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Biological and Fishery-Related Aspects of Overescapement in Alaskan Sockeye Salmon *Oncorhynchus nerka*

by

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December 2007

Alaska Department of Fish and Game **Divisions of Sport Fish and Commercial Fisheries**

Symbols and Abbreviations

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Weights and measures (metric)

centimeter	cm
deciliter	dL
gram	g
hectare	ha
kilogram	kg
kilometer	km
liter	L
meter	m
milliliter	mL
millimeter	mm

Weights and measures (English)

cubic feet per second	ft^3/s
foot	ft
gallon	gal
inch	in
mile	mi
nautical mile	nmi
ounce	oz
pound	lb
quart	qt
yard	yd

Time and temperature

day	d
degrees Celsius	°C
degrees Fahrenheit	°F
degrees kelvin	K
hour	h
minute	min
second	s

Physics and chemistry

all atomic symbols	
alternating current	AC
ampere	A
calorie	cal
direct current	DC
hertz	Hz
horsepower	hp
hydrogen ion activity (negative log of)	pH
parts per million	ppm
parts per thousand	ppt, ‰
volts	V
watts	W

General

Alaska Administrative Code	AAC
all commonly accepted abbreviations	e.g., Mr., Mrs., AM, PM, etc.
all commonly accepted professional titles	e.g., Dr., Ph.D., R.N., etc.
at	@
compass directions:	
east	E
north	N
south	S
west	W
copyright	©
corporate suffixes:	
Company	Co.
Corporation	Corp.
Incorporated	Inc.
Limited	Ltd.
District of Columbia	D.C.
et alii (and others)	et al.
et cetera (and so forth)	etc.
exempli gratia (for example)	e.g.
Federal Information Code	FIC
id est (that is)	i.e.
latitude or longitude	lat. or long.
monetary symbols (U.S.)	$, ¢
months (tables and figures): first three letters	Jan,...,Dec
registered trademark	®
trademark	™
United States (adjective)	U.S.
United States of America (noun)	USA
U.S.C.	United States Code
U.S. state	use two-letter abbreviations (e.g., AK, WA)

Measures (fisheries)

fork length	FL
mideye-to-fork	MEF
mideye-to-tail-fork	METF
standard length	SL
total length	TL

Mathematics, statistics

all standard mathematical signs, symbols and abbreviations	
alternate hypothesis	H_A
base of natural logarithm	*e*
catch per unit effort	CPUE
coefficient of variation	CV
common test statistics	(F, t, χ^2, etc.)
confidence interval	CI
correlation coefficient (multiple)	R
correlation coefficient (simple)	r
covariance	cov
degree (angular)	°
degrees of freedom	df
expected value	*E*
greater than	>
greater than or equal to	≥
harvest per unit effort	HPUE
less than	<
less than or equal to	≤
logarithm (natural)	ln
logarithm (base 10)	log
logarithm (specify base)	$\log_{2,}$ etc.
minute (angular)	'
not significant	NS
null hypothesis	H_O
percent	%
probability	P
probability of a type I error (rejection of the null hypothesis when true)	α
probability of a type II error (acceptance of the null hypothesis when false)	β
second (angular)	"
standard deviation	SD
standard error	SE
variance	
population	Var
sample	var

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ABSTRACT

Overescapement of salmon is defined by the Alaska Department of Fish and Game as escapements that are above the range of the current escapement goal. Our understanding of how overescapement affects long and short term yields is dependent on knowledge of the production relationship and the amount of fishing power. We analyzed brood and run information from 40 Alaska sockeye salmon *Oncorhynchus nerka* stocks to determine the biological and fishery-related effects of overescapement.

For 37 of the 40 stocks we reviewed, overescapement occurred at least once in a recent 15 year period. We examined the long term effects of overescapement on yields relative to MSY for 29 of the 40 stocks. This subset of stocks was chosen because the observed exploitation rate is less than or equal to the exploitation rate at Maximum Sustained Yield (MSY) allowing examination of yields at levels of escapement that would exceed the escapement that produces MSY. Yields from these stocks decreased below MSY as escapements increased beyond that which produces MSY. Averaged across all of these stocks, long term yields decreased and variability in yields increased when current escapement goals were exceeded. This result is consistent with the generic theory of compensatory production, where spawning efficiency decreases with increasing escapement levels and stocks are limited by the carrying capacity of the habitat. Overescapement, in general, is not sustainable as it causes returns and yields to decrease in the next generation, which also result in lower escapements. Lower escapements then result in higher returns and yields in succeeding generations. We also found evidence of delayed density dependence in five Alaskan sockeye salmon stocks. In three of these stocks, returns per spawner fell below replacement for 2 to 5 years following consecutive overescapements that were greater than twice the upper bound of the escapement goal range.

In the remaining 11 of 40 stocks we were unable to examine long term yields at levels of escapement exceeding that which produces MSY. In these cases, yields from these stocks increased above the average yield as escapements increased beyond the upper bound of the current escapement goal. Averaged across all of these stocks, long term yields increased and variability in yields decreased slightly when current escapement goals were exceeded. This result is also consistent with the generic theory of compensatory production. As escapement increases, but is below the level thought to produce MSY, returns and yields will increase even if overescapement occurs. This is due to the high productivity of salmon across a wide range of intermediate escapements so that the long term change in yield due to overescapement is small when exploitation rate is high.

Short term losses in yield were assessed by evaluating foregone annual harvest as a result of overescapement in the most recent 15 years for all 40 stocks. Although foregone harvest due to overescapement was common, on average these harvests typically represented 5% or less of the annual run. Seven of 40 stocks had losses in harvest exceeding 10% of the annual run on average. However, when we examined losses only during years that overescapement occurred, 18 stocks exhibited foregone harvest greater than 10% of the run, and seven of these stocks exhibited foregone harvest greater than 20% of the run. Foregone harvest due to overescapement was more prevalent for stocks with low fishing power.

Although overescapement as defined is occurring on most of the 40 Alaskan sockeye salmon stocks we reviewed, for some of these stocks more information is needed to understand the effect overescapement may or may not have on production and the fishery. Alternative methods for determination of carrying capacity of sockeye salmon watersheds should be developed and validated, especially for highly exploited stocks. Research focused on estimating carrying capacity in select watersheds should include efforts to better define the threshold juvenile salmon densities that cause delayed density-dependent responses in rearing lake ecosystems. From a fishery standpoint, better forecasts of salmon runs and improved inseason management could reduce the incidence of overescapement in highly exploited stocks.

Key words: sockeye salmon, *Oncorhynchus nerka*, overescapement, carrying capacity, exploitation rate, escapement goals, biological reference points, maximum sustained yield, escapement goal policy, sustainable salmon policy

BACKGROUND

The topic of overescapement in Pacific salmon stocks is controversial and complex, especially in regards to the management of Alaskan sockeye salmon *Oncorhynchus nerka*. The controversy has many facets, but three major issues tend to recur in the debate: 1) the definition of overescapement; 2) the effects of overescapement on the stock; and, 3) the effects of overescapement on the fishery. This report attempts to clarify these major issues from the perspective of the Alaska Department of Fish and Game (ADF&G). Our perspective is one that is mandated by the imperatives of Alaskan law, guided by a very simple but useful theory of wild salmon production, based on experience gained through the development of scientifically defensible escapement goals for sockeye salmon stocks throughout the state, and grounded in the sound fishery management principles we have applied to the harvest of these stocks.

The objectives of this report are to: 1) provide definitions of key terms relevant to the issue of overescapement; 2) describe and clarify the process of escapement goal development that is central to the issue of overescapement; 3) discuss the biological and fishery-related aspects of overescapement; and, 4) provide recommendations to address the issue of overescapement in Alaskan sockeye salmon. To aid in clarifying and discussing overescapement, we provide the results from a set of basic, consistent analyses of 40 Alaskan sockeye salmon stocks from fisheries ranging from southeast Alaska to the Kuskokwim Bay region (Figure 1). We also review hypotheses concerning density dependence and present five case studies of delayed-density dependence in sockeye salmon.

RELEVANT POLICIES

From the ADF&G perspective, any discussion of overescapement in salmon stocks must be grounded in the constitutional mandates to provide for sustained yield of fish. Article VIII, section 4 of the Alaska Constitution states that:

> “Fish, forests, wildlife, grasslands, and all other replenishable resources belonging to the State shall be utilized, developed, and maintained on the sustained yield principle, subject to preferences among beneficial uses.”

This mandate for sustainable management of Pacific salmon provided the impetus for development of a scientifically defensible escapement goal policy in Alaska. Along with the statutory functions, powers and duties of the Commissioner of ADF&G (Alaska Statutes 16.05.020 and 16.05.050) and relevant management plans for salmon stocks (Title 5 of the Alaska Administrative Code, various chapters), the development of escapement goals is regulated by the policy for the management of sustainable salmon fisheries and the policy for statewide salmon escapement goals (Title 5 of the Alaska Administrative Code, Chapter 39).

These two regulatory policies define four types of escapement goals, two of which are routinely developed by ADF&G and are most important to sustained yield management of salmon stocks. The biological escapement goal (BEG) is defined as: the escapement that provides the greatest potential for maximum sustained yield (MSY). As an alternative to management for MSY, the sustainable escapement goal (SEG) is defined as: the escapement that is known to provide for sustained yield. Both of these escapement goals must be described as ranges that take into account our uncertainty in the data and variation in stock productivity. The two regulatory policies also stipulate that BEGs and SEGs for Pacific salmon be developed from the best available data and be scientifically defensible.

DEFINITIONS

Some of the confusion and controversy surrounding the effects of overescapement is caused by the lack of a common set of definitions from which to discuss the issue. Basic definitions of salmon population biology are offered here, some of which come directly from statute or regulation, others come from basic texts on fisheries science or from our own experience.

Salmon stock. A locally interbreeding group of salmon that is distinguished by a distinct combination of genetic, phenotypic, life history, and habitat characteristics or an aggregation of two or more interbreeding groups, which occur in the same geographic area and is managed as a unit (from 5 AAC 39.222(f)).

Escapement (or Spawning Abundance or Spawners). The annual estimated size of the spawning salmon stock; quality of escapement may be determined not only by numbers of spawners, but also by factors such as sex ratio, age composition, temporal entry into the system, and spatial distribution within the salmon spawning habitat (from 5 AAC 39.222(f)).

Brood (year). All salmon in a stock spawned in a specific year.

Run. The total number of salmon in a stock surviving to adulthood and returning to the vicinity of the natal stream in any calendar year, composed of both the harvest of adult salmon plus the escapement; the annual run in any calendar year, except for pink salmon is composed of several age classes of mature fish from the stock, derived from the spawning of a number of previous brood years (from 5 AAC 39.222(f)).

Harvest. The number or weight of salmon taken of an annual run from a specific stock.

Harvest rate. The fraction of an annual run from a stock taken in a fishery.

Return (or Total Return or Recruitment or Production). The total number of salmon in a stock from a single brood (spawning) year surviving to adulthood; because the ages of adult salmon (except pink salmon) returning to spawn varies, the total return from a brood year will occur over several calendar years; the total return generally includes those mature salmon from a single brood year that are harvested in fisheries plus those that comprise the salmon stock’s spawning escapement; “return” does not include a run, which is the number of mature salmon in a stock during a single calendar year (from 5 AAC 39.222(f)).

Yield. Defined in regulation as the number or weight of salmon harvested in a particular year or season from a stock (from 5 AAC 39.222(f). However, in this report yield is defined as the return minus the escapement for a particular brood year. This quantity is also known as the surplus production or expected yield. Note that yield is defined in terms of a single brood year, while harvest is defined in terms of the annual run that is composed of components from multiple brood years.

Exploitation rate. Fraction of the return by stock taken in a fishery (specific to a brood year).

Carrying Capacity (or S_{EQ}). Biological reference point that is the highest escapement where the return is expected to equal escapement. This is the point where escapements at or larger than this are expected to produce no yields in the future.

Intrinsic Rate of Increase. Expected number of mature salmon produced per spawner when escapement is close to zero.

Density Dependent Survival. A survival rate affected by abundance of young at the start of a time period or by escapement of their parents.

Density Independent Survival. A survival rate unaffected by abundance of young or by escapement of their parents.

Process Error. Deviations in actual return from expected return given a specific escapement.

Compensatory Mortality. A mortality rate that increases as the initial abundance increases. For example, when the return-per-spawner of a stock decreases as the spawner abundance of that stock increases.

Depensatory Mortality. A mortality rate that decreases as the initial abundance increases.

Sustained Yield. The average annual yield that results from a level of escapement that can be maintained on a continuing basis; a wide range of average annual yield levels is sustainable; a wide range of escapement levels can produce sustained yields (from 5 AAC 39.222(f)).

Sustainable Escapement Goal (or SEG). 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 due to the absence of a stock specific catch estimate; the SEG is the primary management objective for the escapement, unless an optimal escapement goal or inriver run goal has been adopted by the board, and will be developed from the best biological information; the SEG will be determined by the department and will be stated as a range that takes into account data uncertainty; the department will seek to maintain escapements within the bounds of the SEG (from 5 AAC 39.222(f)).

Maximum Sustained Yield (or MSY). 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 (from 5 AAC 39.222(f)).

Biological Escapement Goal (or BEG). 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 goal or inriver run goal has been adopted; BEG will be developed from the best 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 the BEG (from 5 AAC 39.222(f)).

S_{MSY}. Biological reference point that is the escapement that produces the greatest expected yields (i.e., MSY). The BEG range should be based on this reference point.

μ_{MSY}. The exploitation rate for a stock that would on average produce MSY.

Overescapement. Escapements that are above the range of the current escapement goal.

Scientifically Defensible. Relative to an escapement goal for a stock of Pacific salmon, when there is evidence confirming the expectation of sustainable yields from that stock for that escapement goal. Evidence can be empirical (an observed history of yields from the stock), model-based (a model validated with data from one or many stocks), or theoretically-based (a theory validated with experiments from one or many stocks).

GENERIC THEORY OF SALMON PRODUCTION

Any generic theory of salmon production must include the two main ecological processes of an intrinsic rate of increase and a carrying capacity. Similar information can be found in basic texts of fisheries science (Ricker 1975, Hilborn and Walters 1992, Quinn and Deriso 1999).

The intrinsic rate of increase describes the density independent survival of a salmon stock, where survival of the stock is unrelated to size of the escapement. In this case, competition between spawning salmon or juveniles is low so that the survival is not related to the density of the spawners or their offspring. This process is thought to occur when the salmon stock is small relative to its carrying capacity and therefore is described from the left side of the population model where escapements are small (Figure 2).

The intrinsic rate of increase is thought to be specific to species and region. Species-specific influences on salmon productivity include fecundity, maturation schedule, longevity, and growth rate. Regionally specific influences include locally similar freshwater and marine climate, predators, and fisheries.

The intrinsic rate of increase causes a salmon stock to grow indefinitely, but there must be a limit to this growth. The carrying capacity describes the density dependent survival of a salmon stock, where the survival of the stock is directly related to the size of the escapement. In this case, competition between spawning salmon or juveniles increases; consequently survival rate decreases as abundance of spawning adults or juveniles increases. This process is also called compensation and increases as the salmon stock approaches and possibly exceeds its carrying capacity on the right hand side of the production model (Figure 2). Empirically, carrying capacity can be defined as the average size of a salmon stock when it is not being fished.

The carrying capacity of a salmon stock is thought to be watershed and stock specific. There are several potential mechanisms for carrying capacity, including a limitation of rearing or limitation of the spawning grounds. For sockeye salmon, rearing limitation or competition among juveniles can occur through trophic production in lakes by affecting the size, age at smoltification, and survival of fry and smolt (Kyle et al. 1988, Schmidt et al. 1993, Koenings and Kyle 1997). Spawning limitation can also occur in sockeye salmon, with increased competitive interactions among spawning adults causing increased aggressive behavior on the spawning grounds, egg retention, and death prior to spawning (Semenchenko 1988).

More specific but fairly simple models of salmon production result from the generic model. In general, differences among models are due to differences in the relationship between density dependent survival and escapement with the asymptotic (Beverton and Holt 1957), exponential (Ricker 1975), and piece-wise (e.g., hockey stick model of Bradford et al. 2000) forms most commonly used. Although we used the Ricker form of the production model in this report, each of these simple models can be used to estimate parameters that correspond to the intrinsic rate of increase and carrying capacity from a data set composed of escapements and subsequent returns. Once these two quantities are estimated, the biological reference points S_{MSY}, S_{EQ}, and μ_{MSY} can be calculated (see example in Figure 3) and provide information important to development of an escapement goal.

One last consideration in a generic theory of salmon production is the concept of process error. As defined, process error is the variation we observe in the return at any fixed level of escapement. Process error is due to annual variation in survival from spawning adults to returning adults from factors that can change from year-to-year. For example, changes in the fraction of female spawners in the escapement or fecundity of individual spawners, size composition, age composition, the occurrence of floods, drought, freezing, and changes in temperature. Furthermore, errors in estimating the true escapement and return, if not accounted for in our stock assessments end up as process error although they are actually measurement error.

Process error is generally thought of as random through time, but can also be serially correlated (e.g., several years of high survival are grouped together followed by several years of low survival) or correlated with another variable that we may have measured (e.g., escapement in prior years, marine survival rate, environmental variables). Process error is also thought to be distributed log-normally (Peterman 1981) as can be seen in the example in Figure 4. In Figure 4, we see a large amount of variation in returns at any particular level of escapement that obscures the underlying production curve. It is also easy to see why we might observe a large return from a particular escapement in one year and a low return from the same magnitude of escapement in another year. Explanation and prediction of process error in the upcoming year is crucial to forecasting salmon abundance, but is of lesser importance to the development of an escapement goal.

The occurrence of process error in salmon production necessitates a statistical approach to developing reference points for the recommendation of escapement goals. Statistical approaches allow us to view the production curve estimated from the escapement and return data as the expected production we might see on average if escapement was fixed at a certain level (Figure 3). However, there are potential pitfalls with the statistical approach that have been discussed by others in the literature and are relevant when exploitation rate is high (>50% per year) or there is measurement error in estimates of escapement (Walters and Ludwig 1981, Kehler et al. 2002). Specific statistical methods used in this report to estimate the parameters and biological reference points are detailed in Appendix A.

FACTORS IN THE ESTIMATION OF REFERENCE POINTS

As stated above we use accepted statistical techniques to estimate the production curve and biological reference points. From a practical standpoint, our ability to successfully estimate the production curve and the reference points are linked directly back to the history of the fishery and specifically, the range of historical escapements (Walters and Hilborn 1976, Clark et al. in press). Measurement error is also a factor, where imprecision in estimates of escapement can bias estimates of the reference points (Kehler et al. 2002).

The history of fishing on a salmon stock can determine where the production data we gather on that stock lies on a plot of recruits against escapement (stock-recruit plot). This in turn affects our ability to estimate carrying capacity and/or intrinsic rate of increase needed to estimate reference points. Fisheries with a history of very low harvest rates (<15%) tend to have their production data (recruits plotted against escapement) clumped close to the carrying capacity on the right hand side of the plot. In this case we are likely to have very little knowledge of the intrinsic rate of increase, but good knowledge of what the carrying capacity of the stock might be (Figure 5; Walters and Hilborn 1976).

Conversely, fisheries with a history of high harvest rates (>50% harvested per year) tend to have their production data clumped on the left hand side of the stock-recruit plot. In this case, we have very little knowledge of carrying capacity, but good knowledge of the intrinsic rate of increase

(Figure 5). Fisheries with moderate or variable harvest rates can have production data spread across the stock-recruit plot, resulting in good knowledge of both intrinsic rate of increase and carrying capacity.

Measurement error, especially in estimates of escapement can be a factor in the estimation of reference points. Imprecise estimates of escapement will cause bias in estimates of the reference points (Kehler et al. 2002) and the direction of the bias changes as harvest rate increases. The effect of measurement error is especially troublesome for fisheries with high harvest rates, because the bias tends to result in biological reference points that are too low. Precise estimates of escapement (from towers, weirs, sonars, and mark-recapture experiments) are therefore important for fisheries with a history of high harvest rates.

We also use several alternative methods to estimate reference points for comparison with results from spawner-recruit analyses. A tabular Markov approach is often used to compare yields at various levels of spawner abundance (Hilborn and Walters 1992), but results can be sensitive to how spawner abundances are grouped if data are sparse. When limnological data are available, euphotic volume (Koenings and Burkett 1987) and zooplankton biomass (Koenings and Kyle 1997) models are used to estimate lake carrying capacity. The euphotic volume model is based on lake area and the depth of light penetration sufficient to support net primary production. The zooplankton biomass model utilizes seasonal mean total zooplankton biomass to predict smolt production. Both limnological models are based on the assumption that lake carrying capacity is reached when density-dependent growth causes age-1 smolts to emigrate at a threshold size of 60 mm (2 g). In systems that are thought to be spawning limited, a spawning habitat model has been used (Nelson et al. 2005) to estimate the number of spawners at carrying capacity assuming a mean density of one female per m^2 (Burgner 1991).

FACTORS IN THE DEVELOPMENT OF AN ESCAPEMENT GOAL

Although the estimation of reference points is the centerpiece of scientifically defensible escapement goal analysis, many salmon stocks in Alaska lack sufficient information content on them to estimate reference points or do not have production data. Yet, we would like to recommend an escapement goal in these situations.

The Sustainable Escapement Goal (SEG) is used in these circumstances. SEGs are recommended when we lack estimates of reference points for MSY management, but need a goal that preserves the status quo of sustainable fishing practices observed for many years. Examples of these situations occur below in the section Examples from Alaskan Sockeye Salmon. Methods of determining SEGs are many although the common thread in these methods is that the recommended goal must be based on evidence of producing yields that can be sustained into the future.

Conversely, a Biological Escapement Goal (BEG) is used when the reference points can be estimated and there is sufficient fishing power and inseason management capability to harvest annual runs to achieve the BEG.

A REVIEW OF HYPOTHESES CONCERNING DENSITY DEPENDENCE

Short Term Effects of Overescapement – Single Brood

A general theory of salmon production developed by W.E Ricker and others states that survival (e.g., return-per spawner) decreases with increasing spawner abundance, and stock size is limited by the habitat's carrying capacity. When the escapement goal range brackets S_{MSY}, the biological consequence of overescapement is a higher likelihood of lower future production due to compensatory mortality. Different mechanisms cause compensatory mortality in sockeye salmon populations at various life history stages mostly functioning when the fish reside in freshwater. Much less is known about mechanisms causing mortality in the sea, but once these fish disperse into the open ocean, mortality is likely density independent. Although, Ricker's theory predicts that compensatory mortality is the dominant process regulating salmon production, mortality at various lifestages can also be depensatory. The terms compensatory and depensatory refer to the effect of salmon density on their survival, but in the actual system many different factors interact to cause mortality. Salmon density is only one modifying factor affecting the outcome.

During spawning and embryo development, several mechanisms cause compensatory mortality. High spawner densities cause an increase in egg retention and spawning failure, but together these effects reduce embryo deposition by <3% (West and Mason 1987; Quinn et al. 2007). High spawner densities can also result in redd superimposition leading to an asymptotic relation between spawner density and spawning success (McNeil 1964). Embryos displaced by subsequent waves of spawners often die due to mechanical shock (prior to the eyed stage) and predation mostly by various fishes (Selifonov 1987, Ward and Larkin, 1964, Morton 1982). Once deposited in spawning beds, high embryo densities cause higher mortality due to excessive oxygen demand and increases in fungal or parasite infestations (Hunter 1959, Selifonov 1987).

During juvenile lifestages, several different agents function to cause either depensatory or compensatory mortality. The juvenile period can be divided into six distinct lifestages of various lengths: emergent (1 to 7 days), littoral (1 to 2 months), pelagic feeding (5 to 6 months), overwintering (3 to 4 months), smolt (1 to 2 weeks), and early marine (1 to 2 months). We will next examine the mortality processes functioning within each lifestage.

In the emergent stage, fry mortality is likely size-dependent, depensatory, and buffered by the presence of alternative prey. Many emergent fry migrate through streams to lake rearing habitats suffering intense predation losses mostly to various small fishes (Semko 1954, Foerester 1968, Stober and Hamalainen 1980). Mortality at this lifestage (range 13% to 91%) is likely depensatory, because predator populations consume a relatively fixed number of prey causing a greater proportion of fry to survive when their densities are high (Hunter 1959). However, the presence of other prey fishes (pink and chum salmon fry), in systems where they exist, likely buffers sockeye salmon losses (Semko 1954). Mortality at this lifestage is size-dependent (West and Larkin 1987), but size at this lifestage is mostly determined by egg size (Bilton 1971) because there is little time for growth.

In the littoral zone, fry mortality is likely size-dependent and buffered by the presence of alternative prey. In this lifestage, predation and parasitism are likely important agents of mortality. Starvation seems unlikely since emergent fry can survive up to 4 weeks without food (Bilton and Robins 1973). Potential predators include Dolly Varden charr, rainbow trout, lake trout, juvenile coho salmon, northern pike, Arctic terns and gulls (Hartman and Burgner 1972). Predation on juvenile sockeye salmon fry is likely buffered in these habitats by the presence of other prey fish species such as sticklebacks, cottids, trout fry (Burgner 1991), and large numbers of sockeye salmon smolts which cause predators to aggregate near lake outlets (Ward and Larkin 1964). Parasitism by the cestode *Eubothrium salvelini* likely also causes significant mortality among sockeye fry in littoral habitats, because small fry (<45 mm) are much more susceptible to infection (Boyce 1974, West and Larkin 1987). Infected juveniles exhibit reduced growth and impeded swimming performance making them more susceptible to predation (Boyce 1979, 1982, Boyce and Clarke 1983). Since vulnerability to predators and parasites is size dependent, growth becomes an important factor modifying mortality in this lifestage, because it determines the time individuals spend in the vulnerable size range.

Mortality in the pelagic feeding stage is also likely size-dependent and buffered by the presence of alternative prey, but growth at this time also largely determines survival in the next lifestage. Salmon likely encounter fewer predators in the pelagic zone (Burgner 1991), because most of the fish that feed on them tend to be benthic and inshore feeders (Arctic charr, trout, northern pike). Since alternative prey are sometimes abundant (sticklebacks and whitefish), potential predators often have few salmon in their stomachs (Hartman and Burgner 1972). Although predation rate may be low, predation losses over the entire lifestage may still be substantial, because of its relatively long duration. The various diel and seasonal feeding behaviors and depth preferences exhibited by juvenile sockeye salmon (Burgner 1991) to avoid predation (Eggers 1982) support the notion that predation is an important agent of mortality at this lifestage. Inter- and intra-specific competition for food causes growth to be density dependent during this lifestage, extending the time juveniles spend in vulnerable smaller sizes. Sticklebacks and whitefish are also the primary competitors for food in sockeye salmon rearing lakes in Alaska (Burgner 1991). In Babine Lake, fry mortality was strongly size-dependent (91% <median size; 36% >median size) and greatest during the pelagic feeding period in late summer and autumn (West and Larkin 1987). Overall, salmon mortality during lake residence has ranged from 51-93% during 15 years at Babine Lake (McDonald and Hume 1984).

Whether predation mortality in the littoral and pelagic stages is compensatory or depensatory likely depends upon predator size and abundance and juvenile salmon density and growth. Ward and Larkin (1964) proposed that cyclic dominance in Adams River sockeye salmon resulted from depensatory predation caused by predator satiation. However, even in stocks exhibiting cyclic dominance, mortality must become compensatory, because there exists an upper limit on salmon population size. Modeling studies have revealed that juvenile salmon can achieve high survival rates by forming high density aggregations to satiate predators, but this strategy can only succeed if zooplankton densities are sufficient to support high salmon growth rates in high density aggregations (Willette et al. 2001). When predators were satiated, simulated salmon mortality increased when salmon biomass grew slower than predation rate. Conversely, simulated salmon mortality decreased when salmon biomass grew faster than predation rate. Eventually simulated salmon populations declined below the satiation threshold of predators causing mortality to become compensatory. Thus, predation mortality can be depensatory when predator abundance and size are properly scaled with salmon densities and growth rates, and these conditions likely only exist for a relatively short time. In many rearing lakes, juvenile sockeye salmon growth is density dependent (Goodlad et al. 1974, Rogers et al. 1980, Edmundson and Mazumder 2001), indicating that competition for food limits growth, extending the time individuals spend in the vulnerable smaller size range, causing mortality to be compensatory.

During the overwintering stage, mortality is likely size-dependent and most often caused by predation, but at times is caused by starvation when juveniles are very small. Since growth during winter is negligible (Eggers 1978), mortality is likely compensatory and dependent on growth during the previous lifestage. During winter, juvenile salmon likely remain deep in the water column at low light intensities to avoid piscivore predation, living off stored energy reserves (Eggers 1978). However, resumption of active feeding in late winter when zooplankton densities are still low indicates a response to declining energy reserves (Eggers 1978) that likely increases their predation risk. Edmundson et al. (2001) concluded that lipid reserves of juvenile sockeye salmon rearing in Skilak Lake were very near the minimum required to survive the winter fast. Comparison of salmon length distributions between fall 1993 and the following spring indicated that juveniles <48 mm (0.8 g) did not survive the winter (Edmundson et al. 2001). This size threshold needed to survive over winter is similar to that found in other fish species (Carlson and Kaeding 1991, Paul and Paul 1998). Modeling has demonstrated that the fall distribution of sizes and energy contents of juveniles and the duration of winter likely determine survival (Patrick 2000). The distribution of sizes and energy contents of juvenile sockeye salmon in Skilak Lake indicates that the likelihood of surviving over winter declines for individuals <0.5 g body weight, because more of the juveniles in this smallest size class have energy reserves only slightly above the starvation-mortality threshold (Figure 6). We are continuing research to better estimate the threshold size and energy content needed for sockeye salmon to survive the winter and predict overwinter mortality. However in many rearing lakes, juvenile sockeye salmon grow to mean sizes >1.0 g before winter (Kyle 1992b, Willette et al. 1993, Edmundson et al. 2001), so significant overwinter mortality may be rare among sockeye salmon stocks.

During smolt emigrations and the early marine period, mortality is likely size dependent and depensatory. The primary agent of mortality at this lifestage is most often predation. However, small smolts (<50mm, 1.0g) may not be able to osmoregulate successfully in seawater, and this effect is compounded for individuals that have been parasitized (Boyce and Clarke 1983). Predation at this lifestage is often conspicuous as predators aggregate to feed on smolts at lake outlets and river mouths (Hartman and Burgner 1972, Meacham and Clarke 1979, Ruggerone and Rogers 1984). Estimated depensatory mortality rates due to predation have ranged from 95% at low smolt density to <10% at high smolt density (Ruggerone and Rogers 1984). Individuals successfully transitioning into seawater then encounter a much greater abundance of predators mostly fishes and birds (Willette et al. 2001). Since predation by fishes is often size dependent (Willette 2001), smolt-to-adult survival of Alaskan sockeye salmon increases with smolt size from about 10% at 60 mm to 35% at 90 mm (Figure 7; Koenings and Hasbrouck 1994). Although direct predation losses at this lifestage are depensatory, smolt size is the result of compensatory growth during lake residence, so size-dependent smolt-to-adult survival tends to reinforce compensatory effects.

High spawner (and progeny) abundances tend to force individuals into marginal habitats increasing the level of responses to unfavorable environmental or ecological conditions leading to higher variability in production. Spawners utilize less favorable habitat when densities are high leading to greater embryo mortality due to desiccation and freezing if water levels drop (Selifonov 1987). High juvenile densities may force individuals to migrate out of nearshore or deep overwintering predation refugia leading to increased predation losses (Eggers 1978, Willette 2001). Generally, high spawner abundances create a high production potential, which may or may not be realized depending upon the conditions later encountered by offspring.

Long Term Effects of Overescapement – Delayed Density Dependence

Delayed density dependence has been proposed as one mechanism that could account for the cyclic dominance observed in many sockeye salmon populations (Levy and Wood 1992). However, maintenance of population cycles also requires that age at maturity be somewhat constant (Levy and Wood 1992, Walters and Woodey 1992). The mechanisms causing delayed density dependence could function in populations with variable age at maturity leading to delayed density dependent mortality without persistent population cycles. Population cycles can also be maintained by depensatory fishing independent of depensatory mortality during the freshwater period and delayed-density dependent mortality (Eggers and Rogers 1987). It is often not possible to clearly separate single-brood effects from delayed density dependence, because the two processes are highly confounded, particularly when high spawner abundances occur over consecutive brood years.

