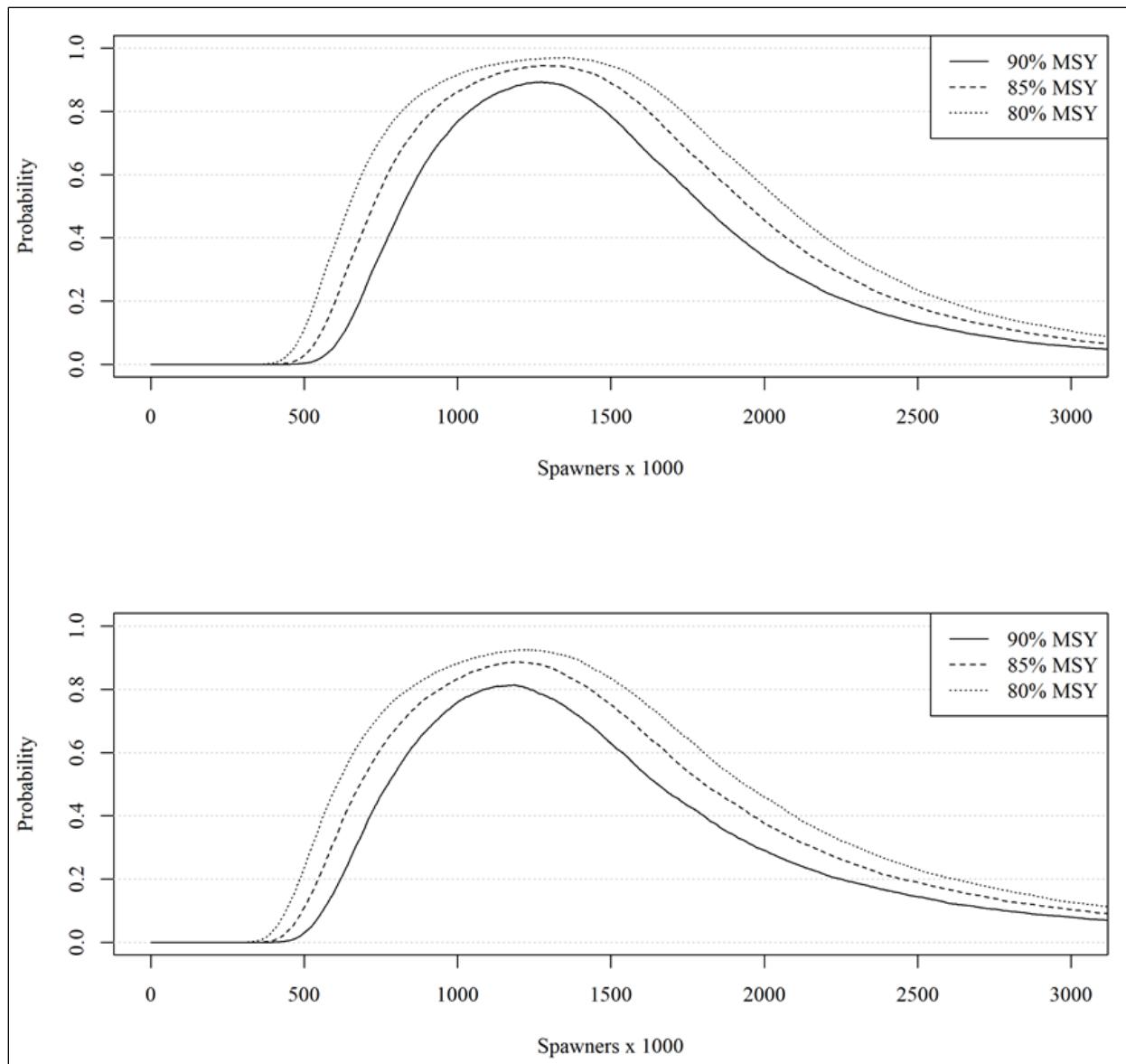


Figure 8.—Estimated yield profiles based on the classic Ricker model using spawner–recruit data from 1968–2012 (top panel) and 1979–2012 (bottom panel).

**APPENDIX A: KENAI RIVER LATE-RUN SOCKEYE
SALMON SPAWNER-RECRUIT DATA**

Appendix A1.—Kenai River late-run sockeye salmon spawner–recruit data.