Four hypotheses have been proposed to explain the ecological mechanisms causing delayed density dependence in sockeye salmon populations:

(1) The delayed-embryo mortality hypothesis states that high salmon egg densities reduce survival of embryos in subsequent years (Hunter 1959).

(2) The delayed-parasitism hypothesis states that large juvenile salmon populations cause an increase in parasite infestations reducing survival of juveniles in subsequent years (Ricker and Smith 1975).

(3) The delayed-predation hypothesis states that large juvenile salmon populations cause an increase in the abundance of predators reducing survival of juveniles in subsequent years (Ricker 1950).

(4) The delayed-food availability hypothesis states that heavy grazing on zooplankton by juvenile salmon from an abundant year class diminishes the food supply available for successive broods in nursery lakes reducing their survival (Koenings and Kyle 1997).

The delayed-embryo mortality hypothesis was first proposed by Hunter (1959) who investigated instream survival of pink and chum salmon embryos and fry over 10 years. He observed that infertile or dead eggs from large spawning populations persisted in spawning beds for 1-2 years. Two very large spawning populations in 1945 and 1954 apparently reduced egg-to-fry survival of subsequent broods for 2 years (Hunter 1959). He postulated that the high oxygen demand from the residual mass of dead eggs reduced subsequent embryo survival, but residual fungal or parasite infestations are other possible explanations.

Direct evidence supporting the delayed-parasitism hypothesis is weak, but this may be due more to a lack of directed research than lack of functioning mechanisms. Ricker and Smith (1975) documented that infestation by the cestode parasite *Eubothrium salvelini* in Skeena River sockeye salmon smolts reduced mean size 18-35%. They postulated that high juvenile salmon densities may lead to cestode infestations that persist for more than one year. But, a 12-year time series showed no correlation between levels of cestode infestation in smolts and smolt abundance in the current or previous years (Ricker and Smith (1975). However, the authors noted that lack of a correlation at the smolt life stage could result if most infected fry died (Ricker and Smith 1975). Boyce (1974) concluded that shedding of eggs, essential to reproduction of *E. salvelini*, occurred in spring when emergent sockeye salmon fry were most vulnerable to infection, providing a plausible mechanism for transmission from smolts to emergent fry. The copepod *Cyclops*, which is common in Alaskan lakes, was also identified as an intermediate host whereby infections could be transmitted to sockeye salmon fry through feeding (Boyce 1974). West and Larkin (1987) suggested that parasitism by *E. salvelini* was one mechanism that could account for strong size-dependent mortality among emergent sockeye salmon fry in Babine Lake. Further studies are needed to examine whether levels of infestation in emergent fry are related to levels of infestation in smolts and subsequent fry survival.

The delayed-predation hypothesis, first proposed by Ricker (1950), is strongly supported by extensive field and modeling studies conducted by Ward and Larkin (1964) in Shuswap Lake, British Columbia (Ricker 1997). The hypothesis involves depensatory predation on the dominant broodline, and a delayed predator response affecting subsequent broods. Ward and Larkin (1964) postulated that large juvenile sockeye salmon populations increased the reproductive success of predacious fishes (primarily rainbow trout) increasing predation losses of subsequent juvenile salmon populations. They documented that rainbow trout fed primarily on juvenile salmon from egg deposition through smoltification, and that trout stomach fullness and condition was correlated with juvenile salmon abundance. They documented a numerical response of trout populations to the abundance of juvenile salmon prey, i.e. cyclic changes in trout abundance that lagged salmon abundance. Levy and Wood (1992) suggested that depensatory predation must occur on emergent fry populations to account for the variable cyclic dominance patterns observed in the various stocks rearing in Shuswap Lake. Larkin (1971) developed a simulation model incorporating a delayed-predation mechanism that successfully reproduced the observed pattern of cyclic dominance in this stock. Ward and Larkin’s (1964) conceptual model had the great merit of accounting for the fact that brood line 2 is usually much more abundant than brood lines 3 or 4 due to the buffering effect of brood line 1 on their predation losses (Ricker 1997). However, more recent estimates of juvenile salmon survival suggest that the overall mortality caused by predators (mostly squawfish) in Shuswap Lake is compensatory not depensatory (Williams et al. 1989). The extent to which this mechanism may function in other sockeye salmon populations is unclear. Although some studies have examined functional responses of fish predators to sockeye salmon abundance (Rogers et al. 1972, Morton 1982, Ruggerone and Rogers 1982), none have provided data sufficient to support a delayed-predation hypothesis.

Whole lake experiments have produced strong evidence supporting the delayed-food availability hypothesis (Koenings and Kyle 1997), but evidence of this mechanism in naturally-producing sockeye salmon populations is limited. In whole-lake experiments, grazing by large juvenile sockeye salmon populations reduced zooplankton biomass up to 90%, created predator-resistant zooplankton communities, and reduced fry-to-smolt survival up to 75% (Koenings and Kyle 1997). Zooplankton communities became resistant to predation as the vulnerable *Daphnia*, *Diaptomus*, and ovigerous *Cyclops* were virtually eliminated, and the more agile nonovigerous *Cyclops* and smaller *Bosmina* became dominant (Koenings and Kyle 1997). The reduction in zooplankton biomass and development of a predator-resistant community increased the second year after initial treatment causing the greatest reduction in fry-to-smolt survival to also be delayed (Koenings and Kyle 1997). Once restructured by excessive grazing, zooplankton communities exhibiting the highest levels of restructuring were slowest to respond to either reduced grazing or nutrient treatment (Koenings and Kyle 1997). These experiments revealed a mechanism causing delayed density-dependent salmon survival when spawner abundances exceed the carrying capacity of rearing lakes for 2 or more consecutive years.

One manifestation of diminished food availability is the tendency for smaller members of a year class to migrate to sea a year later further increasing competition for food in subsequent years. As juvenile densities increased at Leisure Lake, the size of age-1 smolts declined from 97 to 60 mm and the fraction of the population holding over to emigrate at age 2 increased from 3% to 76% (Koenings and Burkett 1987). In the Kvichak watershed, high escapements in the preceding brood year tended to reduce age-1 smolt size and survival in the current year perhaps through exhaustion of the food supply (Burgner 1991). In Becharof Lake, high smolt abundances were correlated with an increase in the proportion of holdover age-2 smolts in the subsequent year class indicating that large juvenile populations reduced the food available for subsequent broods causing them to extend their freshwater residence and increasing competition among broods (Martin and Lloyd 1996).

EXAMPLES FROM ALASKAN SOCKEYE SALMON

The effects of overescapement on Alaskan sockeye salmon were examined by researching existing fisheries and analyzing adult production data from around the state. We searched recent escapement goal analyses for sockeye salmon stocks in Alaska and found published or readily available brood tables for 40 stocks. With some minor exceptions, we attempted to use only published production data (Table 1) so that the fishery descriptions and brood tables need not be reproduced in this report. We coalesced return and escapement data from sockeye salmon stocks from Southeast Alaska and Yakutat (11 stocks), Prince William Sound (3 stocks), upper Cook Inlet (4 stocks), Kodiak (9 stocks), Chignik (2 stocks), the Alaska Peninsula (2 stocks), Bristol Bay (8 stocks) and Kuskokwim Bay (1 stock). Run size for these 40 stocks range from less than 10,000 (Lost) to more than 55 million (Kvichak) fish and represent a wide range of life history characteristics (differing freshwater and ocean ages at return), rearing lakes (stained, glacial, and clear), and drainage area (small to very large drainages). Twenty of the stocks currently have BEGs and 20 stocks have SEGs.

To better compare and describe the effects of overescapement, the same production model was used and the same set of statistical analyses was performed on each stock. Note that the stock-recruit analyses presented herein were only used for comparison purposes in the discussion of overescapement, and may not match the case-specific analyses performed and models used during the cycle of escapement goal reviews (see Table 1 for references to escapement goal reviews by management area). In many cases, the case-specific analyses used a variety of production models, statistical methods, and/or truncated production data sets. Moreover, these case-specific analyses addressed issues such as model selection, changes in data quality over time, and statistical versus practical considerations that could not be replicated in a single analysis of the 40 stocks analyzed in this report.

Simple stock-recruitment analyses were performed on data from each stock to estimate parameters and reference points (see Appendix A for analytical methods). From a long-term biological perspective, we were most interested in estimating: 1) the exploitation rate at MSY or μ_{MSY}, 2) escapement at MSY or S_{MSY}, 3) MSY, and 4) the carrying capacity or S_{EQ}. In our analysis, a Ricker production model was used to estimate these parameters, although other production models have been used to estimate reference points and set escapement goals for some Alaskan sockeye salmon stocks (e.g., a gamma model for Ayakulik River and a brood-interaction model for Kenai River). As an index of sampling error we calculated the non-parametric coefficient of variation (NPCV) for each reference point. From the brood table we also calculated the observed exploitation rate or $\mu_{OBS,}$ and average yields when escapements were within and above the current escapement goal. Note that the observed exploitation rate calculated as in Appendix A is not strictly equivalent to the average harvest rate in the fishery. Observed exploitation rate in this context is used to compare with exploitation rate at MSY in determining the range of data available to estimate the biological reference points and should not be misconstrued as a parameter for management of the fishery. We also plotted returns on escapement and return per spawner on escapement for each stock (Appendix B).

In addition, several metrics were developed to evaluate short-term fishery-related effects of overescapement. We used these analyses to determine the percent occurrence of overescapement, the average loss of harvest due to overescapement, and the percentage of the annual run foregone to overescapement in the most recent 15 run years (see Appendix A for analytical methods). We also plotted the annual run divided into harvest and escapement, and the percent difference between the observed escapement and the upper bound of the goal for the most recent 15 run years (Appendix B).

BIOLOGICAL ASPECTS OF OVERESCAPEMENT

The biological aspects of overescapement can be examined in relation to reliable estimates of the reference points. Although other methods are available for calculating reference points, we used a statistical approach to model production of adult sockeye salmon and based our definition of "reliable" on the non-parametric coefficient of variation (NPCV) of the estimate of S_{EQ} or carrying capacity. We used the arbitrary criterion of NPCV less than 0.25 (similar to a CV of 25% or less) as our measure of reliability.

Based on this approach we could reliably estimate S_{EQ} for 27 of the 40 stocks (Appendix C). In general, we were able to reliably estimate S_{EQ} if the observed exploitation rate was less than or equal to the exploitation rate at MSY (Figure 8). Similarly, 29 of the 40 stocks had observed exploitation rates that were less than or equal to exploitation rate at MSY (Figure 8). Twenty seven of these 29 stocks had a reliable estimate of S_{EQ}, but two stocks did not (East Alsek and Ugashik). Based on these results we ultimately chose the criterion of an observed exploitation rate less than or equal to exploitation rate at MSY to differentiate those stocks with exploitation rates near or below MSY (29 stocks) and those with exploitation rates above MSY (11 stocks). All subsequent analyses were done using these two groups of stocks. Note that our Ricker model estimates of the exploitation rate at MSY can differ from those estimated using other spawner-recruit models. For example, the brood-interaction model used to set the escapement goal range for Kenai River sockeye salmon estimated μ_{MSY} at 0.81 (Carlson et al. 1999); whereas, the Ricker model estimate of μ_{MSY} is 0.74.

OVERESCAPEMENT IN RELATION TO CARRYING CAPACITY

Next we examined whether overescapements, when they occur, are approaching or exceeding carrying capacity. For the 29 stocks with an observed exploitation rate less than or equal to exploitation rate at MSY we calculated the percentage of brood years where the escapement was equal to or exceeded the estimate of S_{EQ} (Appendix B1). The percentage of time the observed escapement was above S_{EQ} ranged from 0% to 25% and was a function of the observed exploitation rate on the stock (Figure 9). Many of the stocks with higher rates (>10% of the time) of escapements approaching carrying capacity are those with low fishery exploitation rates such as Situk, Redoubt, Klukshu, Italio, Akwe, and Speel in Southeast Alaska; Buskin and Afognak on Kodiak Island; Crescent in upper Cook Inlet; as well as Middle Fork Goodnews in Kuskokwim Bay (Figure 9).

OVERESCAPEMENT IN RELATION TO PRODUCING MSY OR SUSTAINED YIELDS

For those stocks with an observed exploitation rate less than or equal to exploitation rate at MSY, we can compare yields at differing levels of escapement to see if yields are reduced as escapement increases above that needed to produce MSY. As expected, a composite graph of the 29 stocks indicates that yields tend to be maximized as escapements approach that needed to produce MSY (Figure 10). Conversely, yields tended to be reduced as escapements exceeded that needed to produce MSY. Also, MSY was achieved at least part of the time over a wide range of escapements until they exceeded 200% of escapement that produces MSY. This result is also confirmed by inspection of the stock-recruitment relationships estimated from brood tables for each stock (upper panels in Appendices B3-B40).

Similar results were obtained when we compared average yields when escapements fell within the current escapement goal to average yields when overescapement occurred. Twenty-two of 29 stocks exhibited a decrease in average yield when overescapement occurred. Averaged across all 29 stocks, yields decreased 48% when overescapement occurred relative to when the current escapement goal was met (Table 2). On average, variability in yields increased 278% as overescapement occurred (Table 2).

Although we could not reliably estimate S_{MSY} using a Ricker model for the 11 of 40 stocks where observed exploitation rate is greater than the exploitation rate at MSY, we were able to compare trends in yields as escapements increased above the upper end of the current escapement goal. For these stocks, yields tended to continue to increase above the average as overescapement occurred (Figure 11). Above average yields tended to occur over the entire range of observed escapements indicating that yields are being sustained from these stocks.

A similar result was obtained when we compared average yields for escapements that fell within the current escapement goal to average yields when overescapement occurred. Seven of 11 stocks exhibited an increase in average yield when overescapement occurred. Averaged across all 11 stocks, yields increased 94% when overescapement occurred relative to when the current escapement goal was met (Table 3). On average, variability in yields decreased 11% as overescapement occurred (Table 3).

DELAYED DENSITY DEPENDENCE

Five examples of delayed-food availability responses can be found among sockeye salmon rearing lakes in Alaska. However, single-brood and delayed-density dependent effects are highly confounded when high spawner abundances occur over consecutive brood years.

In Frazer Lake, three consecutive overescapements (>2 times the upper bound of the escapement goal range) in 1980-1982 resulted in a decline in production from subsequent broods in 1981 and 1982 when returns per spawner fell below replacement (Figure 12). Reduced sockeye salmon production was associated with a decline in macrozooplankton density from 3,590m^{-3} (1970-1976) when escapements were within the current escapement goal range to 140m^{-3} in 1981-1982 (Kyle et al. 1988). The average length of the smallest macrozooplankter (*Bosmina*) shifted below the observed threshold size (0.40 mm) for juvenile sockeye salmon prey, and *Bosmina* became the dominant macrozooplankton species in the lake (Kyle et al. 1988). These changes in the macrozooplankton community were associated with a decline in smolt length from 90 to 70 mm that persisted for 4 years even after escapement levels declined (Kyle et al. 1988). A single overescapement (3 times the upper bound of the escapement goal range) in 1985 resulted in a return per spawner below replacement, but an escapement within the goal range the following year resulted in record high production (Figure 12). Thus at Frazer Lake, consecutive overescapements produced an apparent delayed-density dependent response, but a single overescapement resulted in a single-brood response.

In Afognak Lake, three consecutive overescapements (>2 times the upper bound of the escapement goal range) in 1995-1997 resulted in a decline in production from subsequent broods in 1996 and 1997 when returns per spawner fell below replacement (Figure 12). As in Frazer Lake, reduced sockeye salmon production was associated with a decline in macrozooplankton biomass from 670 mg m^{-2} for brood year 1995 to 221 mg m^{-2} for brood years 1996-1997 (Baer et al. 2007). During this same time period, the biomass of *Daphnia*, a preferred sockeye salmon prey, declined from 44 mg m^{-2} to 15 mg m^{-2}, and the mean length of *Daphnia* declined from 0.78 to 0.57 mm (Baer et al. 2007). A similar overescapement (>2 times the upper bound of the escapement goal range) in 1982 resulted in a return per spawner below replacement from the 1983 year class, but no limnological data is available from this time period. Several other smaller overescapements (<2 times the upper bound of the escapement goal range) in 1984-1985 and 1989-1994 did not result in returns per spawner falling below replacement. However, the production history of Afognak Lake sockeye salmon is confounded by lake fertilization (1990-2000) and fry stocking programs (1992, 1994, 1996-1998).

In Coghill Lake, several consecutive years of overescapement in 1980-1982, 1985, and 1987 (>2 times the upper bound of the escapement goal range) were associated with a decline in production from subsequent broods in 1985-1989 when returns per spawner fell below replacement (Figure 12). Although, no limnological data were available for the period before the overescapement events, Edmundson et al. (1997) postulated that the decline in production could have been caused by overgrazing by large juvenile sockeye salmon populations as had been previously documented in Frazer Lake. The small average size (1.5 g) of smolt emigrating from Coghill Lake in the early 1990's supported this hypothesis (Edmundson et al. 1997). After 1989, escapements were maintained within the escapement goal range, the lake was fertilized for 4 years (1993-1996), and sockeye salmon production returned to normal levels (Figure 12).

In the Chignik watershed, overescapements have occurred in both early and late sockeye salmon runs from 1998 through 2001, with the combined escapements for both runs nearly double the upper range of the goals in 2001. The early run spawns in Black Lake (and tributaries) and the late run spawns in Chignik Lake, but in recent years the juveniles from both runs have overwintered in Chignik Lake. Limnological studies of Chignik Lake documented a threefold decline in macrozooplankton biomass between 1991 (Kyle 1992a) and 2000-2002 (Bouwens and Finkle 2003). During the later period, the zooplankton community was dominated by *Bosmina* and *Cyclops*, both inefficient grazers on phytoplankton, and *Daphnia*, a preferred sockeye salmon prey, was nearly absent (Bouwens and Finkle 2003). In addition, the mean size of *Bosmina* was below the threshold size for juvenile sockeye salmon prey (Bouwens and Finkle 2003). Further, chlorophyll *a* levels were high but macrozooplankton biomass was low indicating inefficient energy transfer from primary producers to primary consumers, attributable to top-down grazing pressure (Bouwens and Finkle 2003). In 2003, only 6.75 million sockeye salmon smolts emigrated from the system compared with an average of 20 million smolts per year from 1997-2002 (Bouwens and Finkle 2003). The adult return from brood year 2001 was about 1.6 million, about 43% below the recent 20-year average (1978-1997).

In the Kenai watershed, overescapements in 1987 through 1989 (~1.5 times the upper bound of the escapement goal range) were associated with below average returns per spawner from brood years 1988-1990 (Figure 12). About 75% of the juvenile sockeye salmon produced in this system rear in glacially turbid Skilak Lake. Limnological studies of this lake documented a 50% decline in spring (May-June) copepod biomass in 1988 and 1990 following these overescapements (Edmundson et al. 2003). These observations led to the hypothesis that grazing by large fry populations reduced the biomass of copepods available for emergent fry the following spring reducing their survival. This hypothesis was supported by a weak statistical relationship between fall fry abundance and copepod biomass the following spring, and a significant statistical relationship between spawner abundance, spring copepod biomass, and fall fry abundance (Edmundson et al. 2003). Subsequently, a brood-interaction model was found to provide the best fit to the spawner-recruit data for this stock (Carlson et al. 1999), and in 1999 a brood-interaction simulation model was used to establish the current escapement goal range (Fried 1999). Edmundson et al. (2003) also found that euphotic zone depths in Skilak Lake had declined over the past 20 years due to increased glacial melt and attendant silt loading. Since euphotic zone depth directly affects primary production, these changes were associated with a 50% reduction in zooplankton biomass and the size of sockeye salmon fry in the fall (Edmundson et al. 2003).

More recent overescapements (~1.5 times the upper bound of the escapement goal range) in the Kenai watershed in 2004-2006 have raised concerns about future production, because productivity in Skilak Lake is currently about 35% lower than in the late 1980s, and the overescapements have occurred consecutively. The 2004 year class produced the largest fall fry population (DeCino and Willette 2004) and the smallest fall fry ever observed in Skilak Lake (Table 4), raising concerns about overwinter mortality (Edmundson et al. 2003). The 2005 year class produced the smallest fall fry population and the lowest egg-to-fry survival ever observed in Skilak Lake (Table 4). Juvenile production data from the 2006 year class are not yet available. The outcome of these overescapements will not be known until adults from these year classes begin to return in 2009.

OVERESCAPEMENT AND JUVENILE SIZE

One manifestation of overescapement is changes in juvenile sockeye salmon size caused by density-dependent growth. The overall relationship between smolt size and production can be viewed within the context of the Beverton-Holt and Ricker production models (Figure 13). In general, the Beverton-Holt model is appropriate when there is a ceiling of abundance imposed by available food or habitat. Whereas, the Ricker model is appropriate when compensatory mortality results from overseeding of spawning beds, or density-dependent growth extends the time in a vulnerable size range (Ricker 1975). As spawner and juvenile abundances increase, juvenile growth becomes density dependent due to competition for limited food resources. In systems that are rearing limited (Beverton-Holt model), smolt size will reach a constant minimum when juvenile abundance reaches a maximum (Figure 13). However, in systems that are spawning limited (Ricker model), smolt size will increase at spawner densities greater than the escapement that produces the maximum return, because juvenile abundance declines due to compensatory mortality of embryos. When top-down effects reduce food available to juveniles and intraspecific competition increases holdovers, age-1 smolt size will continue to decline as spawner abundance increases even though age-1 smolt abundance declines. These top-down effects may only be observed when spawner abundances are more than two times S_{MSY} over consecutive broods and may not be adequately described by a Ricker model (Koenings and Kyle 1997). At very high spawner and juvenile abundances, juveniles cannot sequester sufficient energy reserves to survive over winter, causing smolt size to reach a constant minimum slightly above the starvation-mortality threshold (Figure 6).

FISHERY-RELATED ASPECTS OF OVERESCAPEMENT

The fishery-related aspects of overescapement can be examined for all 40 sockeye salmon stocks and do not require that we know the production relationship or have a reliable estimate of the biological reference points. When overescapement occurs, harvest is foregone and the additional escapement can affect subsequent production and yield as we have shown in the previous section of this report. In this section, we focus on the immediate loss of harvest due to overescapement relative to the magnitude of the run. Plots of the annual run broken into harvest and escapement by run year (lower left panel) and the percent difference between the upper bound of the escapement goal and the observed escapement by run size (lower right panel) are in Appendices B3-B40.

OVERESCAPEMENT IN RELATION TO FOREGONE HARVEST

The simplest metric of overescapement is the frequency of its occurrence. Only three of the 40 stocks did not experience overescapement in at least one year during the most recent 15 years of published data and based on the current escapement goal range (Appendix B2). The percentage of years where overescapement occurred ranged from 0% (Italio, East Alsek, and Upper Station LR stocks) to 93% of the time or 14 out of the 15 years (Karluk ER, Frazer, and Chignik LR stocks). The frequency of overescapement did not appear related to the observed exploitation rate of each stock, although overescapement occurred more frequently in stocks where the observed exploitation rate is less than the exploitation rate at MSY (Figure 14).

A better metric would be to look at the loss in harvest due to overescapement. By averaging the number of fish forgone in the harvest due to overescapement in the most recent 15 years ($\overline{H}_{LOST}$) we see that some loss of harvest occurred in 37 of 40 stocks indicating that some overescapement is occurring with regularity (Appendix B2). Many of the stocks that regularly overescape have fairly low exploitation rates indicating a lack of fishing power, or unexpectedly large runs, or the presence of management or economic constraints on the fishery.

The magnitude of foregone harvest should also be considered since this potentially affects the total benefits (e.g., ex-vessel value, fishing-related employment, economic impact) of the harvest to the fishery. Overescapements may occur more frequently when the run is large (lower right panel of Appendices B3-B40). Moreover, the effect on benefits accrued to the fishery could be significant if foregone harvest is a large percentage of the run. Eighteen of the 40 stocks had average losses ($\overline{\%H}_{LOST}$) that were 5% or greater of the run (Appendix B2). Of these 18 stocks seven had losses that exceeded 10% of the run on average (Speel, Redoubt, Akwe, Karluk ER, Karluk LR, Saltery, and Afognak stocks). Eighteen of the 40 stocks had average losses during the years that overescapement occurred ($\overline{\%H}_{OVER}$) that were 10% or greater of the run (Appendix B2). Of these 18 stocks, seven had losses that exceeded 20% of the run on average (Speel, Redoubt, Lost, Akwe, Ayakulik, Saltery, and Afognak stocks). Foregone harvest was related to fishing power, with stocks that do not achieve the exploitation rate at MSY showing the greatest losses in harvest (Figure 15).

CONCLUSIONS

In this report, overescapement was defined as escapements that are above the range of the current escapement goal. For most of the 40 Alaskan sockeye salmon stocks we reviewed, overescapement occurred at least once in a recent 15 year period. Although overescapement was easy to detect, the biological and fishery-related effects of overescapement were more difficult to detect and assess. Much of the difficulty is due to the life history characteristics of sockeye salmon, with their variable freshwater and marine residence times, dependence on lakes for rearing, and variable size at smoltification causing highly variable, often time-dependent, density independent changes in survival from spawning adult to returning adult. Moreover, Alaska's fixed escapement goal policy and the precautionary nature of the sustainable salmon fisheries management policy dictates that this high variability in survival is largely borne by the fishery as variable harvests that may sometimes be forgone.

We found evidence of delayed density dependence in five Alaskan sockeye salmon stocks. In three of these stocks, returns per spawner fell below replacement for 2 to 5 years following consecutive overescapements that were greater than twice the upper escapement goal range. These observations were consistent with results from whole lake experiments that have shown that overgrazing by large fry populations for 2 or more consecutive years caused the highest level of restructuring of zooplankton populations and the slowest recovery time (Koenings and Kyle 1997).

However, as seen in the review of salmon stocks in British Columbia (Walters et al. 2004) we did not observe long-term stock collapse of any of the 40 stocks that could be attributed to overescapement. We did observe one stock that failed to produce sustained yields on average (Italio, Appendix B7). The watershed that supports this stock (Italio River) has undergone significant natural changes in habitat, leading to a loss of productive capacity and a closure of the fishery.

We were able to assess the density dependent biological effects of overescapement for 29 of the 40 stocks. These are stocks where observed exploitation rate is less than or equal to exploitation rate at MSY. As expected, yields increased as escapements approached the escapement that produces MSY and then decreased as escapements exceeded this value. Although some stocks exhibited increases in yields, when averaged across these 29 stocks, overescapement resulted in a decrease in yields and an increase in the variability in yields.

This result is consistent with the generic theory of compensatory production, where spawning efficiency decreases with increasing escapement levels and stocks are limited by the carrying capacity of the habitat. Overescapement, in general, is not sustainable as it causes returns and yields to decrease in the next generation, which also result in lower escapements. Lower escapements then result in higher returns and yields in succeeding generations.

For the remaining 11 stocks where observed exploitation rate is greater than exploitation rate at MSY, we found that yields tended to increase as escapements increased, even when overescapement occurred. Although four stocks exhibited decreases in yield (McDonald, Kenai, Ayakulik, and Upper Station ER), when averaged across all 11 stocks, overescapement resulted in an increase in yields and a slight decrease in variability in yields.

This result is also consistent with the generic theory of compensatory production. As escapement increases, but is below the level thought to produce MSY, returns and yields will increase even if overescapement occurs. This is due to the high productivity of salmon across a wide range of intermediate escapements so that the long term change in yield due to overescapement is small when exploitation rate is high.

Foregone harvest due to overescapement occurred in 37 of the 40 stocks we reviewed. In many stocks these annual losses were a small percentage of run size, often less than 5% of the run when averaged across all 15 years in the analysis. Seven of these 40 stocks exhibited average annual losses in harvest due to overescapement that ranged from 10% to 21% of the run. When we examined foregone harvest only during years that overescapement occurred, 18 stocks exhibited losses greater than 10% of the run, and seven of these stocks exhibited losses greater than 20% of the run. Lack of fishing power, especially during large runs appears to cause these larger losses.

RECOMMENDATIONS

Although overescapement as defined is occurring on most of the 40 Alaskan sockeye salmon stocks we reviewed, for some of these stocks more information is needed to understand the effect overescapement may or may not have on production and the fishery. Salmon fisheries are not controlled experiments and thus are not easily adapted to the basic tools of science such as replication or the use of controls. However, there are some recommendations we can make to look further into the effects of overescapement.

Alternative methods for determination of carrying capacity of sockeye salmon watersheds should be developed and validated. Limnological methods of determining maximum smolt capacity already exist (e.g., Koenings and Kyle 1997), but should be validated in systems that have independently derived and reliable estimates of carrying capacity. Coring of lake bottoms and measurement of proxies for marine derived nutrients in the sediments has shown considerable promise in systems that support primarily sockeye salmon and have nearby fishless control lakes (e.g., Schindler et al. 2005). Meta-analyses of existing sockeye salmon data should be conducted to see if there are correlates to carrying capacity similar to those shown for Chinook salmon *Oncorhynchus tshawytscha* and watershed area (Parken et al. 2004). The analyses presented herein could form the basis of such a meta-analysis.

Along these same lines, a modeling effort could be attempted that incorporates all of the previously discussed hypotheses concerning density dependence (e.g., predators, zooplankton, spawner densities) as special cases. This model would be formulated as a hierarchical meta-analysis that would produce an analysis of uncertainty in the model outputs such as changes in yield from differing levels of escapement. Similarly, a statistical or graphical analysis of the factors affecting and significance of delayed density dependence could be attempted.

Research focused on estimating carrying capacity in select watersheds should include efforts to better define the threshold juvenile salmon densities that cause delayed density-dependent responses in rearing lake ecosystems. A fundamental assumption of classical spawner-recruit analyses is that productivity of the system does not change over time, processes causing a non-linear response between spawner abundance and future productivity must be understood to properly set escapement goals.

Further research is needed to better define the levels of spawner and fry abundances that can significantly reduce zooplankton biomass, develop a predator-resistant zooplankton community, and reduce sockeye salmon survival. Lack of consensus among salmon biologists regarding the significance of these processes in sockeye salmon population dynamics has been due in part to our lack of understanding of the threshold population densities needed to evoke an ecological response. This has been further complicated by the fact that these threshold salmon densities likely change over time as bottom-up influences change primary productivity. As a result, lack of a response at population densities thought to be sufficient has been interpreted as evidence refuting the mechanism. A program monitoring limnological parameters, zooplankton biomass and species composition, fry and smolt size and abundance should be implemented in sockeye salmon rearing lakes that are likely to experience high escapement levels. These data are needed to improve the efficacy of escapement goal analyses, since responses that only function above a poorly understood threshold are not amenable to statistical time-series analyses typically used to set salmon escapement goals.

From a fishery standpoint, better forecasts of salmon runs and improved inseason management could reduce the incidence of overescapement in highly exploited stocks. Assessments would improve with more accurate catch apportionments in mixed-stock fisheries through the use of genetic stock identification techniques. Our understanding of the factors that affect density independent survival could greatly improve forecasting ability and the management of fisheries to attain escapement goals. Assessments of marine survival of smolts and enumeration of smolt produced from varying levels of escapement would aid in an understanding of the effects of process error in marine versus freshwater environments. In addition to foregone harvests, better economic data from sockeye salmon fisheries statewide could help to determine the effect of overescapement on benefits accrued to these fisheries.

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TABLES AND FIGURES

Table 1.–Sockeye salmon stocks, assessment methods, brood years available, goal type, escapement goals, and source citations used in this report.

Area	Stock	Assessment	Brood yrs	Goal Type	Lower	Upper	Citation[a]
Southeast	Chilkat	Weir/M-R	19	SEG	80,000	200,000	1
	Chilkoot	Weir/M-R	19	SEG	50,000	90,000	1
	Speel	Weir	14	BEG	4,000	13,000	1
	McDonald	Foot survey	17	SEG	70,000	100,000	3
Yakutat	Italio	Peak aerial	26	BEG	5,000	14,000	1
	Situk	Weir	22	BEG	30,000	70,000	1
	Redoubt	Weir	15	BEG	10,000	25,000	1
	East Alsek-Doame	Peak aerial	26	BEG	26,000	57,000	1
	Klukshu	Weir	21	BEG	7,500	15,000	1
	Lost	Peak foot	14	BEG	1,538	3,538	2
	Akwe	Peak aerial	13	BEG	6,000	15,000	2
PWS	Eshamy	Weir	27	BEG	20,000	40,000	4
	Coghill	Weir	37	SEG	20,000	40,000	4
	Copper	Sonar	39	SEG	410,000	760,000	4
Upper Cook Inlet	Kenai	Sonar	32	SEG	500,000	800,000	5
	Kasilof	Sonar	31	BEG	150,000	250,000	5
	Crescent	Sonar	31	BEG	30,000	70,000	5
	Russian ER	Weir	33	SEG	14,000	37,000	5
Kodiak	Karluk ER	Weir	16	BEG	100,000	210,000	6
	Karluk LR	Weir	16	BEG	170,000	380,000	6
	Ayakulik	Weir	33	SEG	200,000	500,000	6
	Upper Station ER	Weir	29	SEG	30,000	65,000	6
	Upper Station LR	Weir	29	BEG	120,000	265,000	6
	Frazer	Weir	30	BEG	70,000	150,000	6
	Saltery	Weir	21	BEG	15,000	30,000	6
	Buskin	Weir	8	SEG	8,000	13,000	6
	Afognak	Weir	16	BEG	20,000	50,000	6
Chignik	Chignik ER	Weir	46	SEG	350,000	400,000	7
	Chignik LR	Weir	46	SEG	200,000	250,000	7

- continued -

Table 1. Page 2 of 2.

Area	Stock	Assessment	Brood yrs	Goal Type	Lower	Upper	Citation[a]
AK Peninsula	Nelson	Weir	23	BEG	97,000	219,000	8
	Bear LR	Weir	16	SEG	117,000	195,000	8
Bristol Bay	Kvichak	Tower	44	SEG	2,000,000	10,000,000	9
	Naknek	Tower	44	SEG	800,000	1,400,000	9
	Egegik	Tower	42	SEG	800,000	1,400,000	9
	Ugashik	Tower	42	SEG	500,000	1,200,000	9
	Wood	Tower	44	SEG	700,000	1,500,000	9
	Igushik	Tower	44	SEG	150,000	300,000	9
	Nushagak	Sonar	21	SEG	340,000	760,000	9
	Togiak	Tower	43	BEG	120,000	270,000	9
Kuskokwim Bay	Middle Fork Goodnews	Weir	18	BEG	18,000	40,000	10

[a] Citations:

1. Geiger et al. 2004.
2. Clark et al. 1995.
3. Johnson et al. 2005.
4. Evenson et al. unpublished.
5. Hasbrouck and Edmundson 2007.
6. Nelson et al. 2005.
7. Witteveen et al. 2005.
8. Nelson et al. 2006/
9. Baker et al. 2006.
10. Molyneaux and Brannian 2006.

Table 2.–Average yields and coefficient of variation within and above current escapement goals for 29 sockeye salmon stocks with observed exploitation rate less than or equal to exploitation rate at MSY. μMSY is calculated from a Ricker model.

					Within goal range			Above goal range			Percent difference	
Stock	Goal Type	μ_{OBS}	μ_{MSY}	Harvest rate	Yield	n	CV	Yield	n	CV	Yield	CV
Chilkat	SEG	0.64	0.69	0.47	131,072	9	64%	209,148	1	0%	60%	-64%
Speel	BEG	0.29	0.86	0.31	6,424	5	104%	-8,390	6	189%	-231%	85%
Italio	BEG	-0.04	0.38	0.06	3,960	11	271%	-6,167	10	171%	-256%	-101%
Situk	BEG	0.33	0.56	0.43	45,648	9	63%	37,053	13	223%	-19%	159%
Redoubt	BEG	0.32	0.75	0.07	27,605	5	141%	-4,680	6	535%	-117%	394%
East Alsek	BEG	0.56	0.58	0.42	68,823	19	120%	83,738	3	30%	22%	-90%
Klukshu	BEG	0.27	0.56	0.35	8,446	8	88%	3,905	12	319%	-54%	231%
Lost	BEG	0.42	0.69	0.43	4,507	6	58%	1,936	8	220%	-57%	162%
Akwe	BEG	0.36	0.58	0.39	15,868	6	95%	-1,337	5	541%	-108%	447%
Eshamy	BEG	0.65	0.77	0.58	33,336	8	84%	60,244	4	187%	81%	103%
Coghill	SEG	0.69	0.78	0.65	179,845	14	172%	87,880	16	190%	-51%	18%
Copper	SEG	0.67	0.70	0.71	1,090,198	23	64%	871,862	3	22%	-20%	-42%
Kasilof	BEG	0.77	0.77	0.70	847,581	12	46%	518,264	5	75%	-39%	30%
Crescent	BEG	0.46	0.62	0.38	64,821	15	85%	46,573	11	195%	-28%	109%
Karluk ER	BEG	0.46	0.69	0.33	270,682	2	4%	197,829	13	85%	-27%	81%
Karluk LR	BEG	0.48	0.74	0.37	305,736	3	22%	356,683	10	143%	17%	121%

-continued-

Table 2. Page 2 of 2.

					Within goal range			Above goal range			Percent difference	
Stock	Goal type	μ_{OBS}	μ_{MSY}	Harvest rate	Yield	n	CV%	Yield	n	CV%	Yield	CV
Frazer	BEG	0.62	0.75	0.36	521,394	6	154%	255,947	13	167%	-51%	12%
Saltery	BEG	0.33	0.64	0.27	51,636	7	70%	3,920	14	1002%	-92%	933%
Buskin	SEG	0.52	0.72	0.41	14,462	6	64%	4,574	2	10%	-68%	-54%
Afognak	BEG	0.22	0.69	0.20	48,490	4	134%	13,504	12	556%	-72%	422%
Chignik LR	SEG	0.71	0.73	0.67	805,354	11	69%	652,871	28	63%	-19%	-6%
Nelson	BEG	0.57	0.71	0.55	367,614	11	38%	224,330	12	89%	-39%	51%
Bear LR	SEG	0.75	0.81	0.73	417,079	4	71%	490,698	7	63%	18%	-8%
Ugashik	SEG	0.69	0.72	0.56	2,089,595	14	105%	2,988,014	10	69%	43%	-36%
Wood	SEG	0.61	0.62	0.57	1,969,359	26	71%	1,989,900	9	117%	1%	46%
Igushik	SEG	0.63	0.73	0.62	866,312	14	120%	482,366	21	178%	-44%	58%
Nushagak	SEG	0.57	0.62	0.65	1,019,529	16	57%	-36,604	3	4727%	-104%	4670%
Togiak	BEG	0.68	0.68	0.63	477,061	23	80%	207,866	6	140%	-56%	60%
MF Goodnews	BEG	0.25	0.53	0.23	15,808	10	153%	5,106	7	424%	-68%	271%
Average		0.50	0.68	0.45	405,801		92%	335,760		370%	-48%	278%

Table 3.–Average yields and coefficients of variation within and above current escapement goals for 11 sockeye salmon stocks with observed exploitation rate greater than exploitation rate at MSY. µMSY is calculated from a Ricker model.

					Within goal range			Above goal range			Percent difference	
Stock	Goal type	μ_{OBS}	μ_{MSY}	Harvest rate	Yield	n	CV%	Yield	n	CV%	Yield	CV
Chilkoot	SEG	0.61	0.58	0.50	85,747	10	156%	171,484	7	61%	100%	-95%
McDonald	SEG	0.50	0.37	0.66	113,250	4	40%	109,000	7	127%	-4%	87%
Kenai	SEG	0.82	0.74	0.74	3,548,945	9	82%	3,192,232	5	89%	-10%	7%
Russian ER	SEG	0.60	0.49	0.44	32,374	16	120%	77,897	7	99%	141%	-21%
Ayakulik	SEG	0.54	0.44	0.39	415,407	20	120%	181,388	2	153%	-56%	33%
U. Station ER	SEG	0.50	0.47	0.39	55,919	14	128%	41,776	7	111%	-25%	-17%
U. Station LR	BEG	0.65	0.62	0.55	274,104	15	81%	948,755	3	39%	246%	-43%
Chignik ER	SEG	0.66	0.52	0.52	860,534	11	72%	991,126	17	79%	15%	7%
Kvichak	SEG	0.52	0.38	0.45	5,002,435	23	178%	16,038,000	8	100%	221%	-78%
Naknek	SEG	0.65	0.59	0.59	2,561,298	23	72%	2,824,304	12	112%	10%	40%
Egegik	SEG	0.83	0.71	0.74	5,546,839	21	104%	8,081,093	9	63%	46%	-41%
Average		0.63	0.54	0.54	1,681,532		105%	2,968,823		94%	62%	-11%

Table 4.–Summary of limnological and juvenile production data for Kenai River late-run sockeye salmon, brood years 1985-2006. Mean annual euphotic zone depth (EZD) in Skilak Lake is provided as an index of interannual changes in primary production. Fry abundance was estimated from acoustic surveys, and fry weight was estimated from trawl samples collected in Skilak Lake in September each year. All abundance estimates are in thousands.

Brood Year	Mainstem Spawners	Potential Egg Deposition	EZD (m)	Fall Fry Wt. (g)	Fall Fry Abundance Skilak	Fall Fry Abundance Total	Egg-to-Fry Survival
1985	234.28	486,196	9.0	1.7	17,877	22,217	0.046
1986	352.66	733,239	8.3	-	9,029	10,182	0.014
1987	1,268.33	3,430,362	12.4	0.9	30,883	37,071	0.011
1988	785.14	1,846,695	11.8	1.2	12,660	13,988	0.008
1989	1,187.54	2,451,806	5.7	1.3	21,850	24,601	0.010
1990	340.81	588,241	6.7	1.5	6,347	7,127	0.012
1991	295.12	553,800	9.6	1.8	8,427	9,541	0.017
1992	675.93	1,739,544	7.7	1.2	31,347	35,687	0.021
1993	565.63	1,260,616	5.9	1.4	8,354	11,159	0.009
1994	769.69	1,682,828	8.3	1.7	7,378	8,813	0.005
1995	452.82	899,797	3.4	1.6	4,830	5,582	0.006
1996	537.88	1,131,986	5.8	0.9	23,000	25,316	0.022
1997	795.73	1,642,865	5.1	0.7	15,332	21,194	0.013
1998	430.10	801,995	7.6	1.3	5,908	8,331	0.010
1999	426.28	857,051	6.9	1.2	18,663	19,950	0.023
2000	318.38	617,640	9.2	1.0	20,416	22,510	0.036
2001	364.36	781,874	8.7	1.0	6,802	8,749	0.011
2002	610.53	1,240,680	4.3	1.3	10,521	12,750	0.010
2003	775.61	1,727,567	6.0	0.6	20,390	22,908	0.013
2004	1,120.00	2,372,232	5.8	0.5	39,500	41,936	0.018
2005	1,113.00	2,357,405	7.3	0.7	4,238	4,478	0.002
2006	1,270.00	2,689,941	-	-	-	-	-
Mean	667.72	1,449,744	7.4	1.2	15,417	17,814	0.015

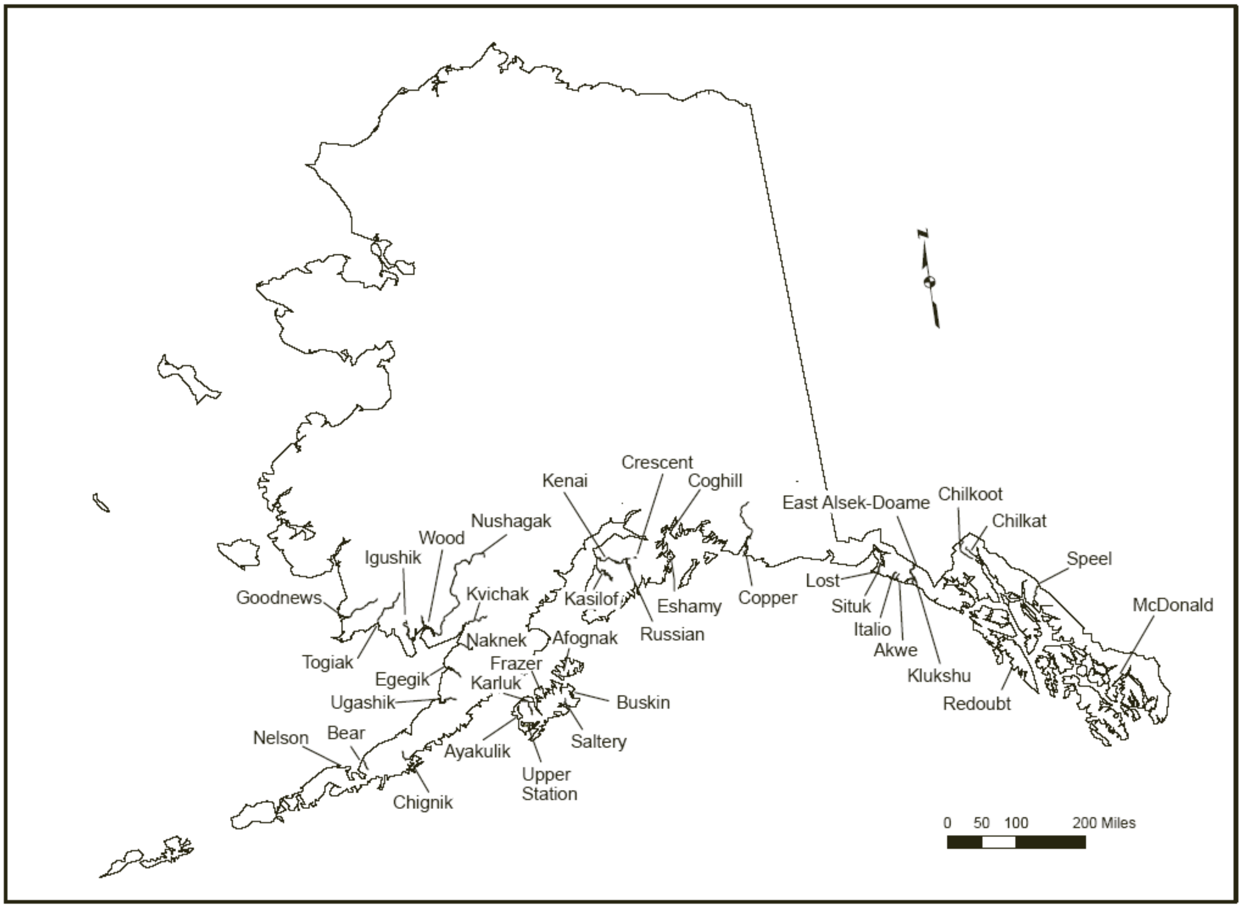


Figure 1.–Map of Alaska with location of the 40 sockeye salmon stocks in this review.

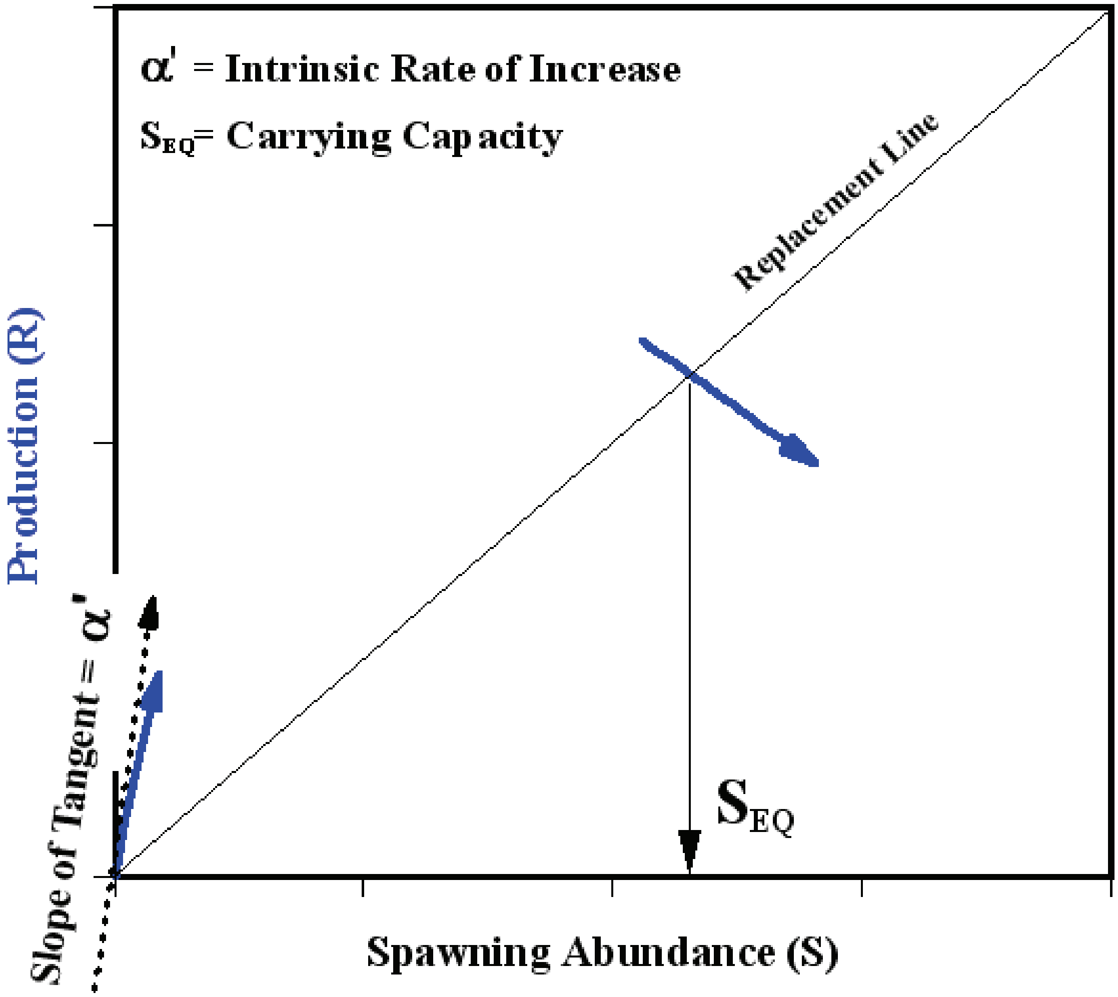


Figure 2.–Schematic representation of a generic production model for salmon.

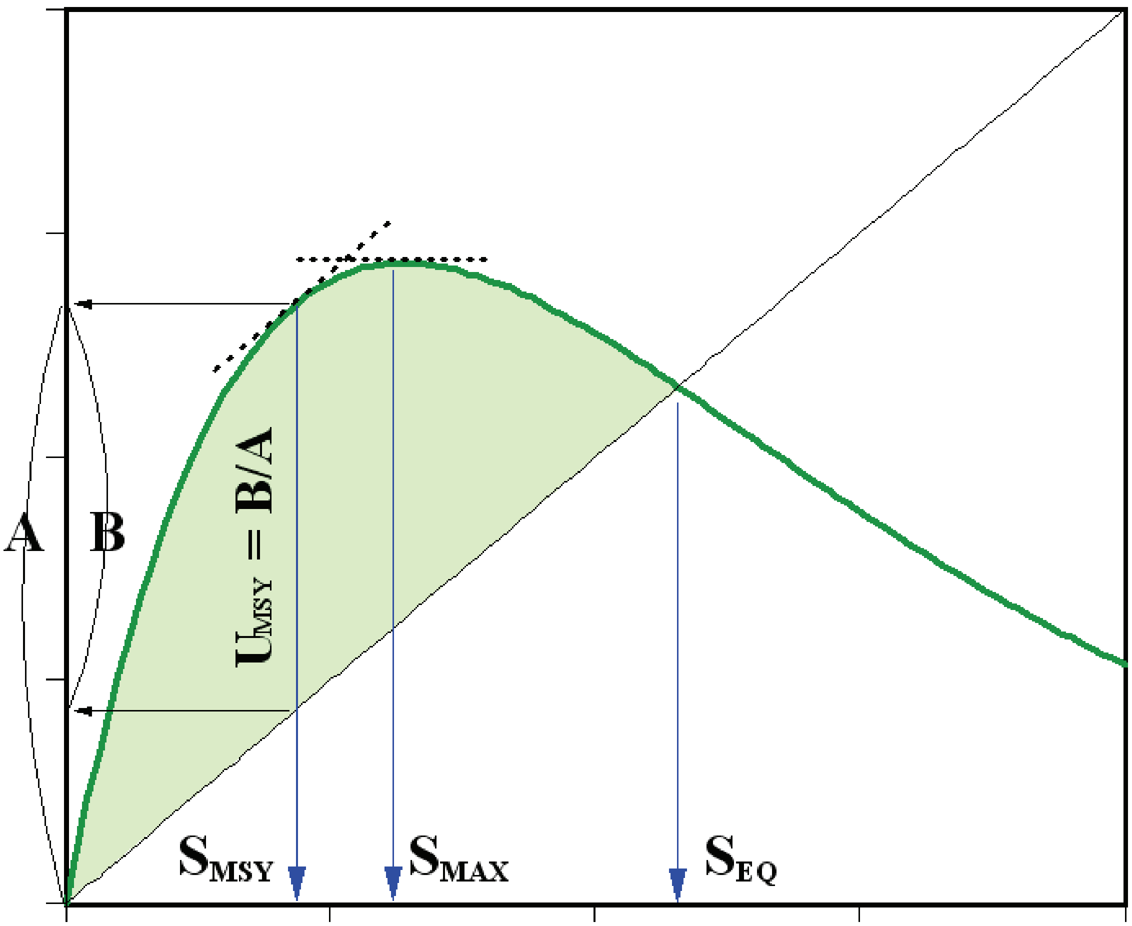


Figure 3.–Schematic representation of a Ricker stock-recruitment curve and relevant biological reference points.

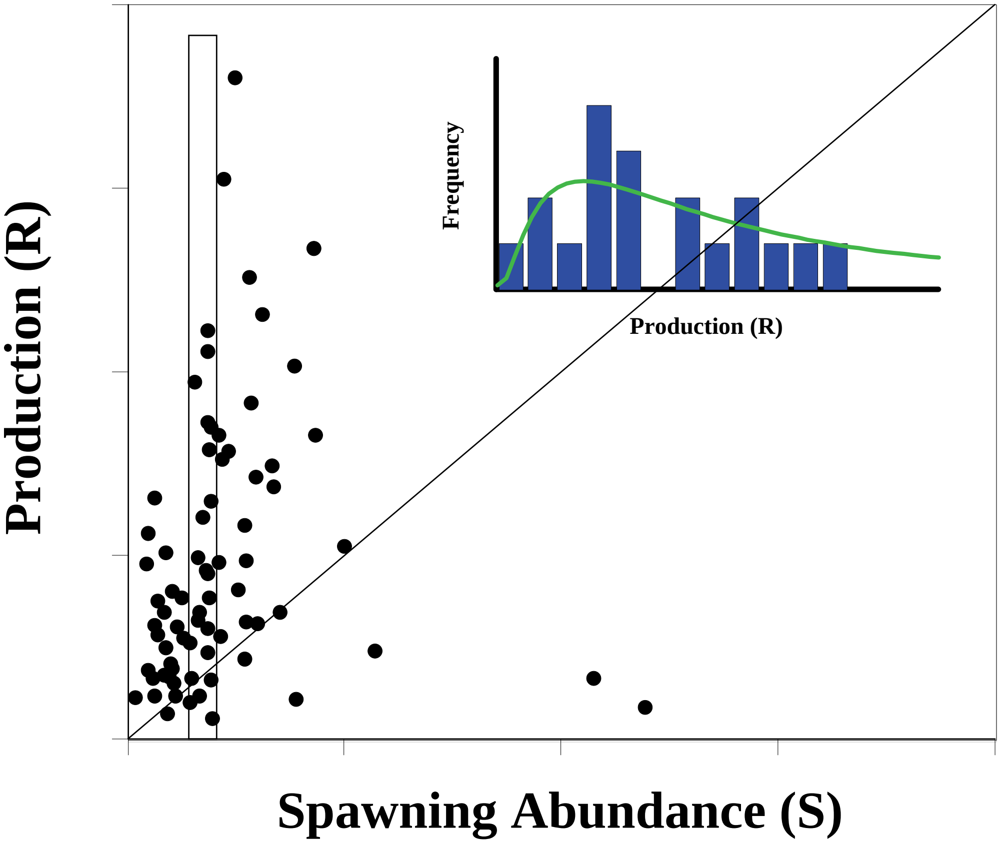
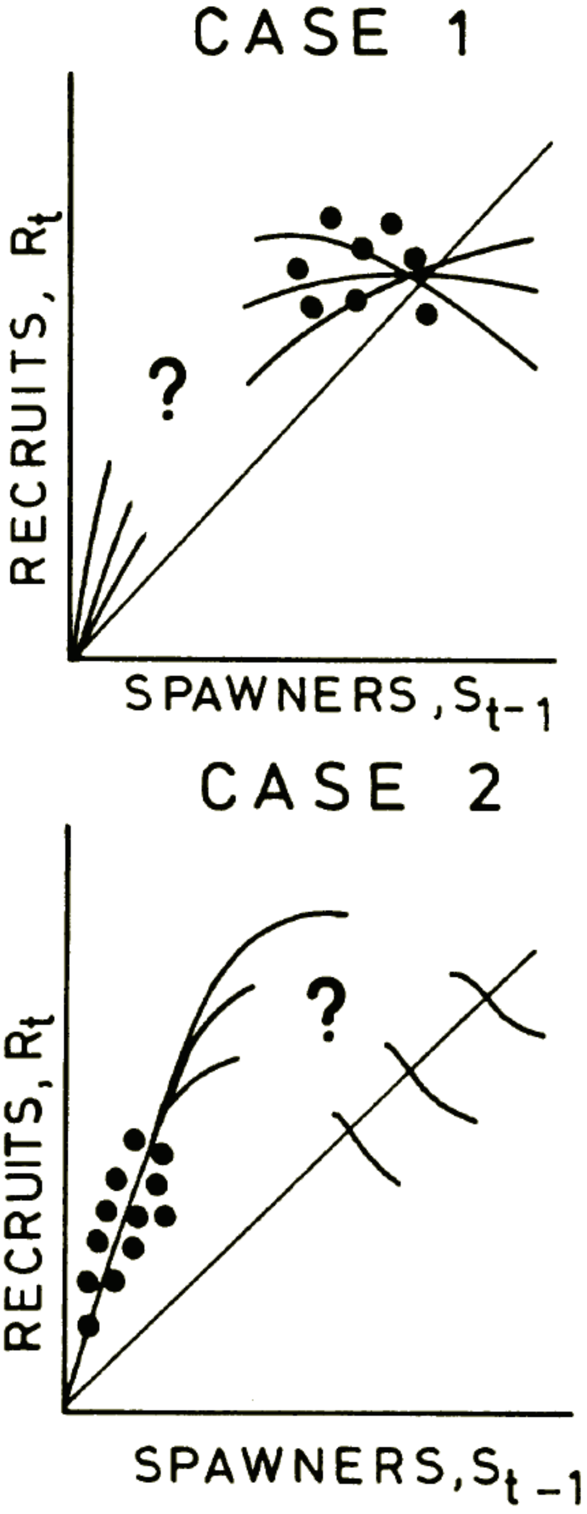


Figure 4.–Schematic representation of log-normal process error of stock-recruitment data.



CASE 1

CASE 2

Figure 5.–Schematic of production data expected from fisheries with very low harvest rates (case 1) and from fisheries with high harvest rates (case 2).

Source: From Walters and Hilborn (1976).

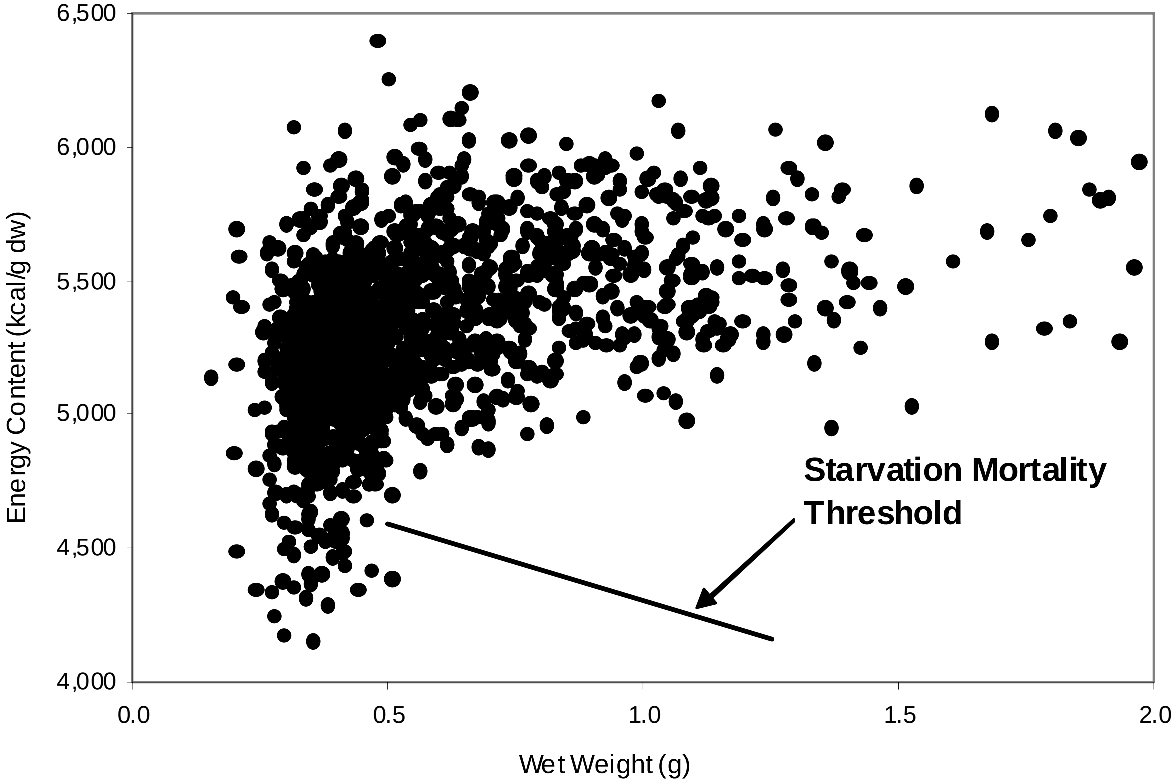


Figure 6.–Distribution of whole-body energy content in relation to wet weight for juvenile sockeye salmon collected in Skilak Lake in the fall, 2000-2005. Bomb calorimetry was used to measure energy content. The solid line indicates the mean (n=64) energy content of juvenile sockeye salmon that died from starvation in the laboratory.

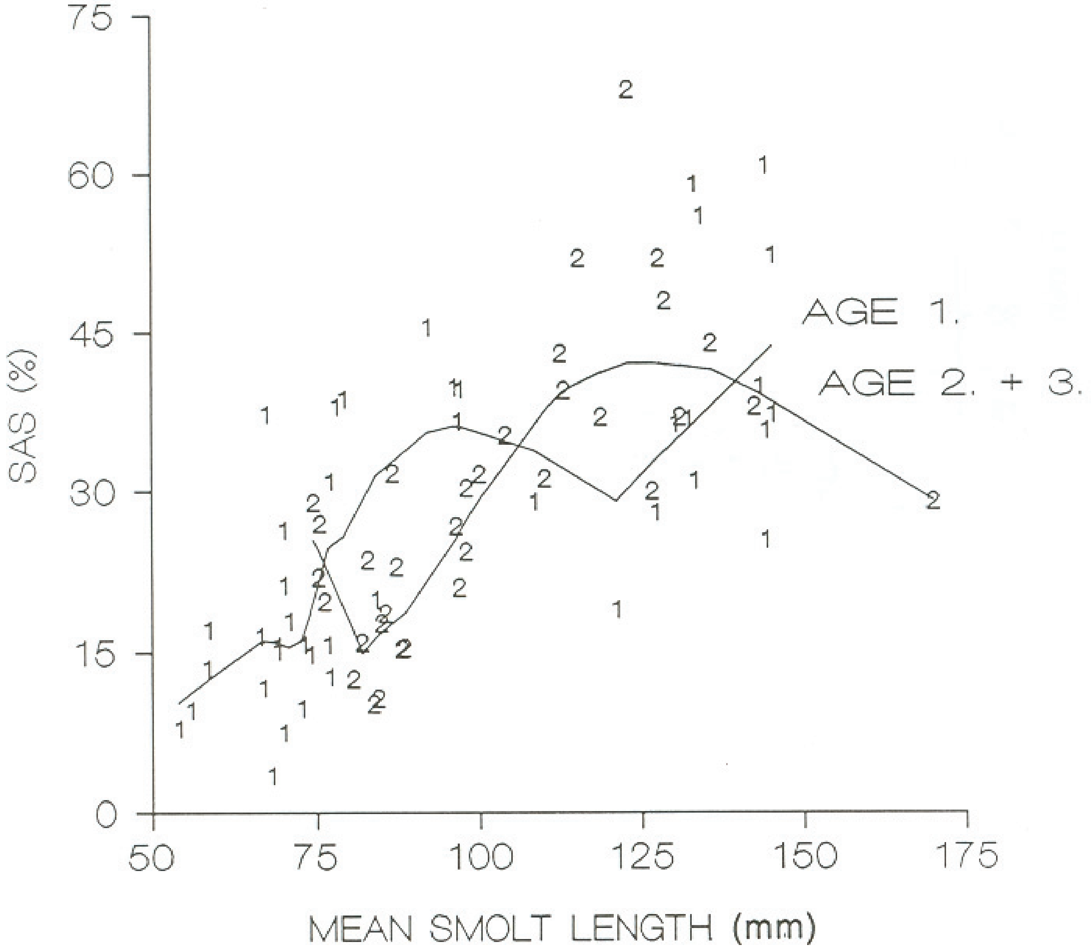


Figure 7.–Loess (F=0.4) models relating smolt-to-adult survival of age 1 and age 2 & 3 smolts to mean lengths of sockeye salmon from 12 nursery systems located in Alaska.