Year	Spawners	Return	R/S	Yield	Harvest rate	Run	Harvest
1968	115,545	960,169	8.3	844,624	0.88		
1969	72,901	430,947	5.9	358,046	0.83		
1970	101,794	550,923	5.4	449,129	0.82		
1971	406,714	986,397	2.4	579,683	0.59		
1972	431,058	2,547,851	5.9	2,116,793	0.83		
1973	507,072	2,125,986	4.2	1,618,914	0.76		
1974	209,836	788,067	3.8	578,231	0.73		
1975	184,262	1,055,373	5.7	871,111	0.83	485,350	301,088
1976	507,440	1,506,012	3.0	998,572	0.66	1,374,607	867,167
1977	951,038	3,112,620	3.3	2,161,582	0.69	2,268,567	1,317,529
1978	511,781	3,785,040	7.4	3,273,259	0.86	2,096,342	1,584,561
1979	373,810	1,321,039	3.5	947,229	0.72	797,838	424,028
1980	615,382	2,673,295	4.3	2,057,913	0.77	1,481,394	866,012
1981	535,524	2,464,323	4.6	1,928,799	0.78	1,176,410	640,886
1982	755,672	9,587,700	12.7	8,832,028	0.92	2,766,442	2,010,770
1983	792,765	9,486,794	12.0	8,694,029	0.92	3,981,411	3,188,646
1984	446,297	3,859,109	8.6	3,412,812	0.88	1,286,678	840,381
1985	573,761	2,587,921	4.5	2,014,160	0.78	2,496,016	1,922,255
1986	555,207	2,165,138	3.9	1,609,931	0.74	2,945,961	2,390,754
1987	2,011,657	10,356,627	5.1	8,344,970	0.81	9,391,896	7,380,239
1988	1,212,865	2,546,639	2.1	1,333,774	0.52	6,054,519	4,841,654
1989	2,026,619	4,458,679	2.2	2,432,060	0.55	6,656,274	4,629,655
1990	794,616	1,507,693	1.9	713,077	0.47	3,224,183	2,429,567
1991	727,146	4,436,074	6.1	3,708,928	0.84	2,182,082	1,454,936
1992	1,207,382	4,271,576	3.5	3,064,194	0.72	8,235,298	7,027,916
1993	997,693	1,689,779	1.7	692,086	0.41	4,446,195	3,448,502
1994	1,309,669	3,052,634	2.3	1,742,965	0.57	3,886,918	2,577,249
1995	776,847	1,899,870	2.4	1,123,023	0.59	2,628,555	1,851,708
1996	963,108	2,261,757	2.3	1,298,649	0.57	3,696,067	2,732,959
1997	1,365,676	3,626,402	2.7	2,260,726	0.62	4,610,042	3,244,366
1998	929,090	4,465,328	4.8	3,536,238	0.79	1,902,219	973,129
1999	949,276	5,755,063	6.1	4,805,786	0.84	2,984,568	2,035,292
2000	696,899	7,058,333	10.1	6,361,435	0.90	1,814,779	1,117,880
2001	738,229	1,697,957	2.3	959,728	0.57	2,189,670	1,451,441
2002	1,126,616	3,628,712	3.2	2,502,096	0.69	3,466,762	2,340,146
2003	1,402,292	1,919,813	1.4	517,521	0.27	4,439,571	3,037,279
2004	1,690,547	3,236,600	1.9	1,546,053	0.48	5,705,141	4,014,594
2005	1,654,003	4,804,018	2.9	3,150,015	0.66	6,109,173	4,455,170
2006	1,892,090	5,006,280	2.6	3,114,190	0.62	2,848,597	956,507
2007	964,243	4,378,678	4.5	3,414,435	0.78	3,601,777	2,637,535
2008	708,805	3,380,397	4.8	2,671,592	0.79	2,082,431	1,373,626
2009	848,117	3,809,455	4.5	2,961,339	0.78	2,430,414	1,582,297
2010	1,038,302	3,625,388	3.5	2,587,086	0.71	3,596,458	2,558,156
2011	1,280,733	4,513,815	3.5	3,233,082	0.72	6,263,091	4,982,359
2012	1,212,921	1,490,134	1.2	277,212	0.19	4,769,681	3,556,760
2013	980,208					3,628,121	2,647,914
2014	1,218,342					3,404,034	2,185,693
2015	1,400,047					3,819,016	2,418,696
2016	1,118,155					3,711,842	2,593,688
2017	1,056,773					2,595,720	1,538,947
2018	831,096					1,867,998	1,036,902

Note: Shaded area indicates 1968–1978 brood years were used in earlier spawner–recruit analyses.

APPENDIX B: JAGS CODE

Classic Ricker

```
parameters.CR <- c('lnalpha','beta','sigma')
jag.model.CR <- function(){
  for(y in 1:nyrs){
    s[y] <- S[y]/(10^d)
    lnRm[y] = log(S[y]) + lnalpha - beta * s[y]
  }
  # Define Priors
  lnalpha ~ dunif(0,10)
  beta ~ dunif(0,10)
  sigma ~ dunif(0,10)
  phi ~ dunif(-1,1)
  Tau <- 1/(sigma*sigma)
  # Likelihood
  for(y in 1:nyrs){
    R[y] ~ dlnorm(lnRm[y],Tau)
  }
}
```