Source: From (Koenings et al. 1993).

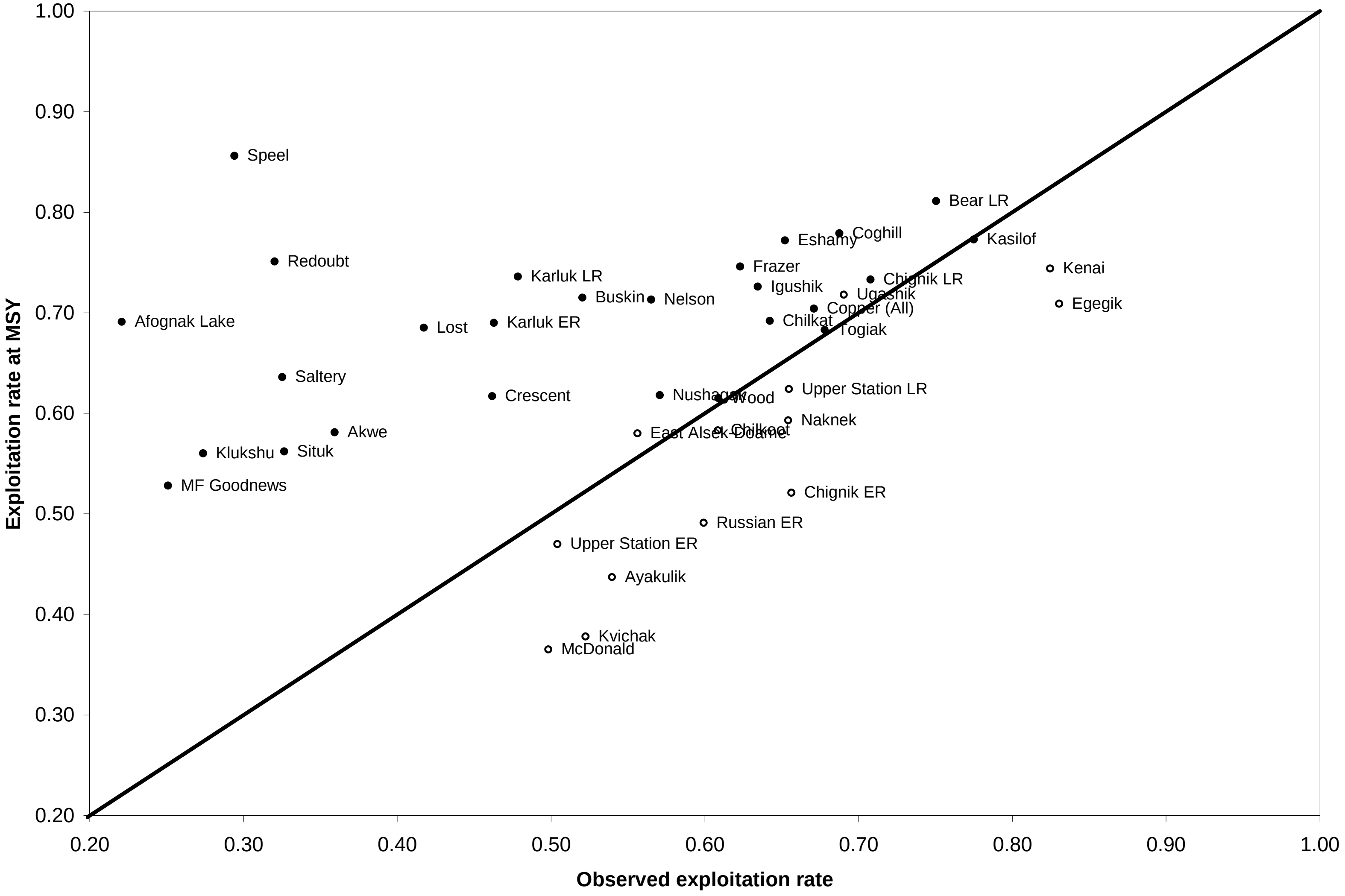


Figure 8.–Estimated exploitation rate at MSY determined from lnα’ plotted against the observed exploitation rate for 40 Alaskan sockeye stocks (Italio stock not visible in this plot). Open circles designate stocks that do not have a reliable estimate of carrying capacity (NPCV of $S_{EQ} > 0.250$) and closed circles designate stocks that do have a reliable estimate of carrying capacity (NPCV of $S_{EQ} \leq 0.250$).

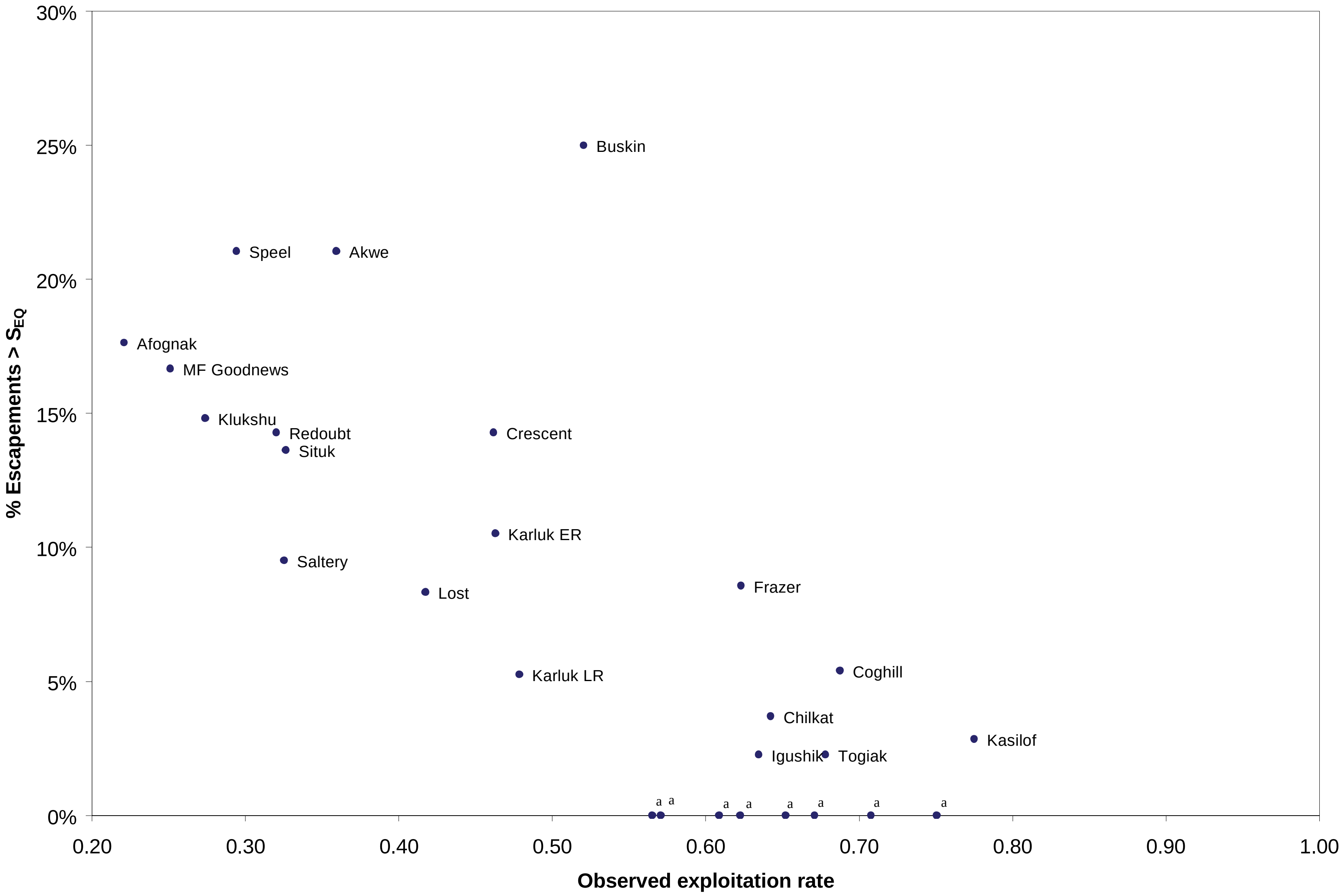


Figure 9.–Percentage of escapements greater than carrying capacity (S_{EQ}) plotted against the observed exploitation rate for 29 sockeye salmon stocks with a reliable estimate of S_{EQ} (Italio stock not shown).

[a] Stocks with no escapements greater than carrying capacity plotted on the x-axis are: East Alsek, Nelson, Bear LR, Chignik LR, Wood, Nushagak, Ugashik, Eshamy and Copper.

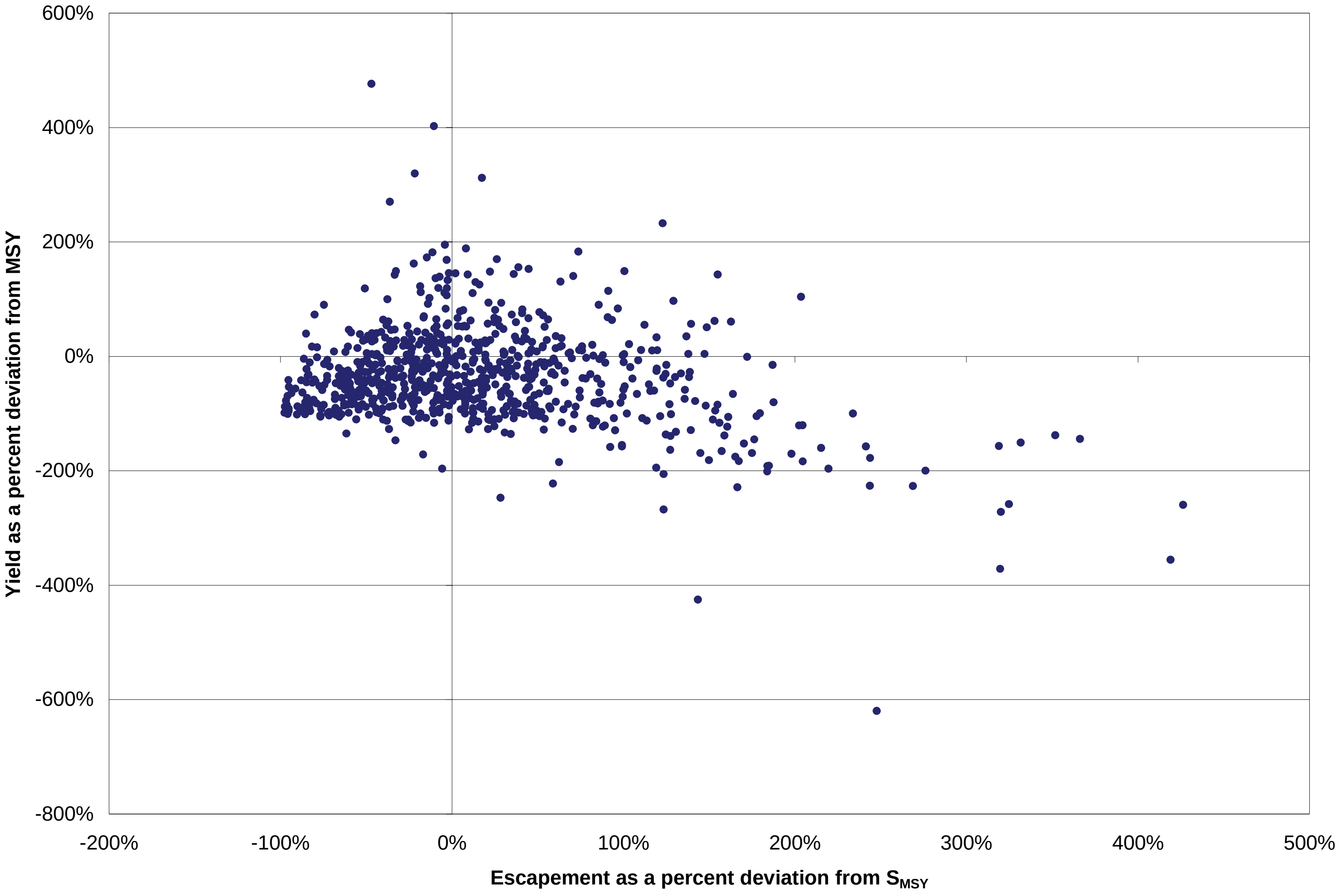


Figure 10.–Composite scatterplot of yields as a percent deviation from MSY on escapement as a percent deviation from S_{MSY} for 29 sockeye salmon stocks with observed exploitation rate less than or equal to exploitation rate at MSY.

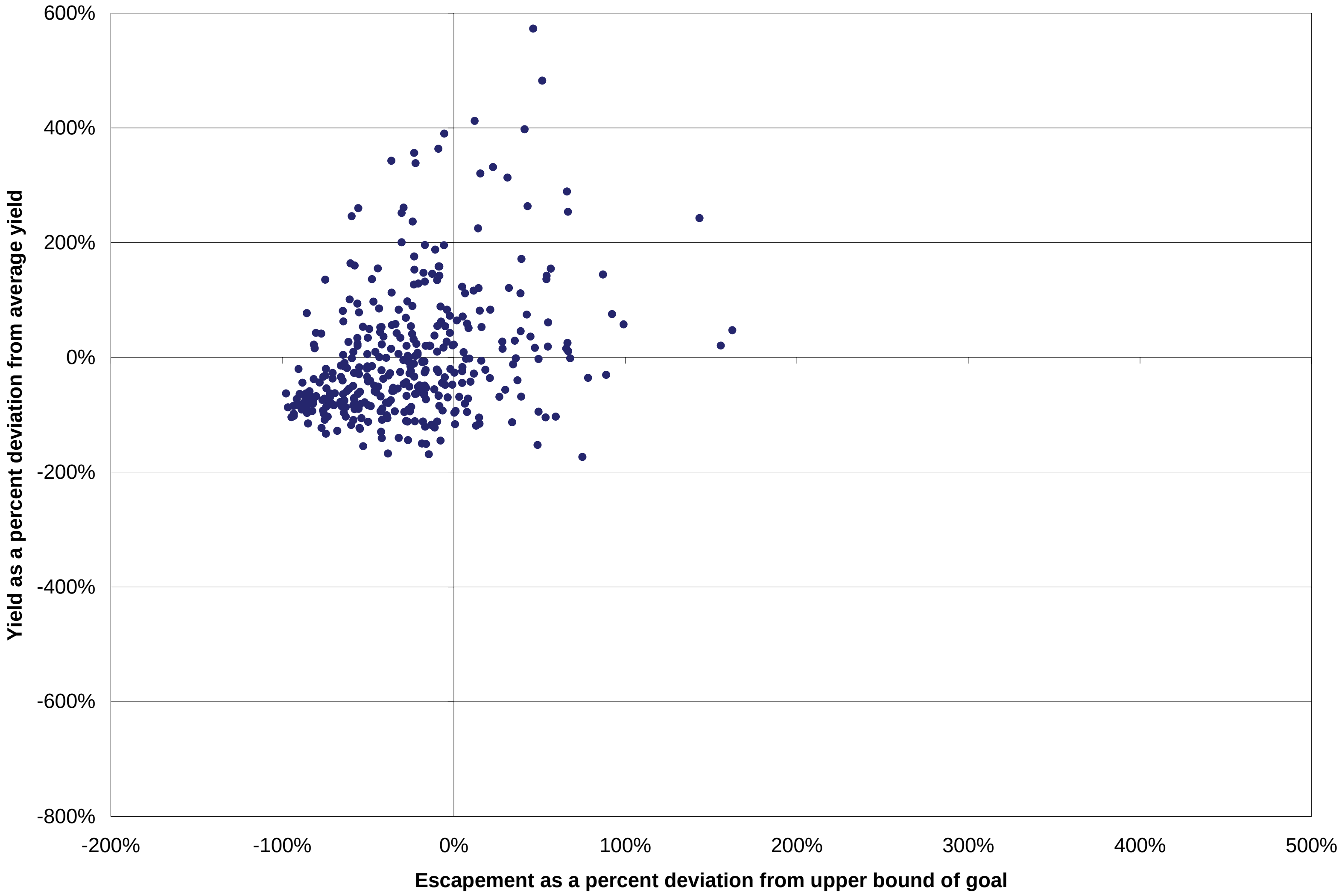


Figure 11.–Composite scatterplot of yields as a percent deviation from average yield on escapement as a percent deviation from the upper bound of the escapement goal for 11 sockeye salmon stocks with observed exploitation rate greater than exploitation rate at MSY.

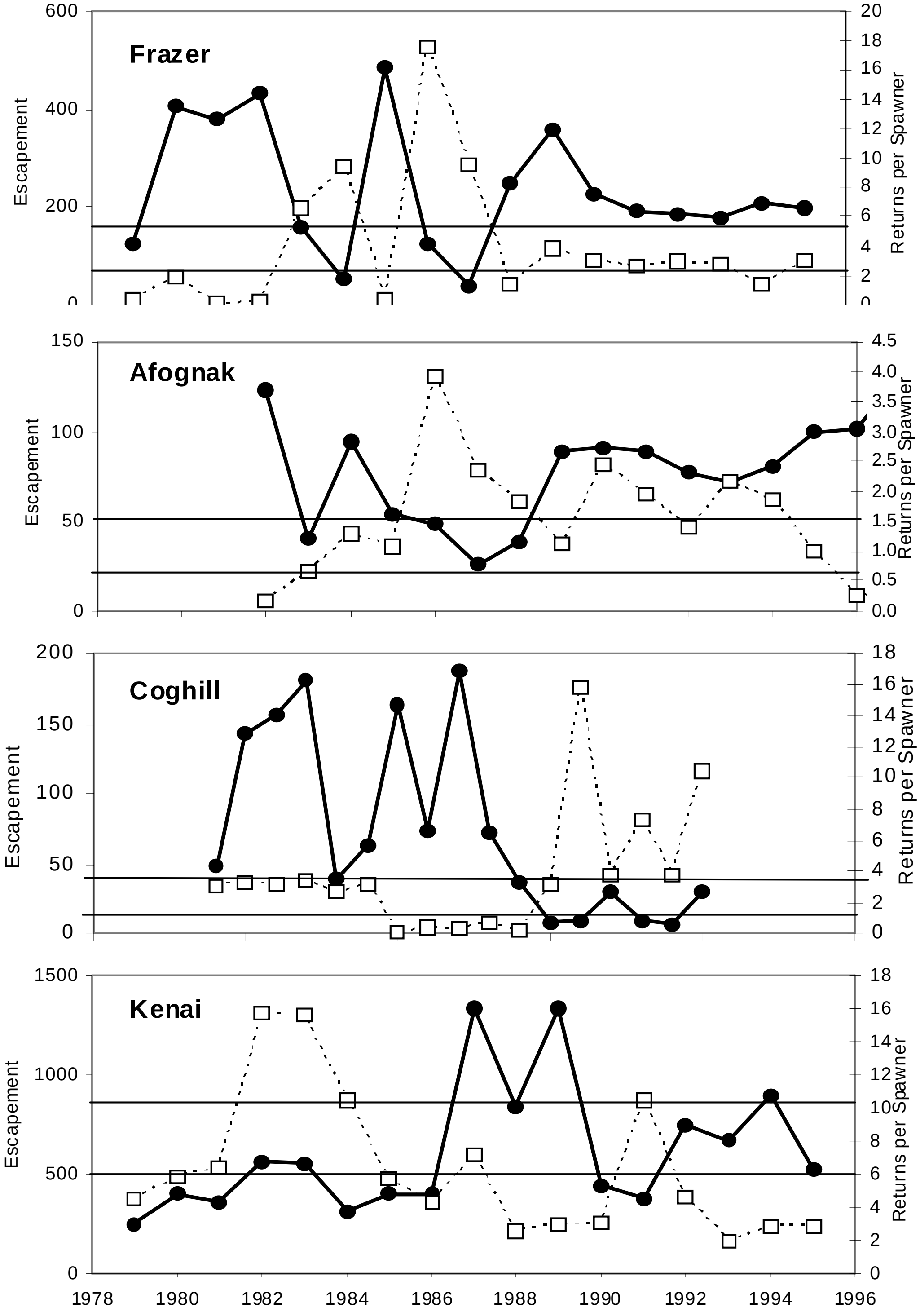


Figure 12.–Escapements (solid circles; in thousands) and returns per spawner (open squares) for Frazer, Afognak, Coghill, and Kenai river sockeye salmon stocks, 1978-1996. Solid horizontal lines indicate escapement goal ranges for each stock.

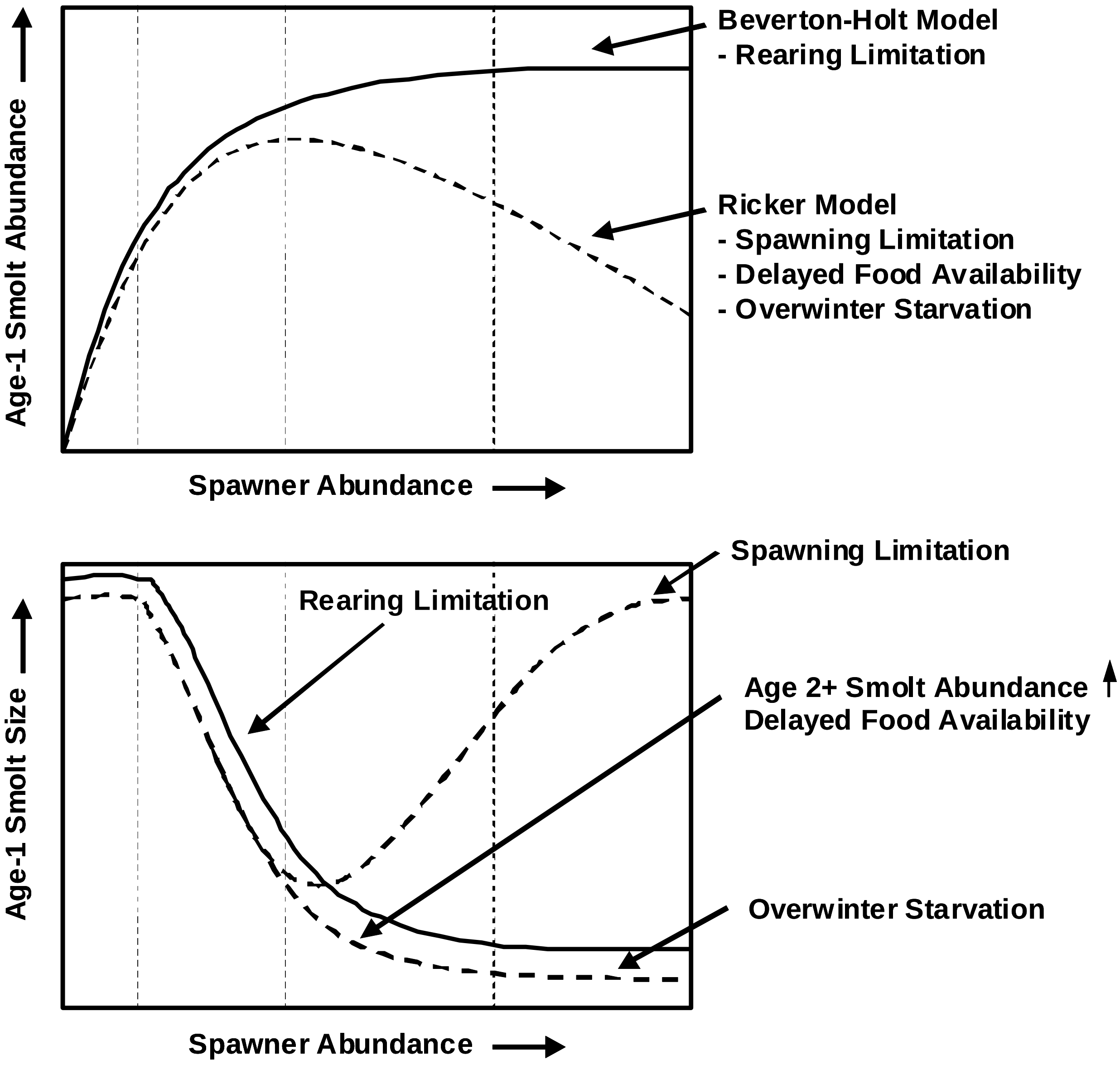


Figure 13.–Theoretical relationships between sockeye salmon spawner abundance, and juvenile abundance and size viewed within the context of the Beverton-Holt (solid line) and Ricker (dashed line) production models.

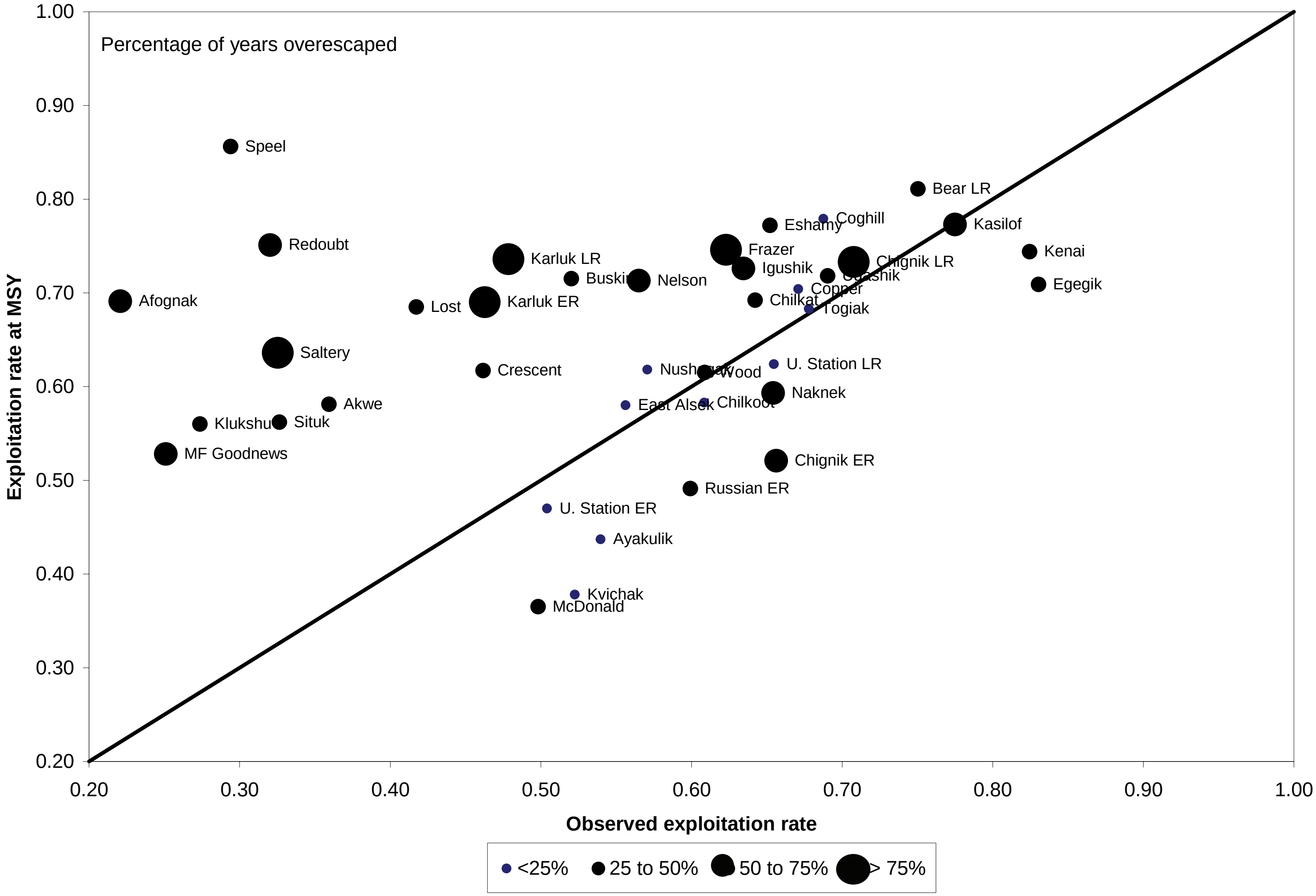


Figure 14.–Exploitation rate at MSY plotted against observed exploitation rate for 40 sockeye salmon stocks. Size of each point represents the percentage of years when overescapement occurred during the most recent 15 years.

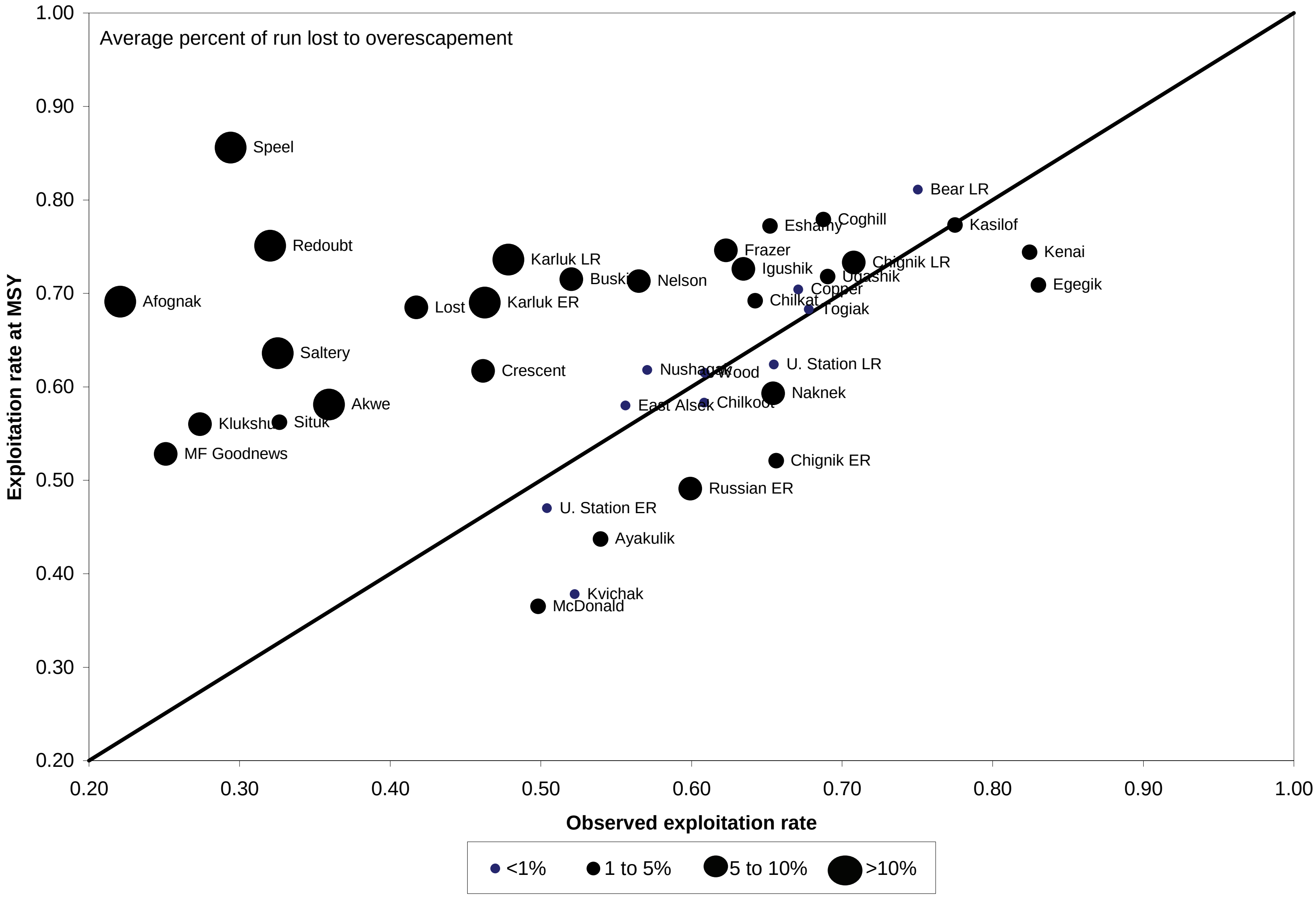


Figure 15.–Exploitation rate at MSY plotted against observed exploitation rate for 40 sockeye salmon stocks. Size of each point represents the average percentage of the run lost to overescapement during the most recent 15 years.

APPENDIX A
Stock-Recruitment Methodology and Overescapement Metrics

Appendix A1.–Stock-recruit analysis methodology and overescapement metrics.

Simple stock-recruitment analyses were performed on each brood table using the linearized form of the Ricker relationship with multiplicative process error (Hilborn and Walters 1992) to estimate parameters (Equation 1) and reference points (Equations 2 through 4). Beginning with the familiar non-linear form of the stochastic Ricker equation,

$$R = \alpha S \exp(-\beta S)\exp(\varepsilon), \tag{1a}$$

where S is the escapement and R is the resultant return. We then divide by S and take natural logs to form the simple linear regression recipe (SLR)

$$\ln\left(\frac{R}{S}\right) = \ln\alpha - \beta S + \varepsilon;\ \varepsilon \sim N\left(0, \sigma_{\varepsilon}^{2}\right). \tag{1b}$$

A linear regression of ln(R/S) on S will estimate the parameters lnα (y-intercept), β (slope), and σ_{ε}^{2} (mean squared residual error). We then adjust $\widehat{\ln\alpha}$ for asymmetrical log-normal process error (Hilborn 1985),

$$\widehat{\ln\alpha}' = \widehat{\ln\alpha} + \hat{\sigma}_{\varepsilon}^{2} / 2 \tag{1c}$$

and estimate the relevant reference points for salmon management from the regression parameters:

$$\hat{S}_{EQ} = \frac{\widehat{\ln\alpha}'}{\hat{\beta}}, \tag{2}$$

$$\hat{S}_{MSY} \approx \hat{S}_{EQ}\left(0.5 - 0.07\,\widehat{\ln\alpha}'\right), \text{ and} \tag{3}$$

$$\hat{\mu}_{MSY} \approx \widehat{\ln\alpha}'\left(0.5 - 0.07\,\widehat{\ln\alpha}'\right). \tag{4}$$

In this formulation, the estimate of S_{EQ} is the carrying capacity and the estimate of α' is the intrinsic rate of increase. The estimate of σ_{ε}^{2} is the process error. The estimate of S_{MSY} is the escapement that produces MSY and μ_{MSY} is the exploitation rate at MSY.

Statistical uncertainty about the parameters and reference points was assessed with a bootstrap technique (Efron and Tibshirani 1993); resampling the residuals of the linear regression with replacement, calculating all parameter estimates and reference points for each bootstrap replicate, omitting replicates with negative values of lnα or β[1], and using percentiles of the bootstrap values to obtain interval estimates. Here, for comparison among stocks we also calculated a nonparametric analog of the coefficient of variation (NPCV) for each parameter and reference point (Prager and Mohr 1999):

$$NPCV = \frac{\left(69.15^{th}\ percentile - 30.85^{th}\ percentile\right)}{median}; \tag{5}$$

where an NPCV of 0.250 (25%) or less was considered precise.

In addition, serial correlation in process error with a lag of one year was examined for each of the stocks with a time series regression of the simple model in equation (1). In this model, process errors are not independent, but serially dependent on the process error from the previous brood year (Noakes et al. 1987). The linear form of the model is then (AR1):

$$\ln\left(\frac{R}{S}\right) = \ln\alpha - \beta S + \varepsilon_{by};\ \varepsilon_{by} = \phi_1 \varepsilon_{by-1} + a_{by} \text{ or,} \tag{6a}$$

$$\ln\left(\frac{R_{by}}{S_{by}}\right) = \left(1-\phi_1\right)\ln\alpha + \phi_1 \ln\left(\frac{R_{by-1}}{S_{by-1}}\right) + \phi_1 \beta S_{by-1} - \beta S_{by} + a_{by},\ a_{by} \sim Norm\left(0, \sigma_a^2\right) \tag{6b}$$

The time series regression includes an additional parameter (ϕ_1) that controls the strength of the correlation between the process error in two adjacent brood years (*by* and *by-1*) and can range from -1 to 1. The adjustment to $\overset{\wedge}{\ln\alpha}$ for asymmetric log-normal process error is then:

$$\overset{\wedge}{\ln\alpha'} = \overset{\wedge}{\ln\alpha} + \hat{\sigma}_a^2 \Big/ 2\left(1-\hat{\phi}_1^2\right) \tag{6c}$$

The remaining reference points are then calculated as in equations 2 through 4. Statistical uncertainty was handled with a model-based resampling bootstrap technique (Davison and Hinckley 1997) and estimation of NPCV's as above. Three stocks that were missing production data from consecutive brood years (Lost, Akwe, Eshamy) were not included in the time series analysis.

Several metrics were calculated to describe the difference in observed yield from expected yields and the difference in observed escapements from the reference points where we could reliably estimate S_{MSY} and S_{EQ} (NPCV ≤ 0.250). First, simple averages of annual escapement and yield were calculated for each brood table. One metric of overescapement is the percentage of brood years when the observed escapement was equal to or greater than the carrying capacity (S_{EQ}):

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[1] Negative values of lnα correspond to stocks with the intrinsic rate of increase less than one, and negative values of β correspond to R/S increasing with increasing S. Since neither of these situations have biological analogs (they cannot occur in nature), these replicates must be omitted before calculating interval estimates.

$$\% \geq \hat{S}_{EQ} = \frac{number\ of\ brood\ years\ S \geq \hat{S}_{EQ}}{number\ of\ brood\ years} \times 100\% \tag{7}$$

We also compared $\hat{\mu}_{MSY}$ to observed exploitation rate in the brood table:

$$\mu_{OBS} = \frac{average\ yield}{average\ return}, \text{ where} \tag{8a}$$

$$average\ yield = \frac{\sum_{by=1}^{n}(return_{by} - escapement_{by})}{n}, \text{ and} \tag{8b}$$

$$average\ return = \frac{\sum_{by=1}^{n} return_{by}}{n} \tag{8c}$$

as a method of determining if the range of data in the brood table was sufficient to reliably estimate the biological reference points. The more familiar average annual harvest rate was also calculated for each stock from the annual harvest as a proportion of the annual run (*i*):

$$Harvest\ rate = \frac{\sum_{i=1}^{n}\left(harvest_i \middle/ run_i \right)}{n} \tag{9}$$

Several metrics were calculated to describe the short-term loss of harvest when overescapement occurs. Because escapement goals can change over time, only the most recent 15 years of run, harvest, and escapement data for each stock were used and only the currently published escapement goal was evaluated. Note that these calculations are for data from calendar year runs and not the brood table of returns. One simple metric of overescapement is the percentage of years (out of the 15 most recent years) that overescapement occurred:

$$\%Overescapement = \frac{number\ of\ run\ years\ that\ overescapement\ occurred}{15\ years} \times 100\%. \tag{10}$$

However, overescapement can be very small in some years (i.e., a few fish over the escapement goal) or very large. To account for this, the average harvest foregone was calculated for the most recent 15 years:

$$\overline{H}_{LOST} = \frac{\sum_{i=1}^{15} \begin{cases} Escapement_i - Upper\ bound\ of\ goal & if\ Escapement_i > Upper\ bound\ of\ goal \\ 0 & if\ Escapement_i \leq Upper\ bound\ of\ goal \end{cases}}{15}, \tag{11}$$

so that zeros indicate that overescapement did not occur on average and positive values indicate that overescapement occurred on average. Overescapement is more likely to occur during large runs than small runs. To measure the effect of run size on overescapement, the average percentage of the run foregone to overescapement was also calculated for the most recent 15 years:

$$\overline{\%H}_{LOST} = \left. \sum_{i=1}^{15} \frac{\begin{cases} Escapement_i - Upper\, bound\, of\, goal & if\ Escapement_i > Upper\, bound\, of\, goal \\ 0 & if\ Escapement_i \leq Upper\, bound\, of\, goal \end{cases}}{Run_i} \times 100\% \middle/ 15 \right., \qquad (12)$$

so that percentages of zero indicate that overescapement did not occur on average and positive percentages indicate that overescapement did occur on average.

An alternative method of examining foregone harvest due to overescapement was to average the harvest foregone only in those years when overescapement occurred:

$$\overline{H}_{OVER} = \frac{\sum_{i=1}^{15} Escapement_i - Upper\, bound\, of\, goal, if\ Escapement_i > Upper\, bound\, of\, goal}{number\, of\, years\, overescapement\, occurred} \qquad (13)$$

Similar to equation 12, the average percentage of the run foregone to overescapement was calculated, but only for those years when overescapement occurred:

$$\overline{\%H}_{OVER} = \frac{\sum_{i=1}^{15} \frac{Escapement_i - Upper\, bound\, of\, goal, if\ Escapement_i > Upper\, bound\, of\, goal}{Run_i} \times 100\%}{number\, of\, years\, overescapement\, occurred}. \qquad (14)$$

APPENDIX B
Summary of Reference Points, Overescapement Metrics and Data Plots

Appendix B1.–Goal type, escapement goal, biological reference points and biological performance metrics for 40 sockeye salmon stocks.

Stock	Goal	Lower	Upper	Model Used	S_{EQ}	% ≥ S_{EQ}	S_{MSY}	MSY	μ_{MSY}	μ_{OBS}
Chilkat	SEG	80,000	200,000	SLR	239,156	4%	88,147	200,439	0.69	0.64
Chilkoot	SEG	50,000	90,000	AR1	NE[a]	NE	NE	NE	0.58	0.61
Speel	BEG	4,000	13,000	SLR	25,616	21%	7,707	48,625	0.86	0.29
McDonald	SEG	70,000	100,000	SLR	NE	NE	NE	NE	0.37	0.50
Italio	BEG	5,000	14,000	SLR	18,329	19%	8,055	5,028	0.38	-0.04
Situk	BEG	30,000	70,000	SLR	128,231	14%	51,578	67,320	0.56	0.33
Redoubt	BEG	10,000	25,000	SLR	49,969	14%	17,466	53,198	0.75	0.32
East Alsek	BEG	26,000	57,000	SLR	148,811	0%	59,223	83,125	0.58	0.56
Klukshu	BEG	7,500	15,000	SLR	22,462	15%	9,044	11,717	0.56	0.27
Lost	BEG	1,538	3,538	SLR	6,619	8%	2,454	5,392	0.69	0.42
Akwe	BEG	6,000	15,000	SLR	29,454	21%	11,716	16,504	0.58	0.36
Eshamy	BEG	20,000	40,000	SLR	58,111	0%	19,863	68,055	0.77	0.65
Coghill	SEG	20,000	40,000	SLR	175,143	5%	59,413	211,660	0.78	0.69
Copper	SEG	410,000	760,000	AR1	1,275,428	0%	465,612	1,118,266	0.70	0.67
Kenai	SEG	500,000	800,000	SLR	NE	NE	NE	NE	0.74	0.82
Kasilof	BEG	150,000	250,000	AR1	572,807	3%	195,667	672,519	0.77	0.77
Crescent	BEG	30,000	70,000	SLR	116,461	14%	45,313	74,039	0.62	0.46
Russian ER	SEG	14,000	37,000	SLR	NE	NE	NE	NE	0.49	0.60
Karluk ER	BEG	100,000	210,000	SLR	401,757	11%	148,289	334,193	0.69	0.46
Karluk LR	BEG	170,000	380,000	SLR	770,164	5%	273,255	768,279	0.74	0.48
Ayakulik	SEG	200,000	500,000	SLR	NE	NE	NE	NE	0.44	0.50
Station ER	SEG	30,000	65,000	SLR	NE	NE	NE	NE	0.47	0.50
Station LR	BEG	120,000	265,000	SLR	NE	NE	NE	NE	0.62	0.65
Frazer	BEG	70,000	150,000	SLR	402,117	9%	141,325	418,283	0.75	0.62
Saltery	BEG	15,000	30,000	SLR	60,181	10%	23,121	40,897	0.64	0.33
Buskin	SEG	8,000	13,000	SLR	18,219	25%	6,585	16,714	0.72	0.52
Afognak	BEG	20,000	50,000	SLR	97,101	18%	35,811	81,057	0.69	0.22
Chignik ER	SEG	350,000	400,000	SLR	NE	NE	NE	NE	0.52	0.66
Chignik LR	SEG	200,000	250,000	AR1	737,660	0%	262,357	728,271	0.73	0.71

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Stock	Goal	Lower	Upper	Model Used	S_{EQ}	% ≥ S_{EQ}	S_{MSY}	MSY	μ_{MSY}	μ_{OBS}
Nelson	BEG	97,000	219,000	SLR	422,374	0%	152,992	383,704	0.71	0.57
Bear LR	SEG	117,000	195,000	SLR	410,506	0%	133,669	583,423	0.81	0.75
Kvichak	SEG	2,000,000	10,000,000	AR1	NE	NE	NE	NE	0.38	0.52
Naknek	SEG	800,000	1,400,000	SLR	NE	NE	NE	NE	0.59	0.65
Egegik	SEG	800,000	1,400,000	AR1	NE	NE	NE	NE	0.71	0.83
Ugashik	SEG	500,000	1,200,000	AR1	4,613,891	0%	1,663,994	4,279,316	0.72	0.69
Wood	SEG	700,000	1,500,000	AR1	3,113,860	0%	1,212,565	1,969,471	0.62	0.61
Igushik	SEG	150,000	300,000	SLR	1,055,001	2%	377,765	1,011,125	0.73	0.63
Nushagak	SEG	340,000	760,000	SLR	2,009,201	0%	780,914	1,282,898	0.62	0.57
Togiak	BEG	120,000	270,000	SLR	525,452	2%	194,973	426,047	0.68	0.68
Goodnews	BEG	18,000	40,000	SLR	53,358	17%	21,870	24,862	0.53	0.25

[a] NE = no estimate due to NPCV > 0.250 and $\mu_{OBS} > \mu_{MSY}$.

Appendix B2.–Fishery performance metrics in the most recent 15 years for 40 sockeye salmon stocks.

Stock	Goal	Lower	Upper	Harvest rate	%Overescape	H_{LOST}	$\%H_{LOST}$	H_{OVER}	$\%H_{OVER}$
Chilkat	SEG	80,000	200,000	0.42	33%	10,592	3%	31,775	9%
Chilkoot	SEG	50,000	90,000	0.48	7%	43	<1%	638	<1%
Speel	BEG	4,000	13,000	0.31	47%	5,979	16%	12,811	35%
McDonald	SEG	70,000	100,000	0.68	20%	5,600	2%	28,000	8%
Italio	BEG	5,000	14,000	0.02	0%	0	0%	0	0%
Situk	BEG	30,000	70,000	0.56	27%	1,906	1%	7,829	5%
Redoubt	BEG	10,000	25,000	0.09	67%	10,899	19%	16,348	29%
East Alsek	BEG	26,000	57,000	0.38	0%	0	0%	0	0%
Klukshu	BEG	7,500	15,000	0.32	40%	2,371	8%	5,927	20%
Lost	BEG	1,538	3,538	0.38	40%	892	9%	2,229	22%
Akwe	BEG	6,000	15,000	0.40	47%	5,507	13%	11,800	28%
Eshamy	BEG	20,000	40,000	0.42	40%	2,659	5%	6,647	12%
Coghill	SEG	20,000	40,000	0.61	13%	3,649	2%	27,369	17%
Copper	SEG	410,000	760,000	0.71	20%	17,731	<1%	88,654	2%
Kenai	SEG	500,000	800,000	0.75	40%	96,128	3%	240,319	7%
Kasilof	BEG	150,000	250,000	0.70	53%	50,281	4%	94,276	7%
Crescent	BEG	30,000	70,000	0.32	40%	11,491	7%	28,728	18%
Russian ER	SEG	14,000	37,000	0.48	40%	7,797	7%	19,492	17%
Karluk ER	BEG	100,000	210,000	0.37	93%	87,785	16%	94,055	17%
Karluk LR	BEG	170,000	380,000	0.40	87%	151,682	15%	175,017	17%
Ayakulik	SEG	200,000	500,000	0.46	7%	17,873	2%	268,101	35%
Station ER	SEG	30,000	65,000	0.54	13%	865	1%	6,485	6%
Station LR	BEG	120,000	265,000	0.55	0%	0	0%	0	0%
Frazer	BEG	70,000	150,000	0.61	93%	54,160	9%	58,029	9%
Saltery	BEG	15,000	30,000	0.30	80%	14,184	17%	17,731	22%
Buskin	SEG	8,000	13,000	0.41	50%	3,046	9%	6,092	19%
Afognak	BEG	20,000	50,000	0.22	73%	27,247	21%	40,685	32%
Chignik ER	SEG	350,000	400,000	0.62	53%	85,311	5%	159,958	9%
Chignik LR	SEG	200,000	250,000	0.71	93%	95,584	8%	102,412	8%

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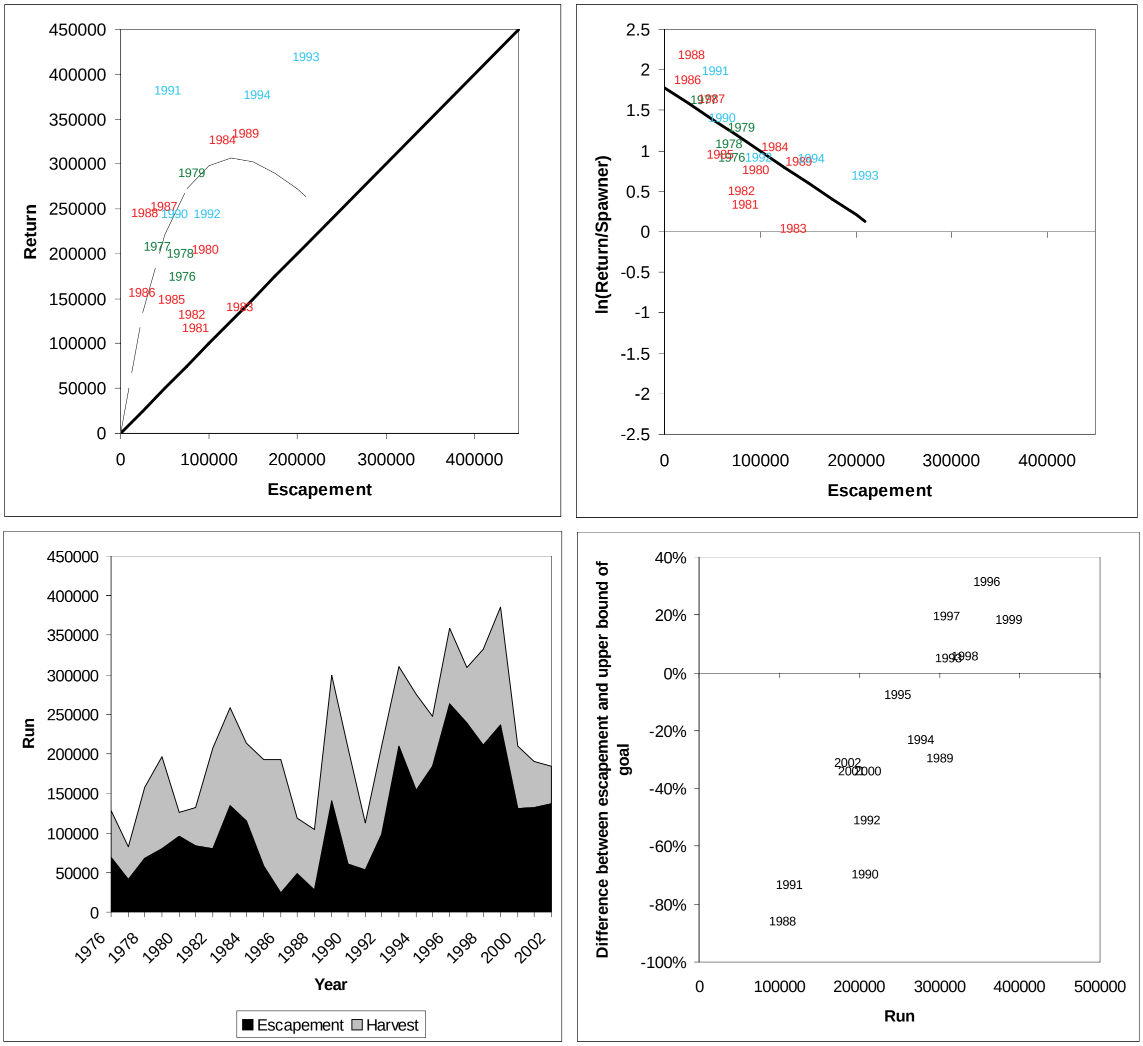
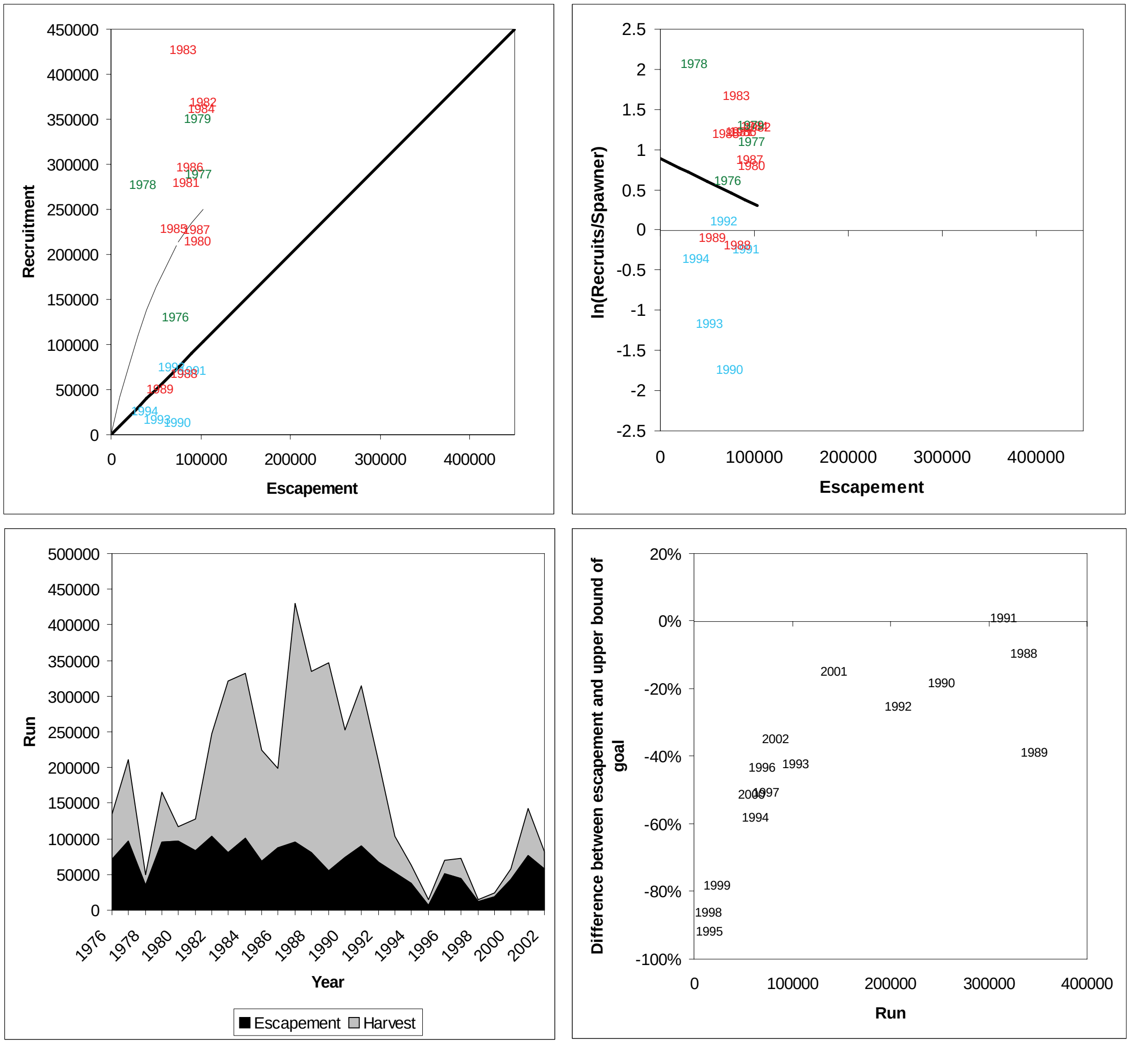
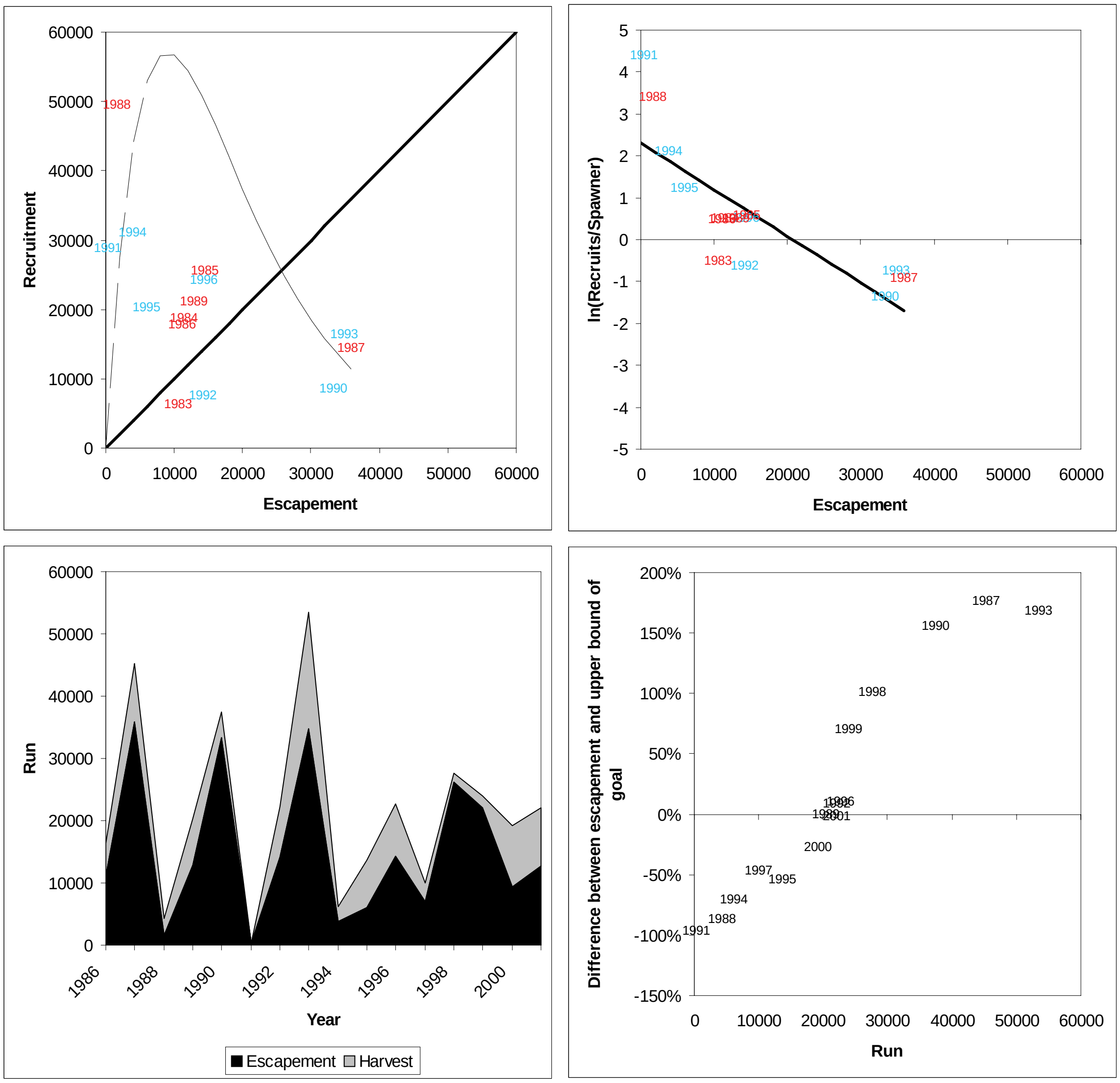
Stock	Goal	Lower	Upper	Harvest rate	%Overescape	H_{LOST}	%H_{LOST}	H_{OVER}	%H_{OVER}
Nelson	BEG	97,000	219,000	0.55	53%	42,100	6%	78,938	12%
Bear LR	SEG	117,000	195,000	0.75	33%	6,067	1%	18,202	2%
Kvichak	SEG	2,000,000	10,000,000	0.39	7%	2,600	<1%	39,000	<1%
Naknek	SEG	800,000	1,400,000	0.63	53%	366,133	5%	686,500	10%
Egegik	SEG	800,000	1,400,000	0.84	40%	206,533	2%	516,333	4%
Ugashik	SEG	500,000	1,200,000	0.68	33%	204,867	4%	614,600	11%
Wood	SEG	700,000	1,500,000	0.66	33%	31,533	1%	94,600	2%
Igushik	SEG	150,000	300,000	0.70	67%	94,800	5%	142,200	8%
Nushagak	SEG	340,000	760,000	0.67	13%	25,800	1%	193,500	6%
Togiak	BEG	120,000	270,000	0.67	13%	7,667	1%	57,500	5%
Goodnews	BEG	18,000	40,000	0.24	53%	5,339	8%	10,010	15%



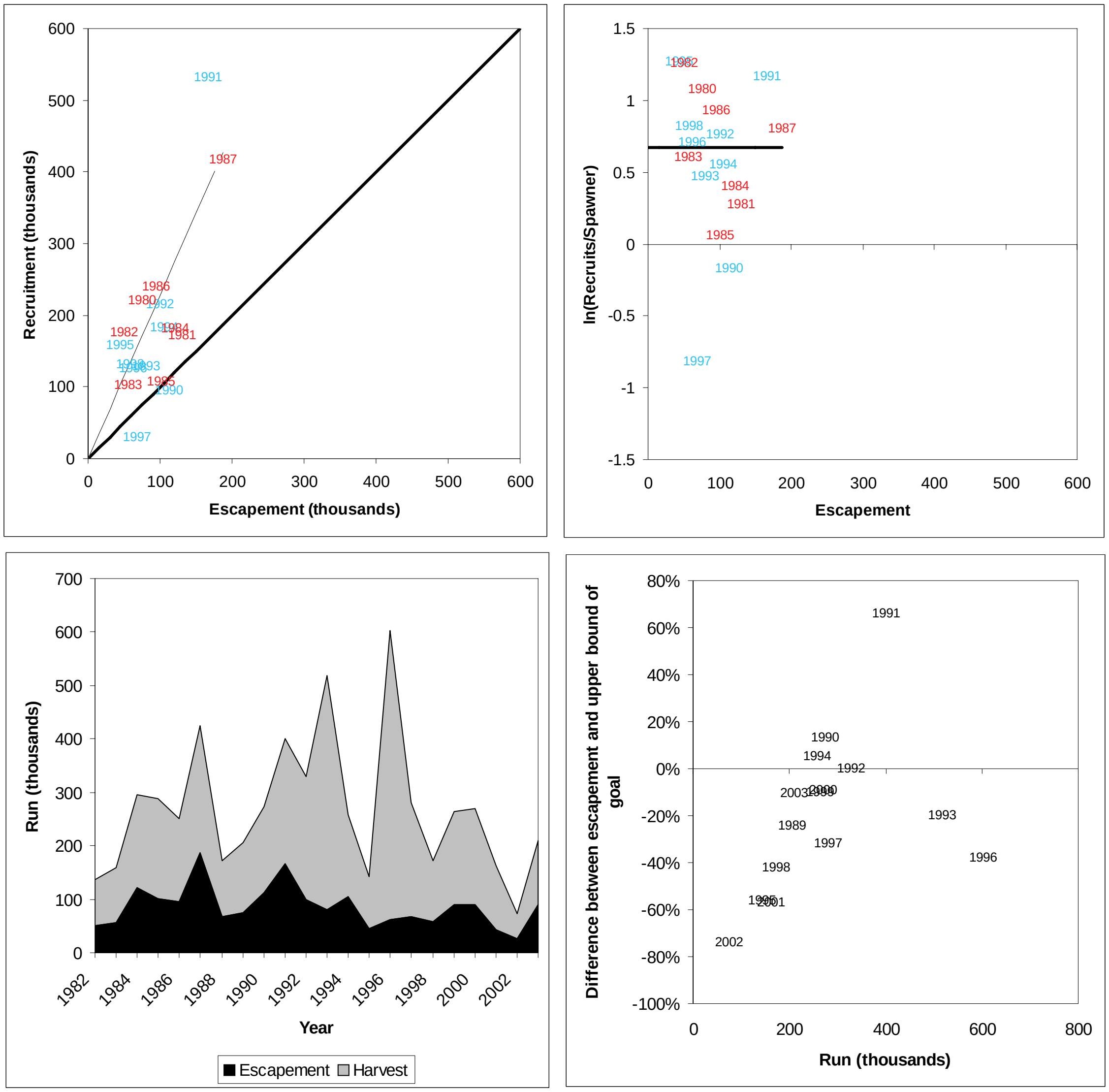
Appendix B3.–Ricker stock-recruitment relation (top panels) and fishery performance data (bottom panels) for the 1976-1994 brood years and 1976-2002 run years for the Chilkat stock. Bottom right panel depicts run data from the most recent 15 years (1988-2002).