AR1 Ricker

```
parameters.AR1 <- c('lnalpha','beta','phi','lnresid0','sigma')
jag.model.AR1 <- function(){
  for(y in 1:nyrs){
    s[y] <- S[y]/(10^d)
    lnRm1[y] = log(S[y]) + lnalpha - beta * s[y]
    lnResid[y] = log(R[y]) - lnRm1[y]
  }
  lnRm[1] = lnRm1[1] + phi * lnresid0;
  for(y in 2:nyrs){
    lnRm[y] = lnRm1[y] + phi * lnResid[y-1]
  }
  # Define Priors
  lnalpha ~ dunif(0,10)
  beta ~ dunif(0,10)
  sigma ~ dunif(0,10)
  phi ~ dunif(-1,1)
  lnresid0 ~ dnorm(0,0.001)
  Tau <- 1/(sigma*sigma)
  # Likelihood
  for(y in 1:nyrs){
    R[y] ~ dlnorm(lnRm[y],Tau)
  }
}
```

-continued-

Beverton-Holt

```
parameters.BH <- c('lnalpha','beta','sigma')
jag.model.BH <- function(){
  for(y in 1:nyrs){
    s[y] <- S[y]/(10^d)
    lnRm[y] <- lnalpha + log(S[y]) -log(1+beta*s[y])
  }
  # Define Priors
  lnalpha ~ dunif(0,10)
  beta ~ dunif(0,10)
  sigma ~ dunif(0,10)
  Tau <- 1/(sigma*sigma)
  # Likelihood
  for(y in 1:nyrs){
    R[y] ~ dlnorm(lnRm[y],Tau)
  }
}
```

Deriso-Shunute

```
parameters.DS <- c('lnalpha','beta','c','sigma')
jag.model.DS <- function(){
  for(y in 1:nyrs){
    s[y] <- S[y]/(10^d)
    lnS[y] <- log(S[y])
    lnR[y] <- log(R[y])
    lnRm[y] = lnS[y] + lnalpha - log(1 + beta*c*s[y])/c
  }
  # Define Priors
  lnalpha ~ dunif(0,10)
  beta ~ dunif(0,10)
  sigma ~ dunif(0,10)
  c ~ dunif(0,1)
  Tau <- 1/(sigma*sigma)
  # Likelihood
  for(y in 1:nyrs){
    R[y] ~ dlnorm(lnRm[y],Tau)
  }
}
```

Additive Brood Interaction

```
parameters.BI <- c('lnalpha','beta1','beta2','lnS0','sigma')
jag.model.BI<- function(){
```

-continued-

```

for(y in 1:nyrs){
  s[y] <- S[y]/(10^d)
  lnRm1[y] <- log(S[y]) + lnalpha - beta1*s[y]
}
lnRm[1] <- lnRm1[1] + beta2*exp(lnS0)/(10^d)
for(y in 2:nyrs){
  lnRm[y] <- lnRm1[y] + beta2*s[y-1]
}

# Define Priors
lnalpha ~ dunif(0,10)
beta1 ~ dunif(0,10)
sigma ~ dunif(0,10)
beta2 ~ dunif(-10,10)
lnS0 ~ dunif(0,16)
Tau <- 1/(sigma*sigma)
# Likelihood
for(y in 1:nyrs){
  R[y] ~ dlnorm(lnRm[y],Tau)
}
}

Multiplicative Brood Interaction
parameters.BI2 <- c('lnalpha','beta3','lnS0','sigma')
jag.model.BI2<- function(){
  for(y in 1:nyrs){
    s[y] <- S[y]/(10^d)
  }
  lnRm[1] <- log(S[1]) + lnalpha - beta3*(s[1])*exp(lnS0)/(10^d)
  for(y in 2:nyrs){
    lnRm[y] <- log(S[y]) + lnalpha - beta3*s[y]*s[y-1]
  }
}

# Define Priors
lnalpha ~ dunif(0,10)
sigma ~ dunif(0,100)
beta3 ~ dunif(-10,10)
lnS0 ~ dunif(0,16)
Tau <- 1/(sigma*sigma)
# Likelihood
for(y in 1:nyrs){
  R[y] ~ dlnorm(lnRm[y],Tau)
}
}

```

-continued-

```
JAGS model running code
nmodels <- 6
models <- list()
models$model1 = jag.model.CR
models$model2 = jag.model.AR1
models$model3 = jag.model.BH
models$model4 = jag.model.DS
models$model5 = jag.model.BI
models$model6 = jag.model.BI2

# Store Model Parameters
parlist <- list()
parlist$par1 = parameters.CR
parlist$par2 = parameters.AR1
parlist$par3 = parameters.BH
parlist$par4 = parameters.DS
parlist$par = parameters.BI
parlist$par6 = parameters.BI2

# Run JAGS Model
simlist <- list()
for (i in 1:nmodels){
  sim <- jags(data=datnew, parameters.to.save=parlist[[i]],    model.file= models[[i]],n.chains=1,
  n.iter=100000,n.burnin=20000,n.thin=10,DIC=TRUE, working.directory=data_dir)
  simlist[[i]] <- sim
}
```