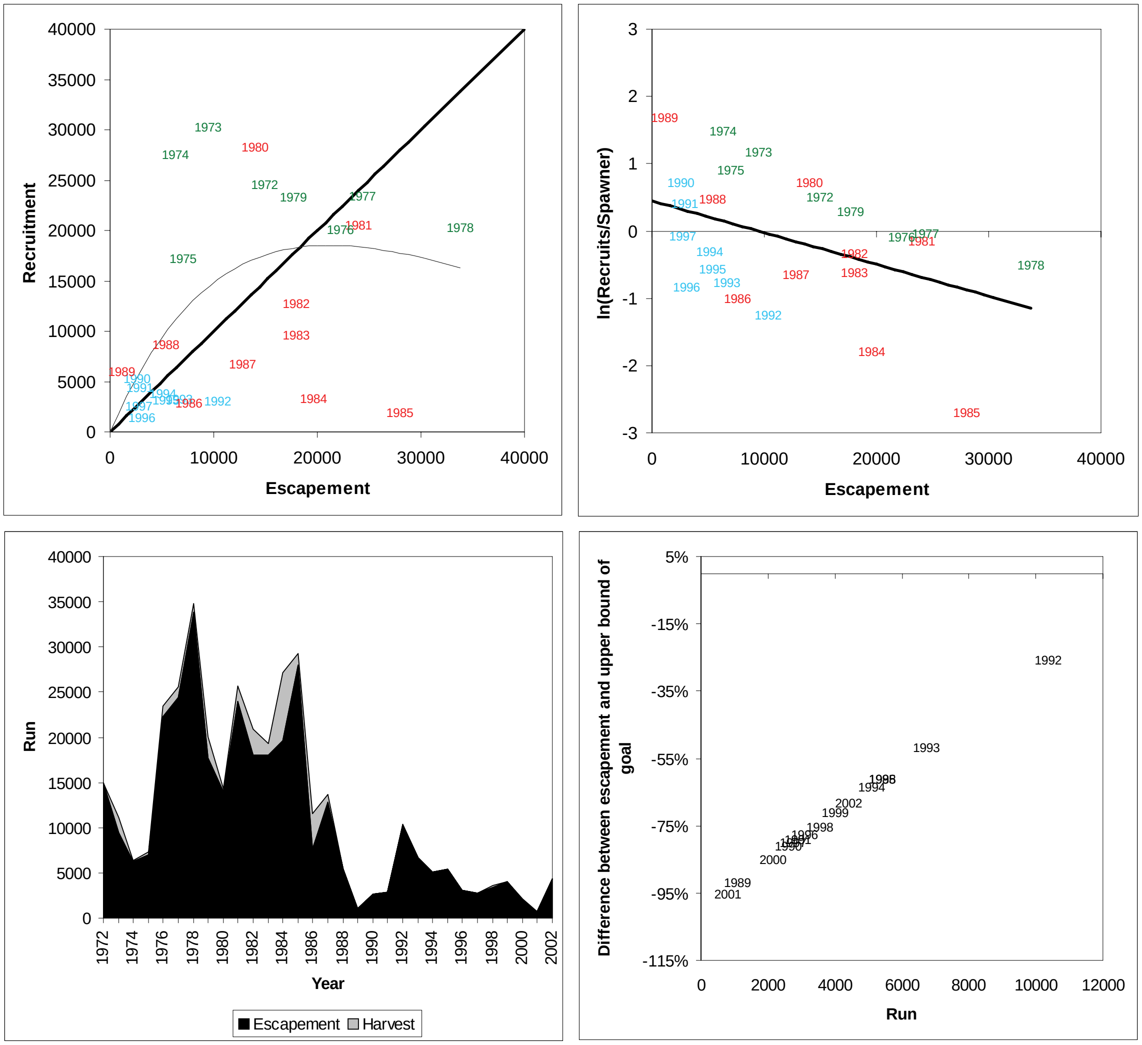
Appendix B4.–Ricker stock-recruitment relation (top panels) and fishery performance data (bottom panels) for the 1976-1994 brood years and 1976-2002 run years for the Chilkoot stock. Bottom right panel depicts run data from the most recent 15 years (1988-2002).



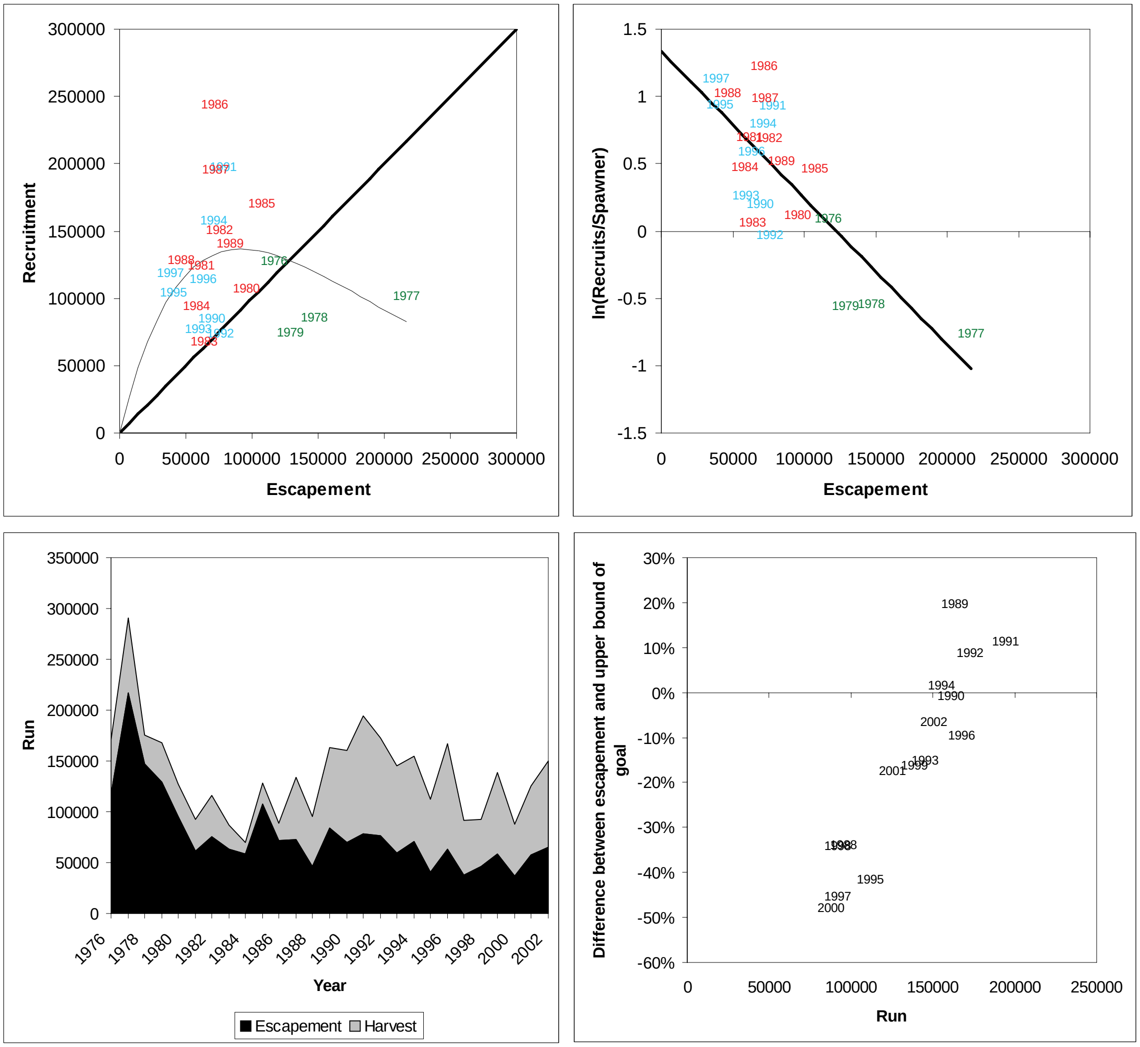
Appendix B5.–Ricker stock-recruitment relation (top panels) and fishery performance data (bottom panels) for the 1983-1996 brood years and 1983-2001 run years for the Speel stock. Bottom right panel depicts run data from the most recent 15 years (1987-2001).



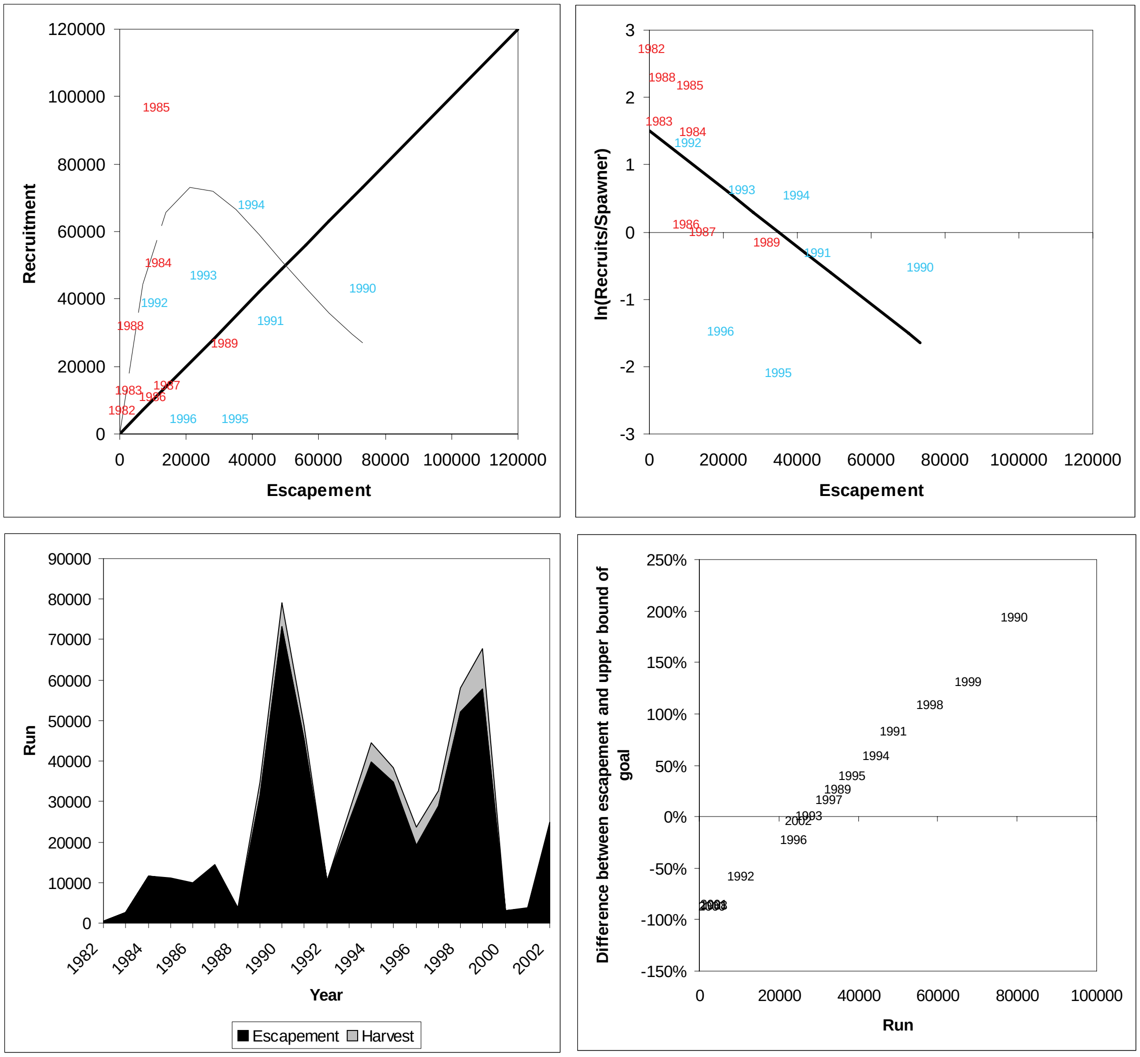
Appendix B6.–Ricker stock-recruitment relation (top panels) and fishery performance data (bottom panels) for the 1980-1987 and 1990-1998 brood years and 1982-2003 run years for the McDonald stock. Bottom right panel depicts run data from the most recent 15 years (1989-2003).



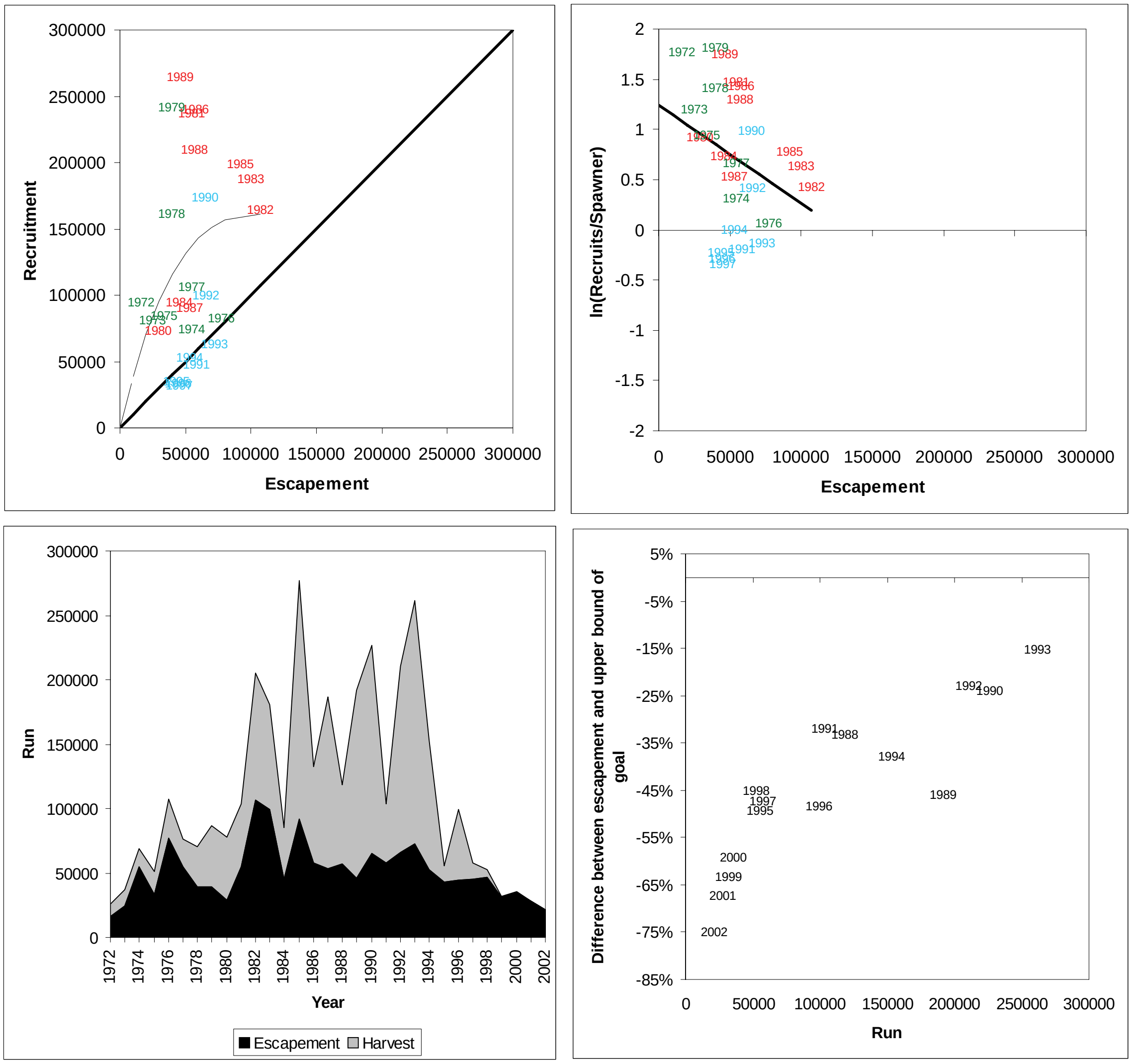
Appendix B7.–Ricker stock-recruitment relation (top panels) and fishery performance data (bottom panels) for the 1972-1997 brood years and 1972-2002 run years for the Italio stock. Bottom right panel depicts run data from the most recent 15 years (1988-2002).



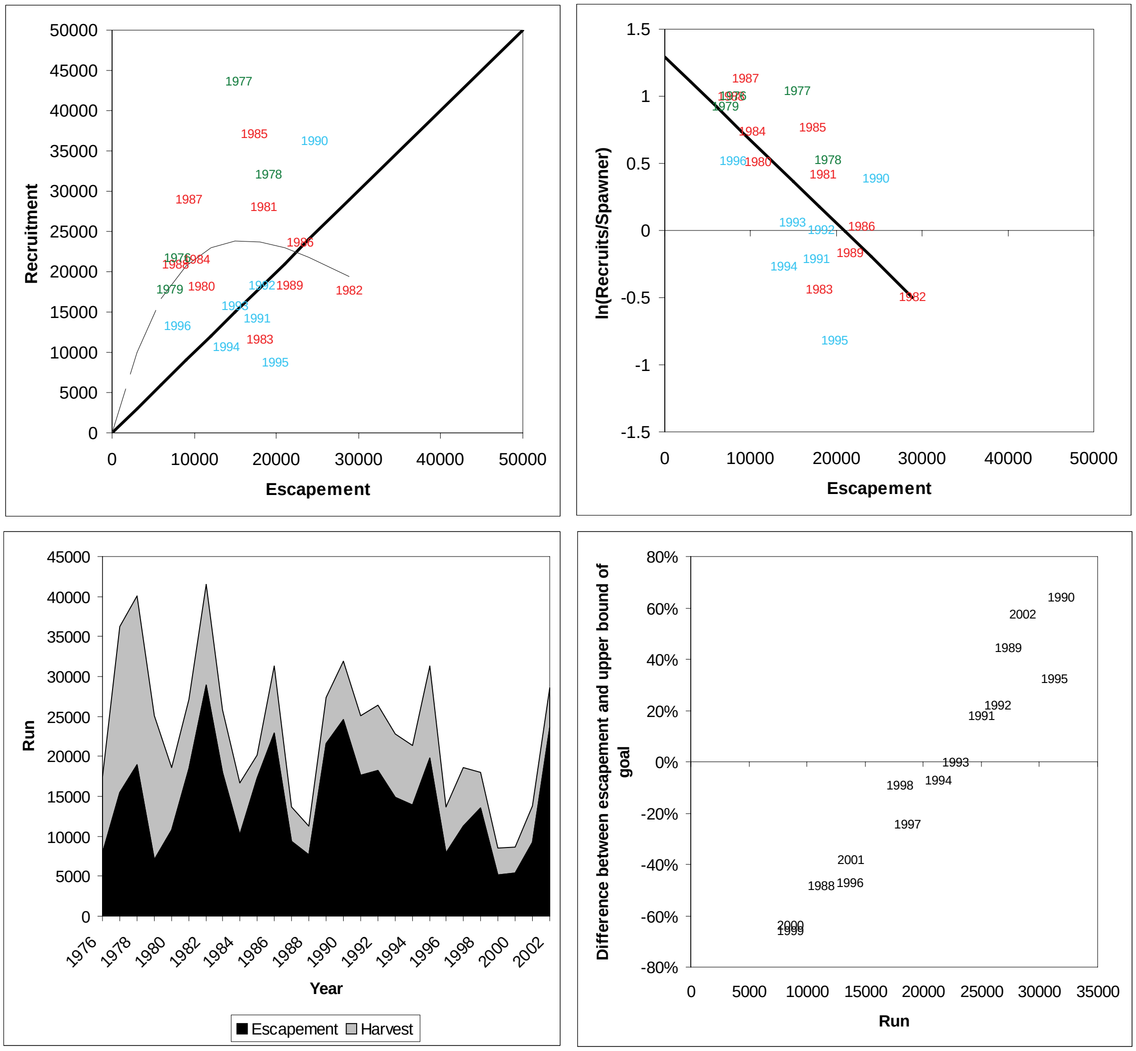
Appendix B8.–Ricker stock-recruitment relation (top panels) and fishery performance data (bottom panels) for the 1976-1997 brood years and 1976-2002 run years for the Situk stock. Bottom right panel depicts run data from the most recent 15 years (1988-2002).



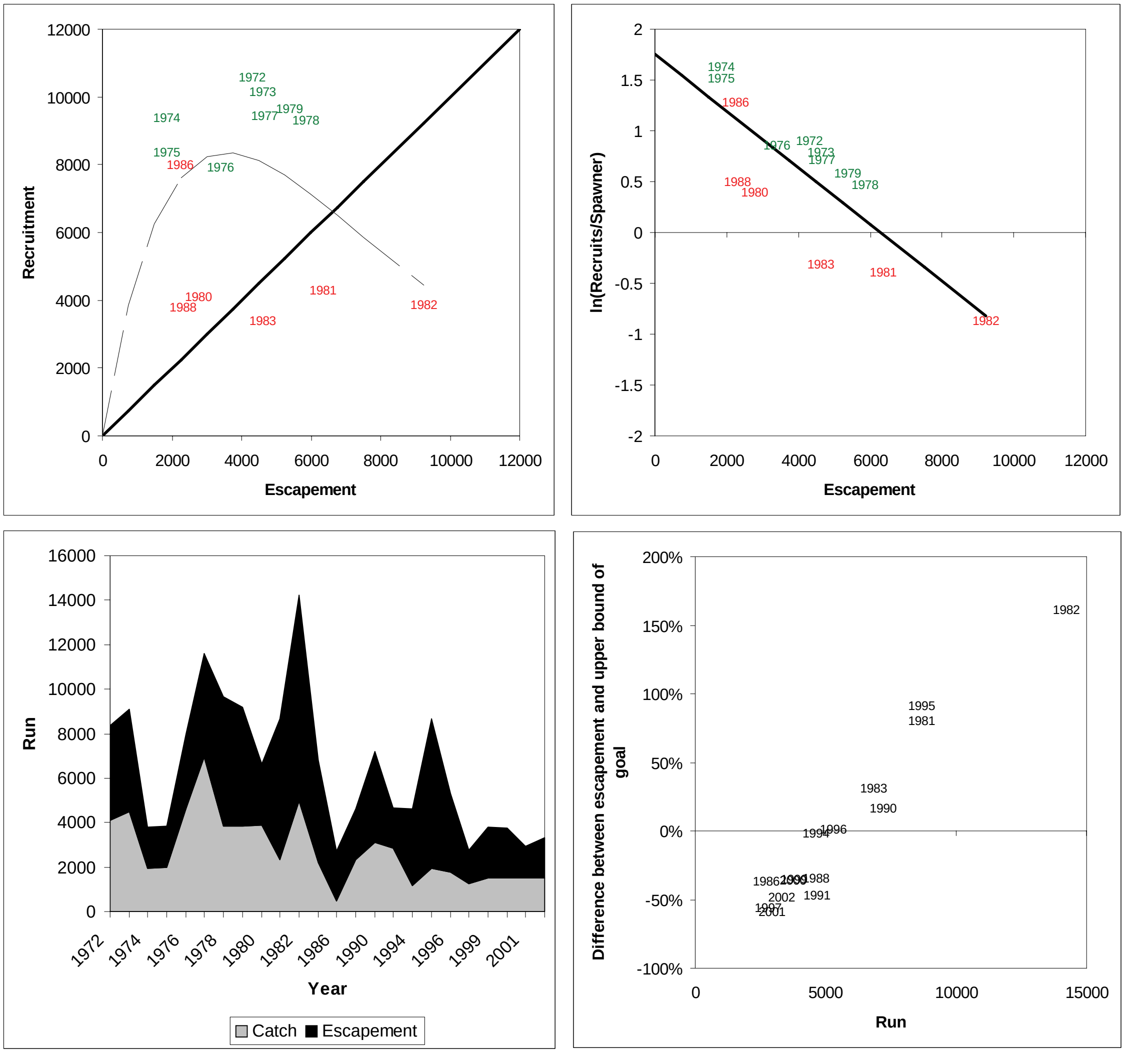
Appendix B9.–Ricker stock-recruitment relation (top panels) and fishery performance data (bottom panels) for the 1982-1996 brood years and 1982-2002 run years for the Redoubt stock. Bottom right panel depicts run data from the most recent 15 years (1988-2002).



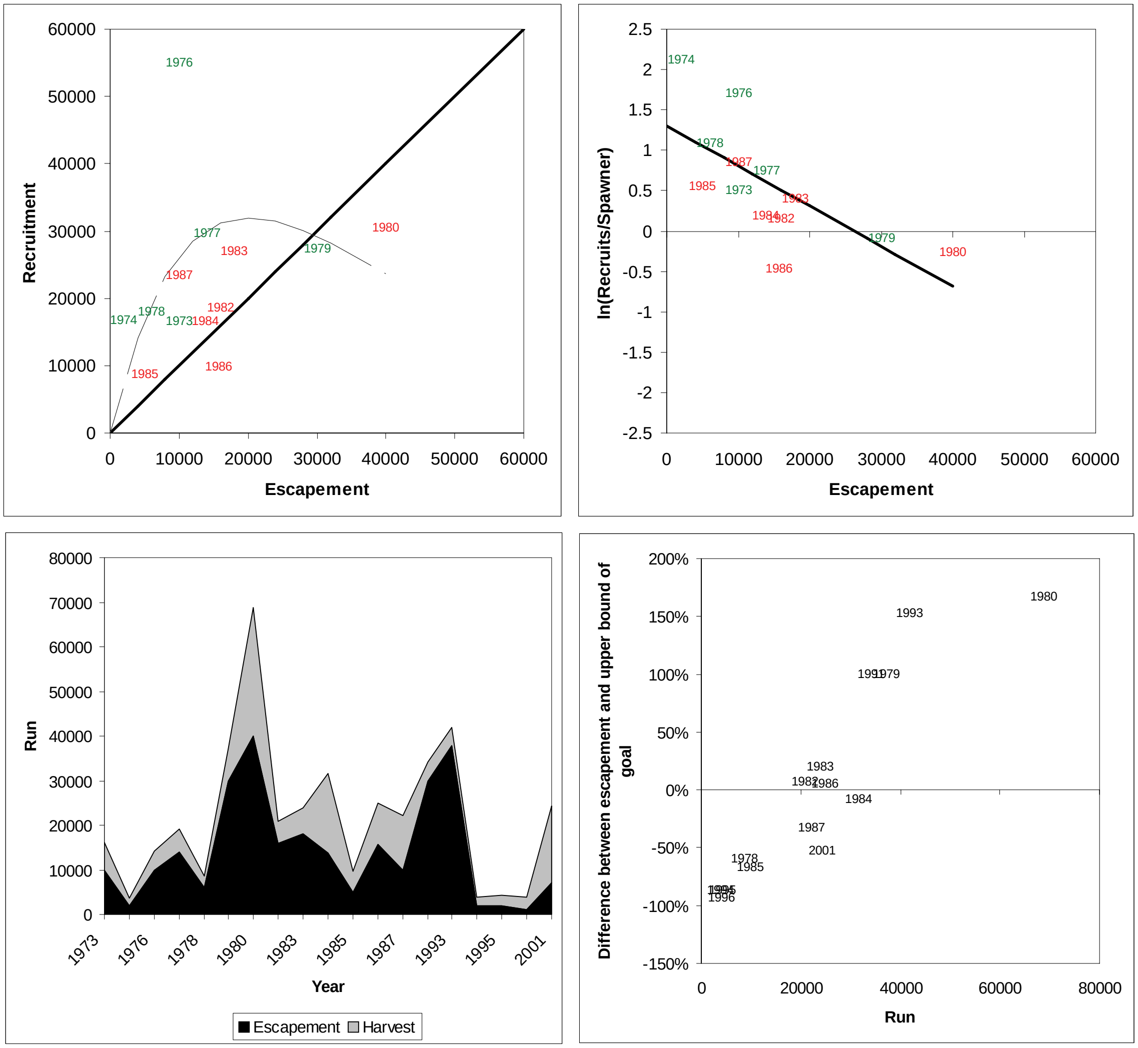
Appendix B10.–Ricker stock-recruitment relation (top panels) and fishery performance data (bottom panels) for the 1972-1997 brood years and 1972-2002 run years for the East Alsek-Doame stock. Bottom right panel depicts run data from the most recent 15 years (1988-2002).



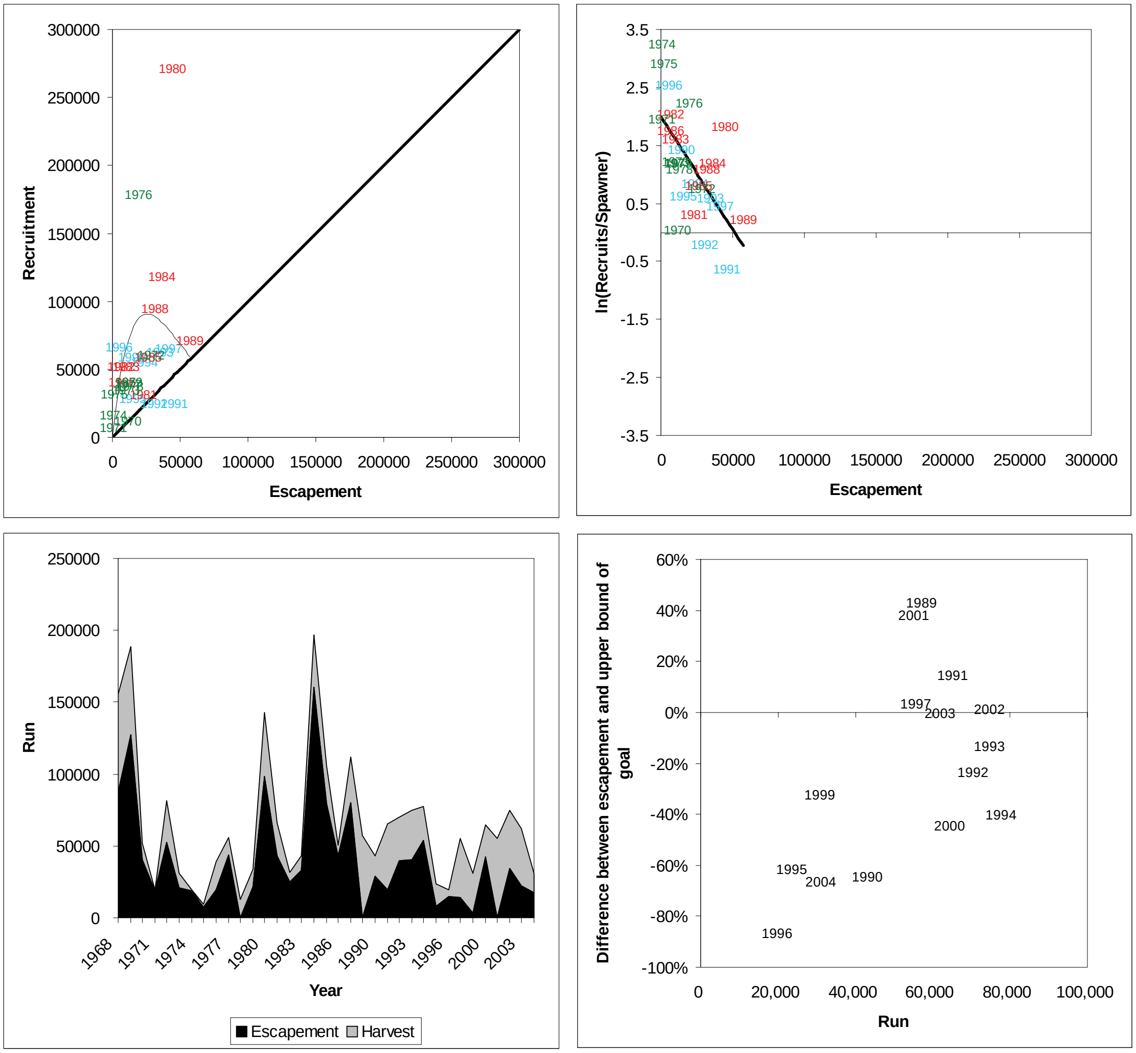
Appendix B11.–Ricker stock-recruitment relation (top panels) and fishery performance data (bottom panels) for the 1976-1996 brood years and 1976-2002 run years for the Klukshu (Alsek) stock. Bottom right panel depicts run data from the most recent 15 years (1988-2002).



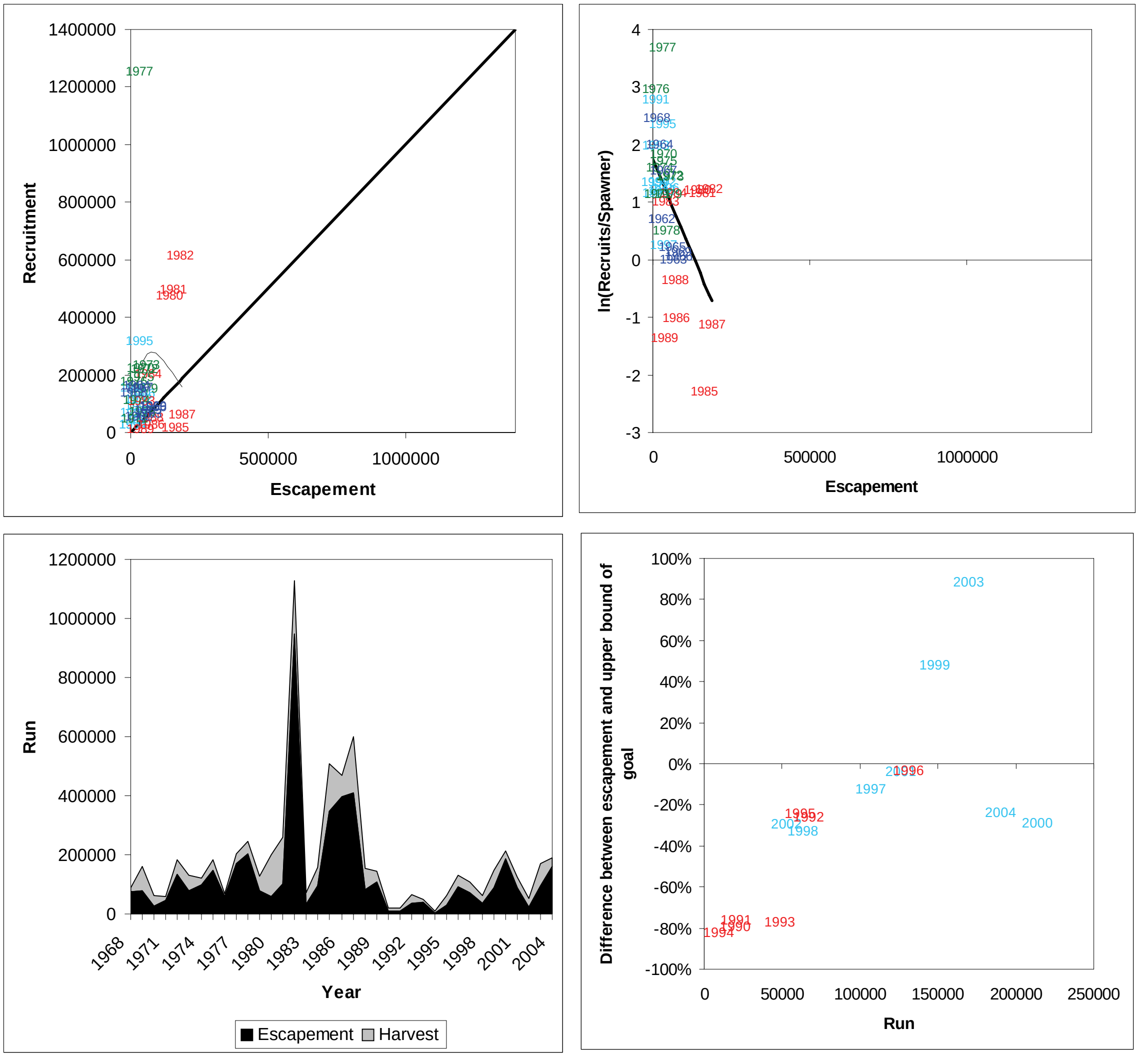
Appendix B12.–Ricker stock-recruitment relation (top panels) and fishery performance data (bottom panels) for the 1972-1983, 1986, and 1988 brood years and 1972-1983, 1986, 1988, 1990-1991, 1994-1997 and 1999-2002 run years for the Lost stock. Bottom right panel depicts run data from the most recent 15 years (1981-1983, 1986, 1988, 1990-1991, 1994-1997, and 1999-2002).



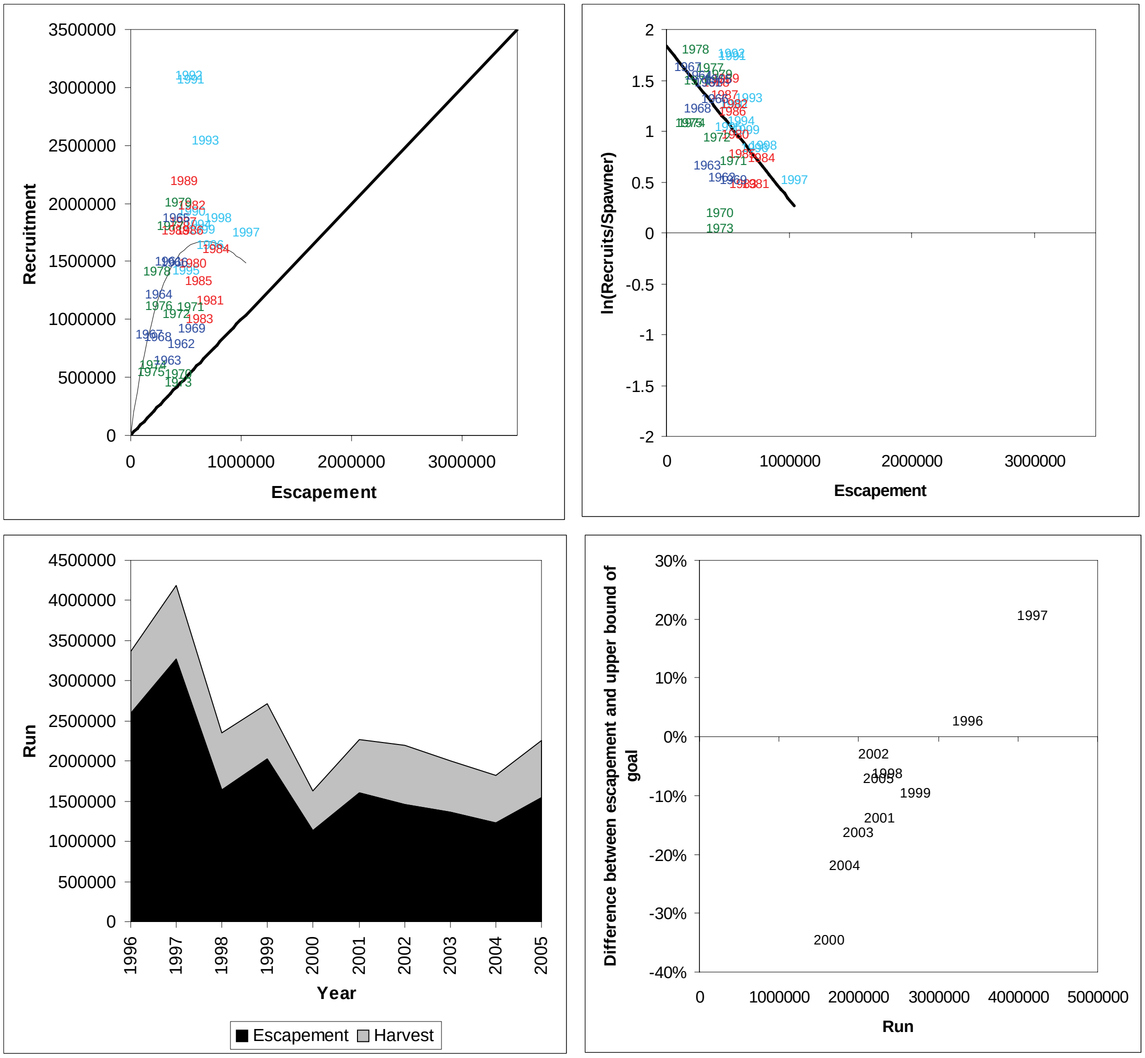
Appendix B13.–Ricker stock-recruitment relation (top panels) and fishery performance data (bottom panels) for the 1973, 1974, 1976-1980 and 1982-1987 brood years and 1972, 1973, 1976-1980, 1982-1987, 1991, 1993-1996 and 2001 run years for the Akwe stock. Bottom right panel depicts run data from the most recent 15 years (1978-1980, 1982-1987, 1991, 1993-1996 and 2001).



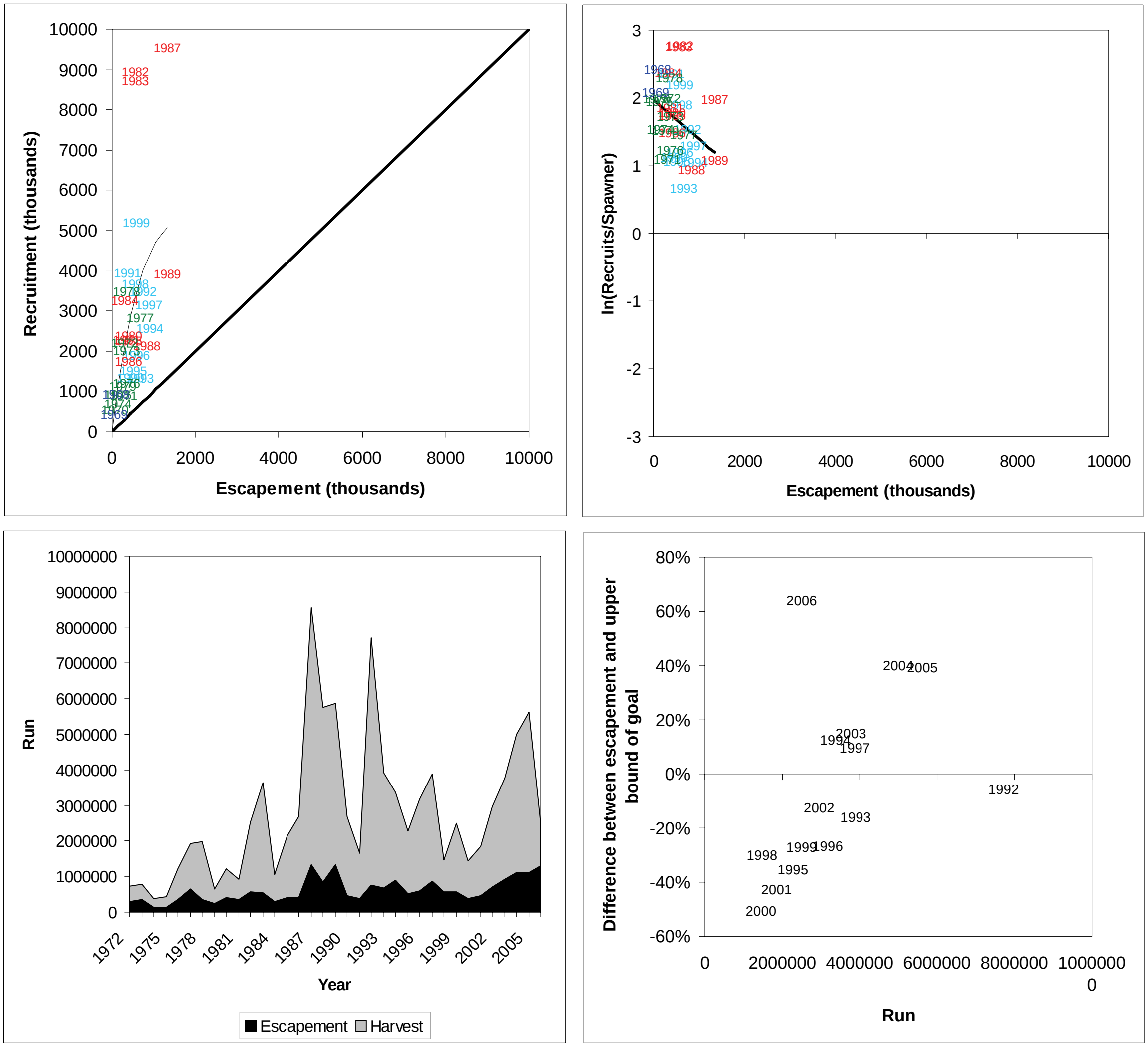
Appendix B14.–Ricker stock-recruitment relation (top panels) and fishery performance data (bottom panels) for the 1970-1986 and 1988-1997 brood years and 1968-1986, 1988-1997, and 1999-2004 run years for the Eshamy stock. Bottom right panel depicts run data from the most recent 15 years (1989-1997 and 1999-2004).



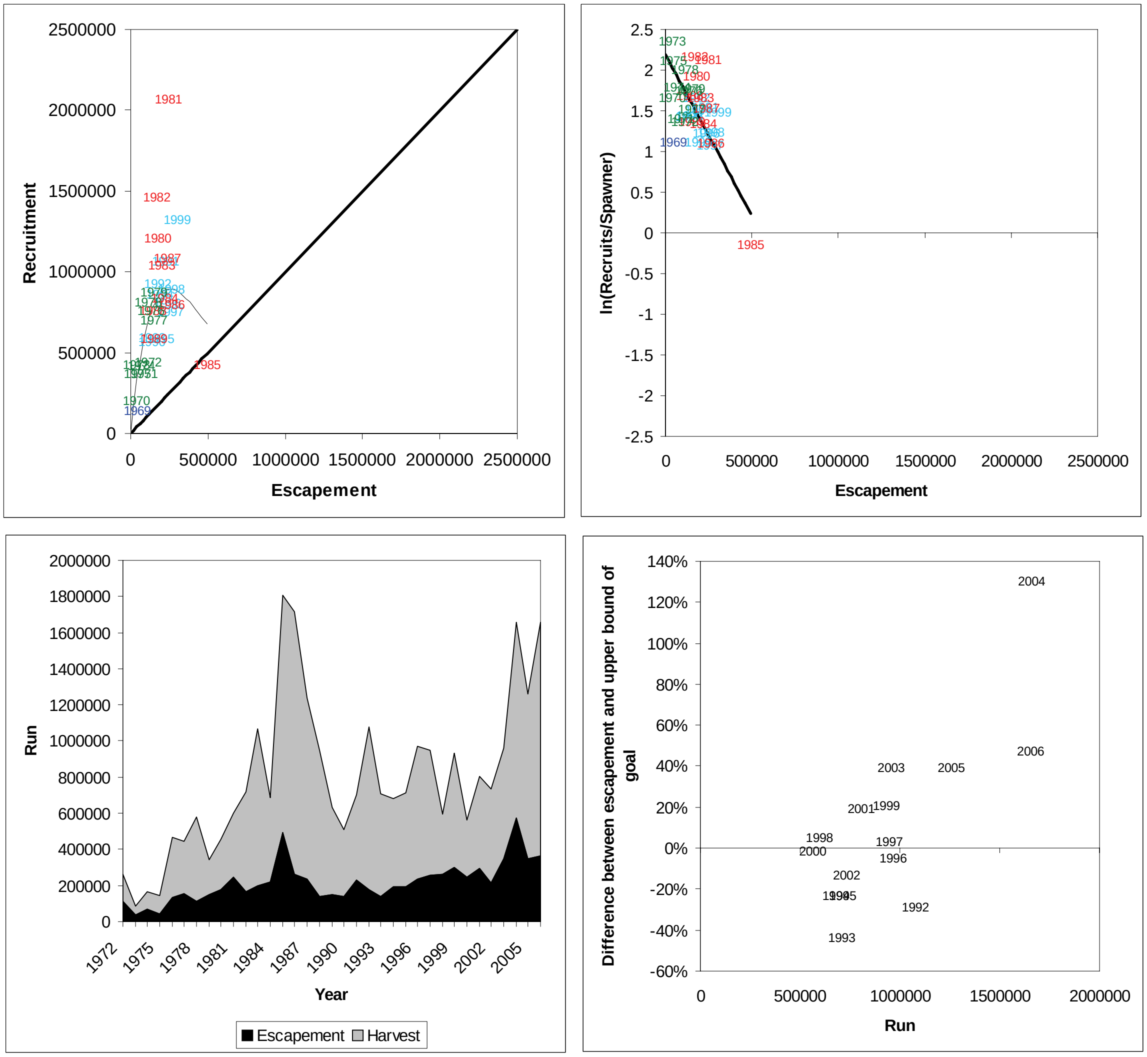
Appendix B15.–Ricker stock-recruitment relation (top panels) and fishery performance data (bottom panels) for the 1962-1998 brood years and 1968-2004 run years for the Coghill stock. Bottom right panel depicts run data from the most recent 15 years (1990-2004).



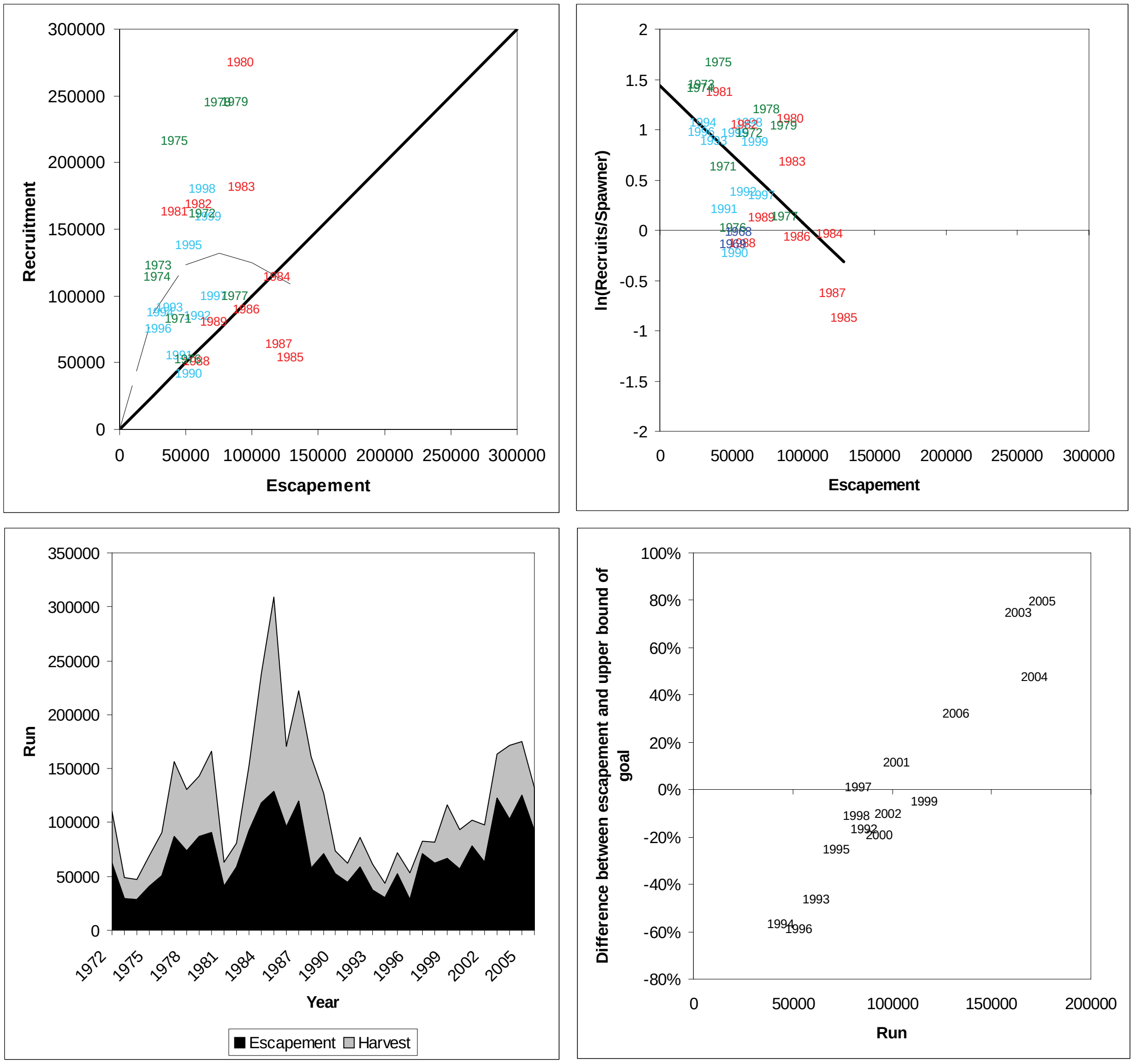
Appendix B16.–Ricker stock-recruitment relation (top panels) and fishery performance data (bottom panels) for the 1961-1999 brood years and 1996-2005 run years for the Copper stock. Bottom right panel depicts run data from the most recent 10 years (1996-2005).



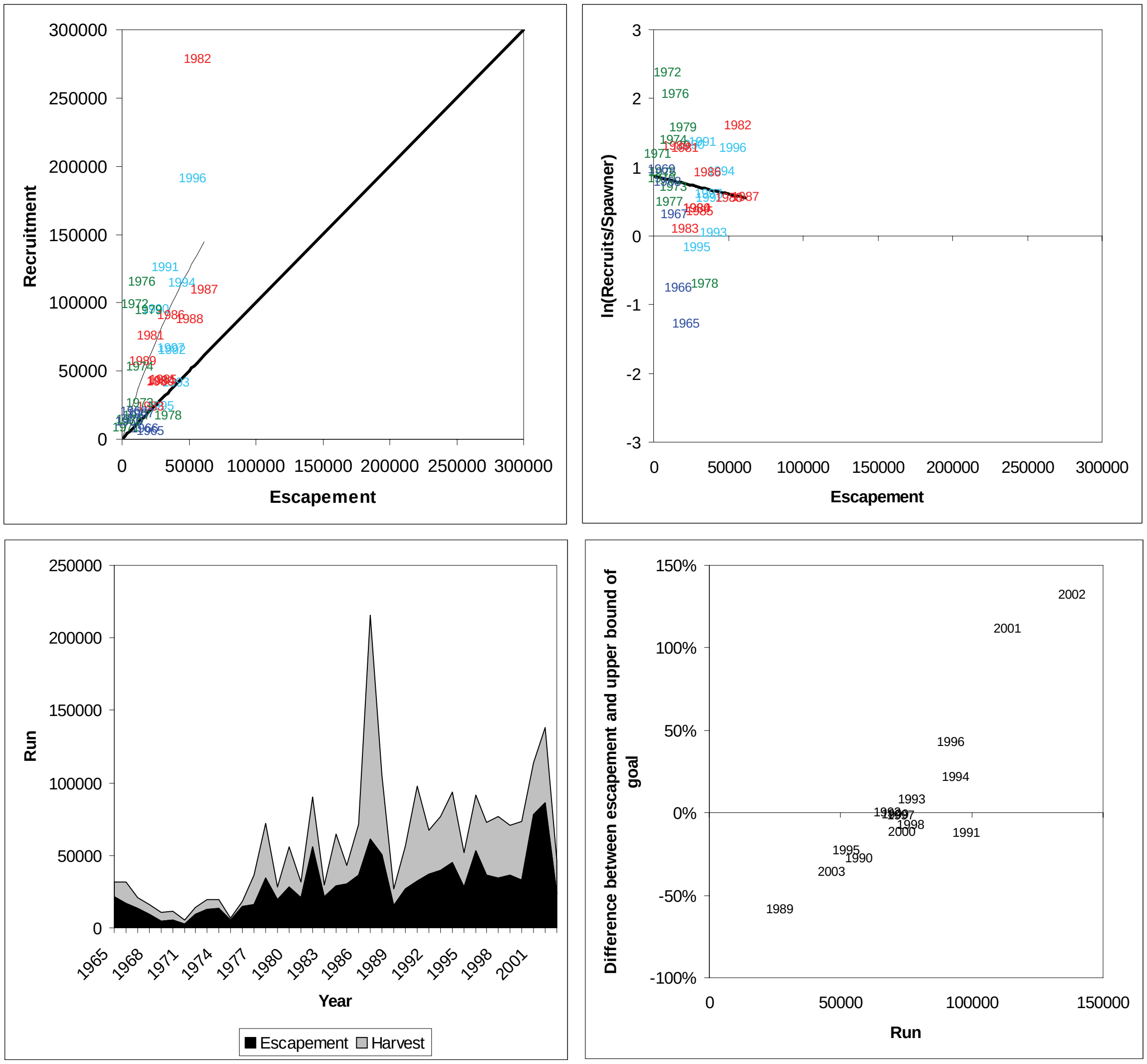
Appendix B17.–Ricker stock-recruitment relation (top panels) and fishery performance data (bottom panels) for the 1968-1999 brood years and 1968-2006 run years for the Kenai stock. Bottom right panel depicts run data from the most recent 15 years (1992-2006).



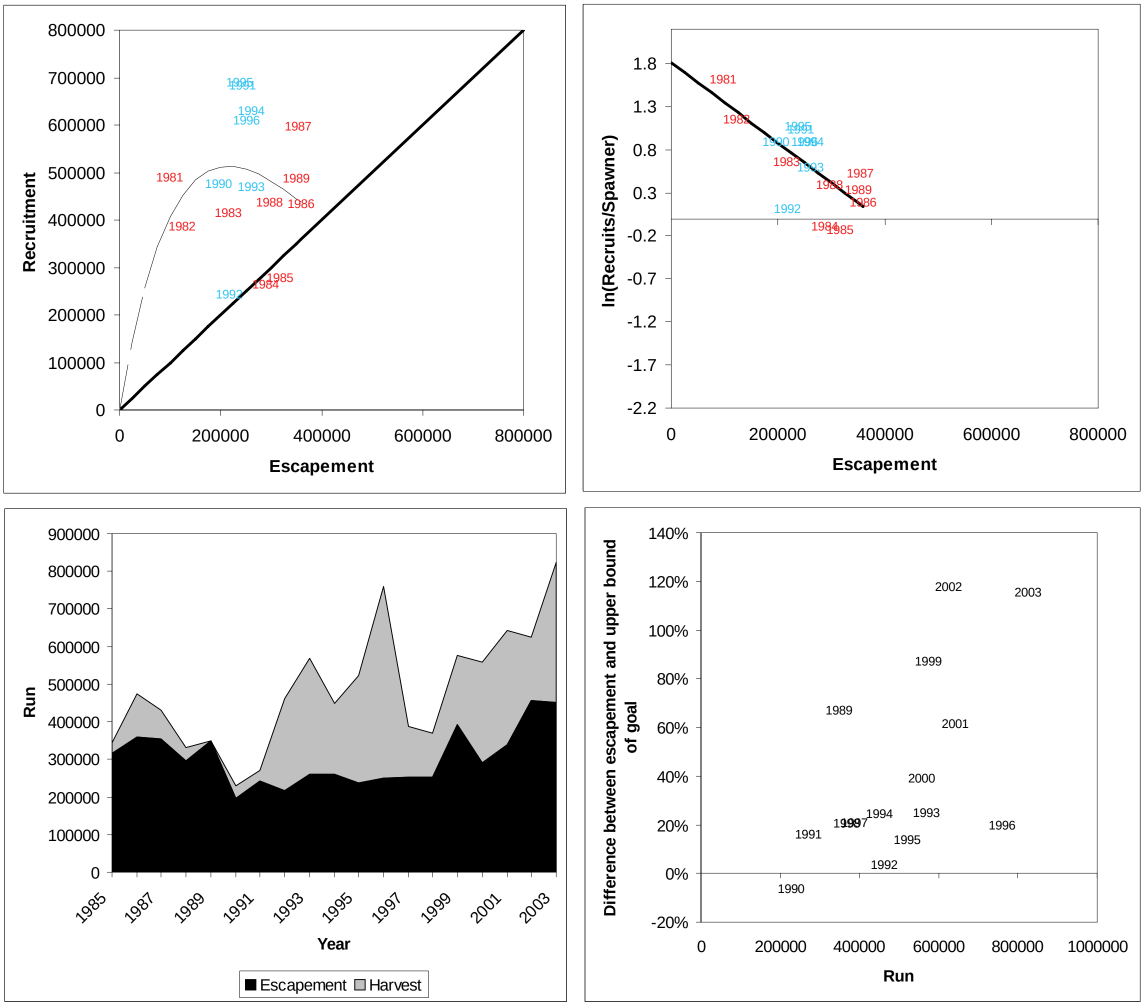
Appendix B18.–Ricker stock-recruitment relation (top panels) and fishery performance data (bottom panels) for the 1969-1999 brood years and 1969-2006 run years for the Kasilof stock. Bottom right panel depicts run data from the most recent 15 years (1992-2006).



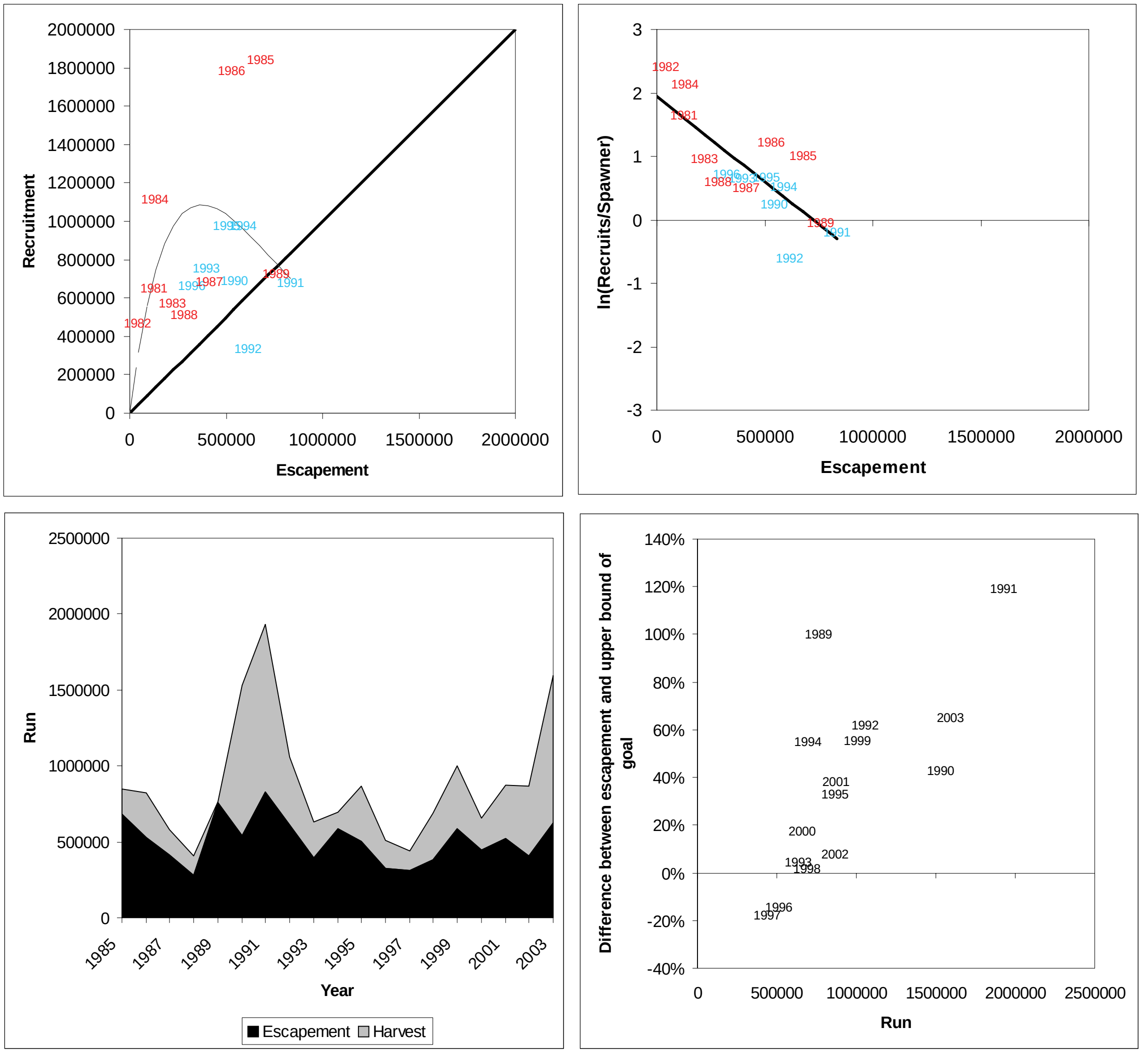
Appendix B19.–Ricker stock-recruitment relation (top panels) and fishery performance data (bottom panels) for the 1968, 1969 and 1971-1999 brood years and 1972-2006 run years for the Crescent stock. Bottom right panel depicts run data from the most recent 15 years (1992-2006).



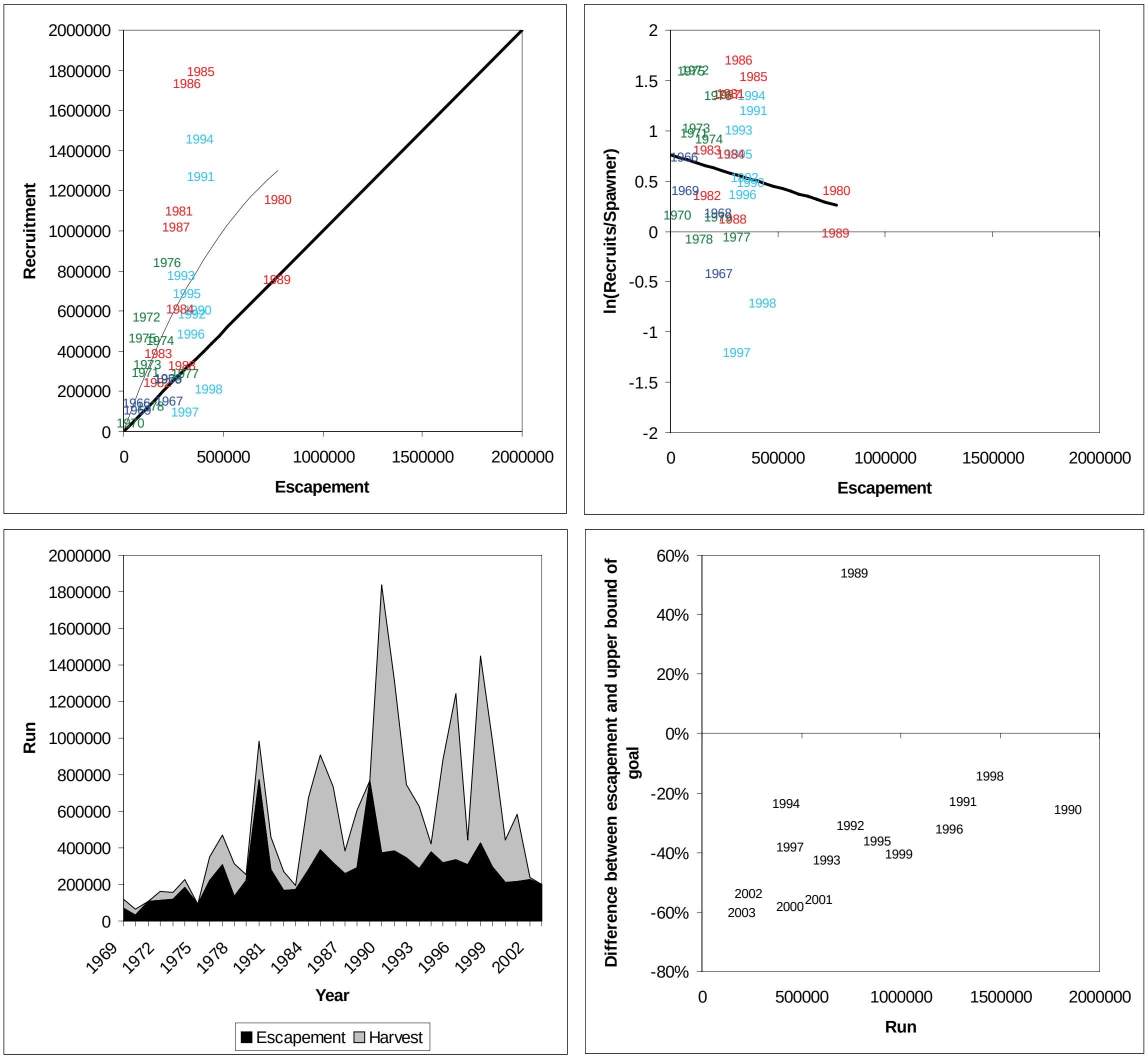
Appendix B20.–Ricker stock-recruitment relation (top panels) and fishery performance data (bottom panels) for the 1965-1997 brood years and 1965-2003 run years for the Russian early run (ER) stock. Bottom right panel depicts run data from the most recent 15 years (1989-2003).



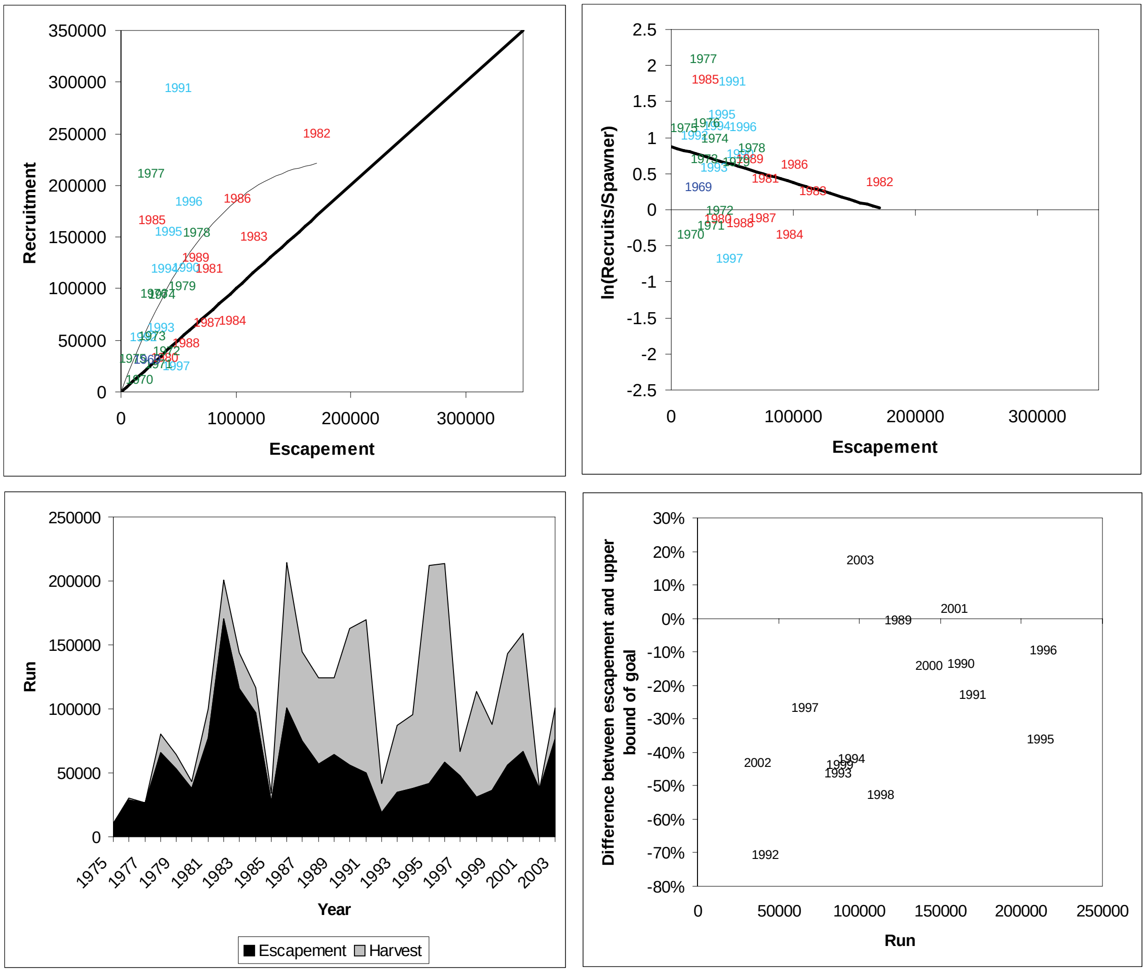
Appendix B21.–Ricker stock-recruitment relation (top panels) and fishery performance data (bottom panels) for the 1981-1996 brood years and 1985-2003 run years for the Karluk ER stock. Bottom right panel depicts run data from the most recent 15 years (1989-2003).



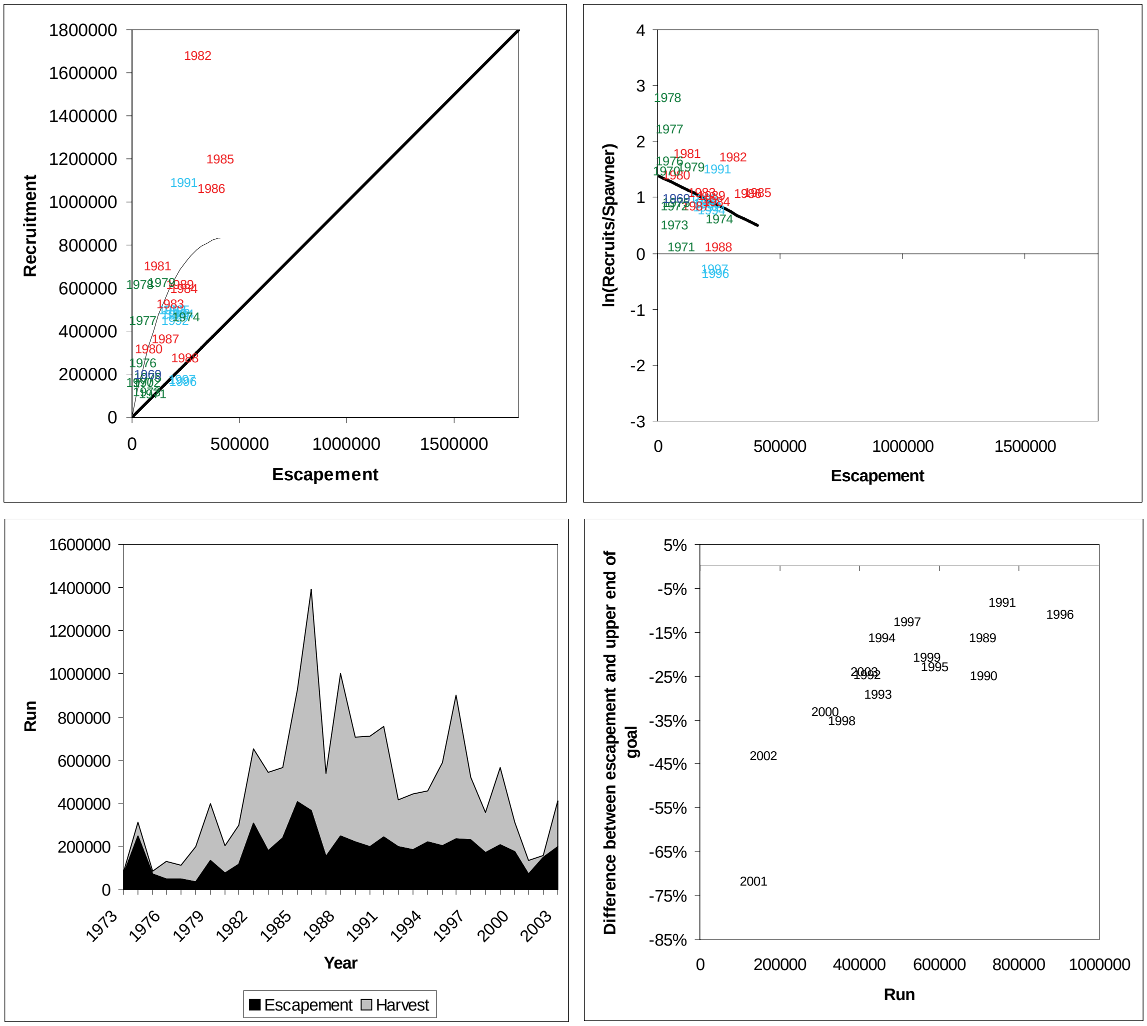
Appendix B22.–Ricker stock-recruitment relation (top panels) and fishery performance data (bottom panels) for the 1981-1996 brood years and 1985-2003 run years for the Karluk late run (LR) stock. Bottom right panel depicts run data from the most recent 15 years (1989-2003).



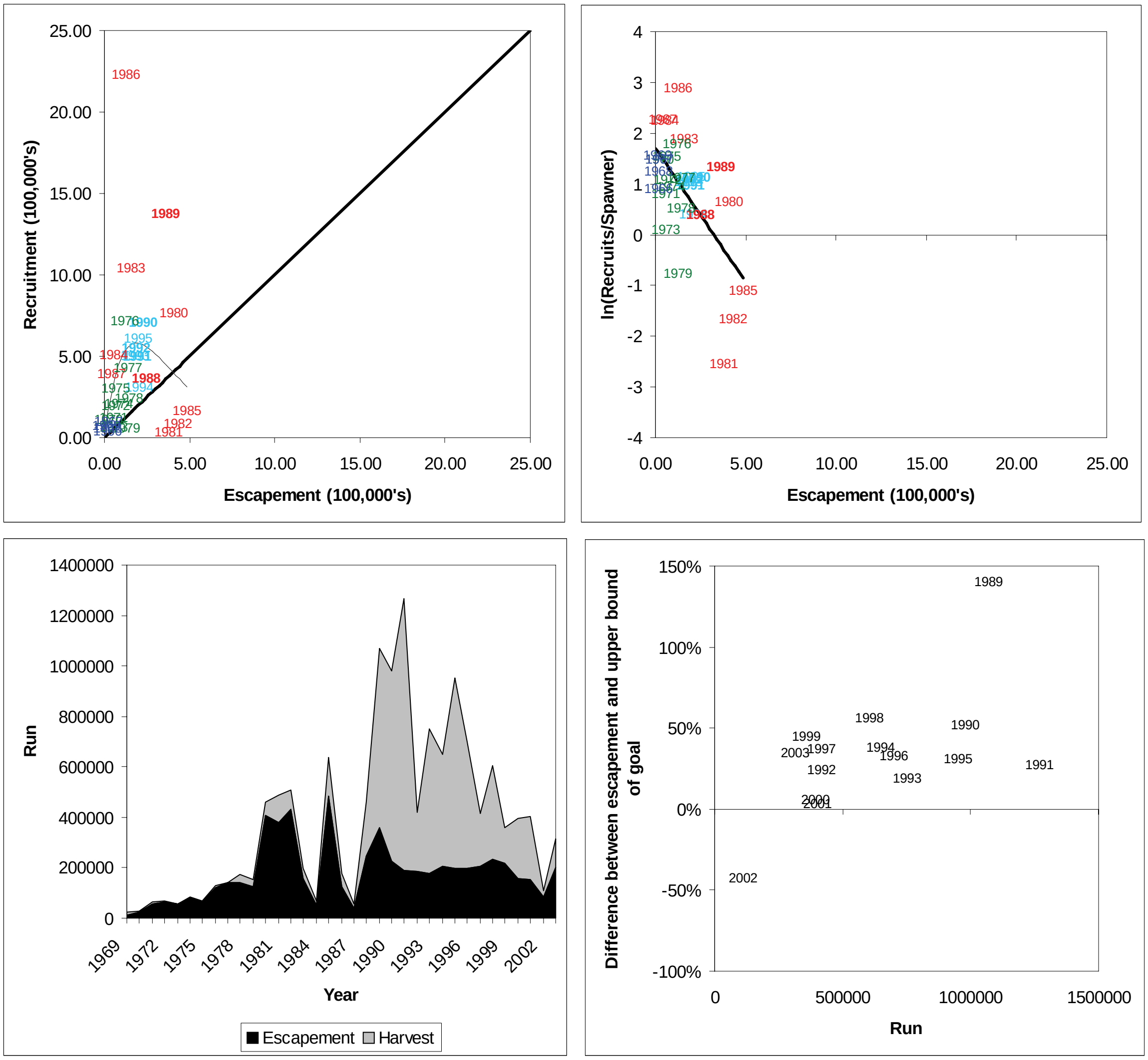
Appendix B23.–Ricker stock-recruitment relation (top panels) and fishery performance data (bottom panels) for the 1966-1996 brood years and 1969-2003 run years for the Ayakulik stock. Bottom right panel depicts run data from the most recent 15 years (1989-2003).



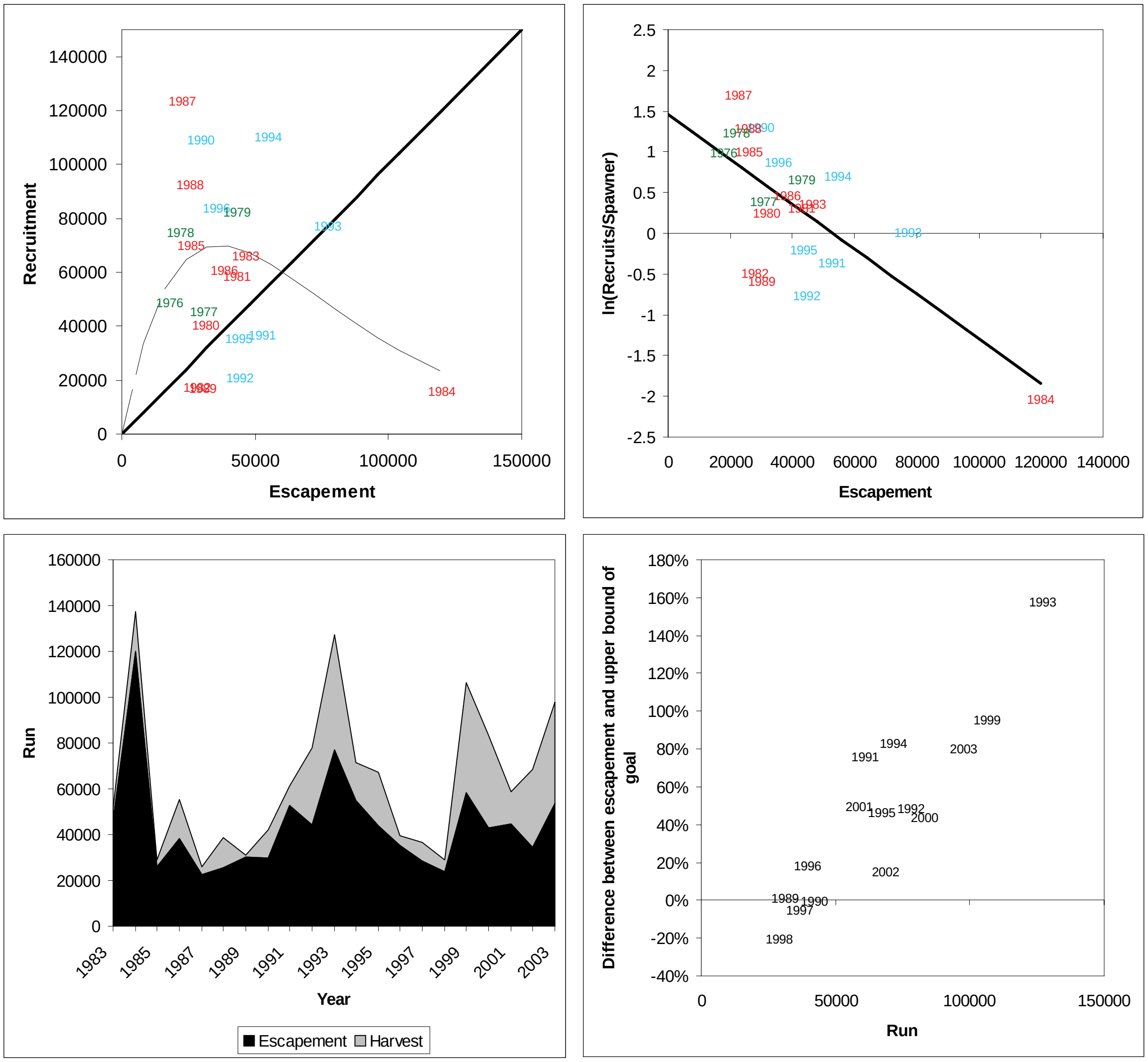
Appendix B24.–Ricker stock-recruitment relation (top panels) and fishery performance data (bottom panels) for the 1969-1997 brood years and 1975-2002 run years for the Upper Station ER stock. Bottom right panel depicts run data from the most recent 15 years (1988-2002).



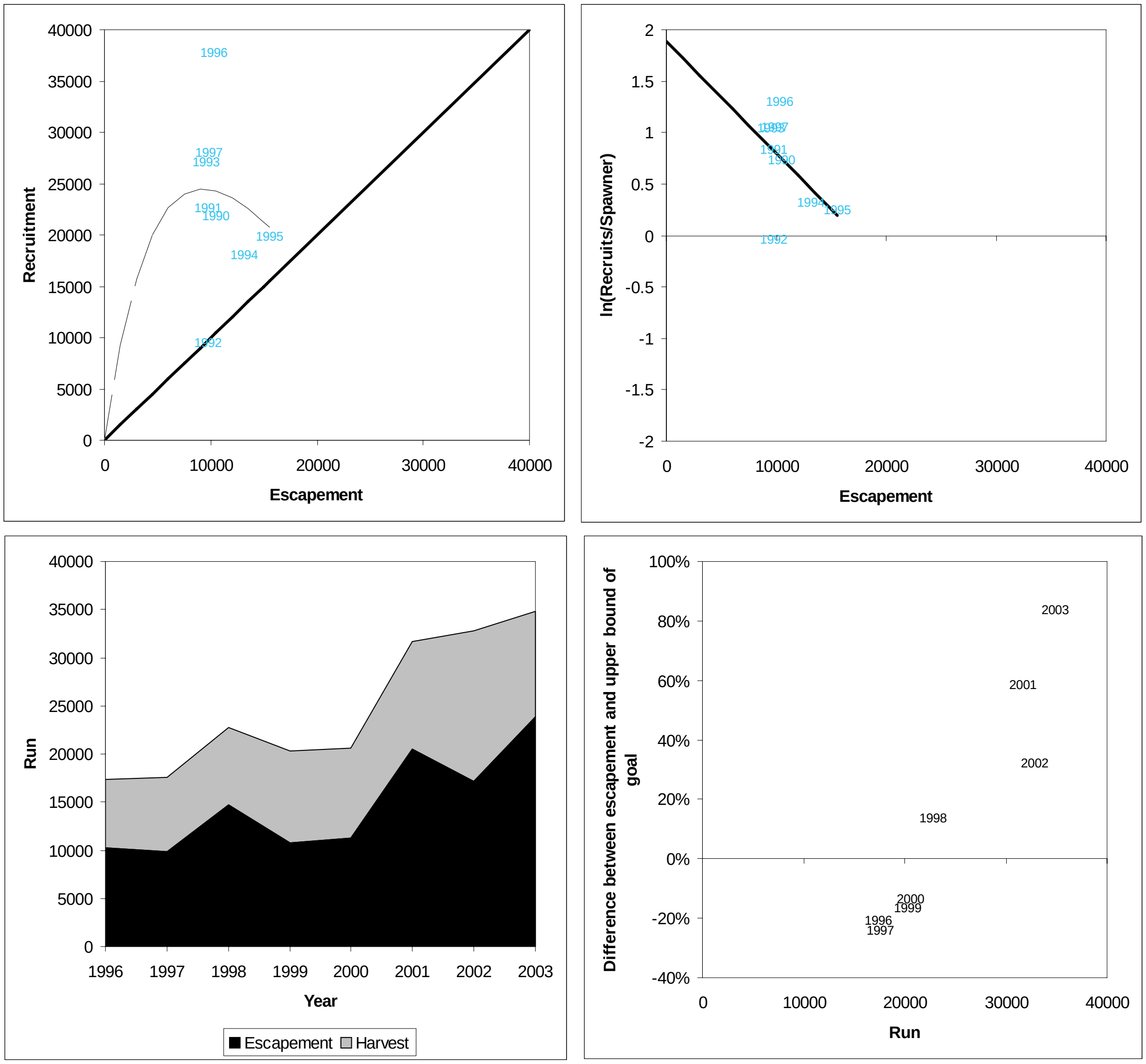
Appendix B25.–Ricker stock-recruitment relation (top panels) and fishery performance data (bottom panels) for the 1969-1997 brood years and 1975-2002 run years for the Upper Station LR stock. Bottom right panel depicts run data from the most recent 15 years (1988-2002).



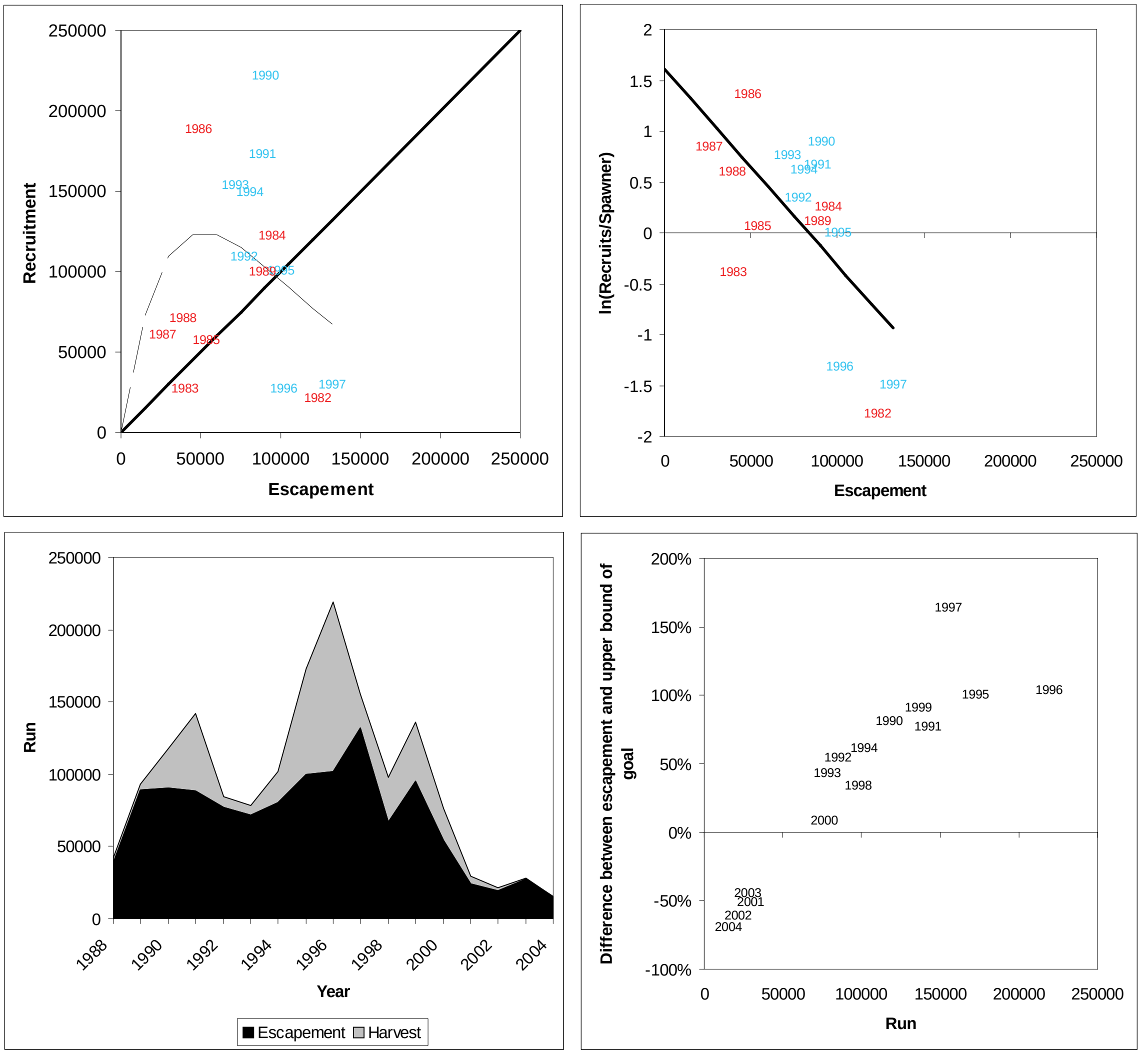
Appendix B26.–Ricker stock-recruitment relation (top panels) and fishery performance data (bottom panels) for the 1966-1995 brood years and 1969-2003 run years for the Frazer stock. Bottom right panel depicts run data from the most recent 15 years (1989-2003).



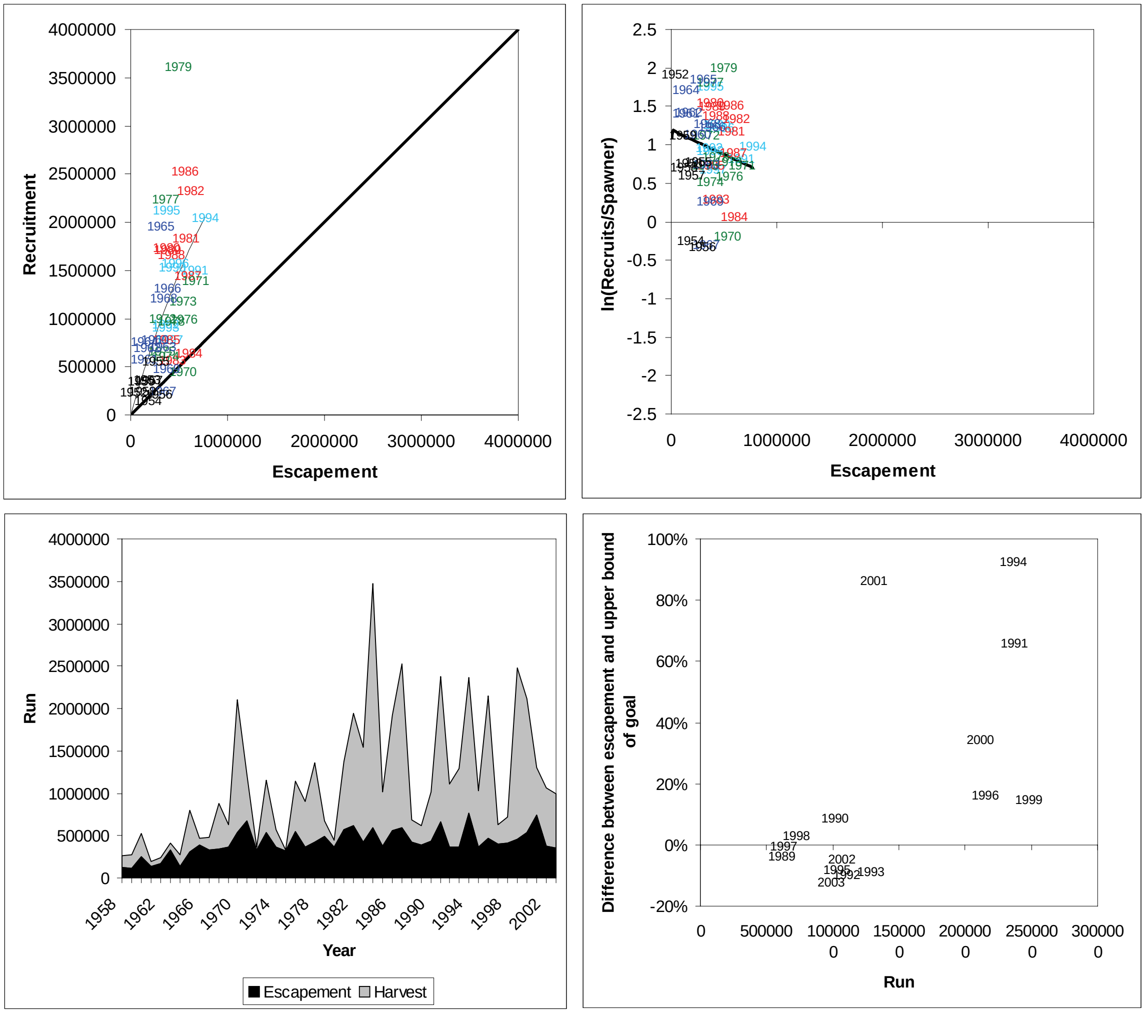
Appendix B27.–Ricker stock-recruitment relation (top panels) and fishery performance data (bottom panels) for the 1976-1996 brood years and 1983-2003 run years for the Saltery stock. Bottom right panel depicts run data from the most recent 15 years (1989-2003).



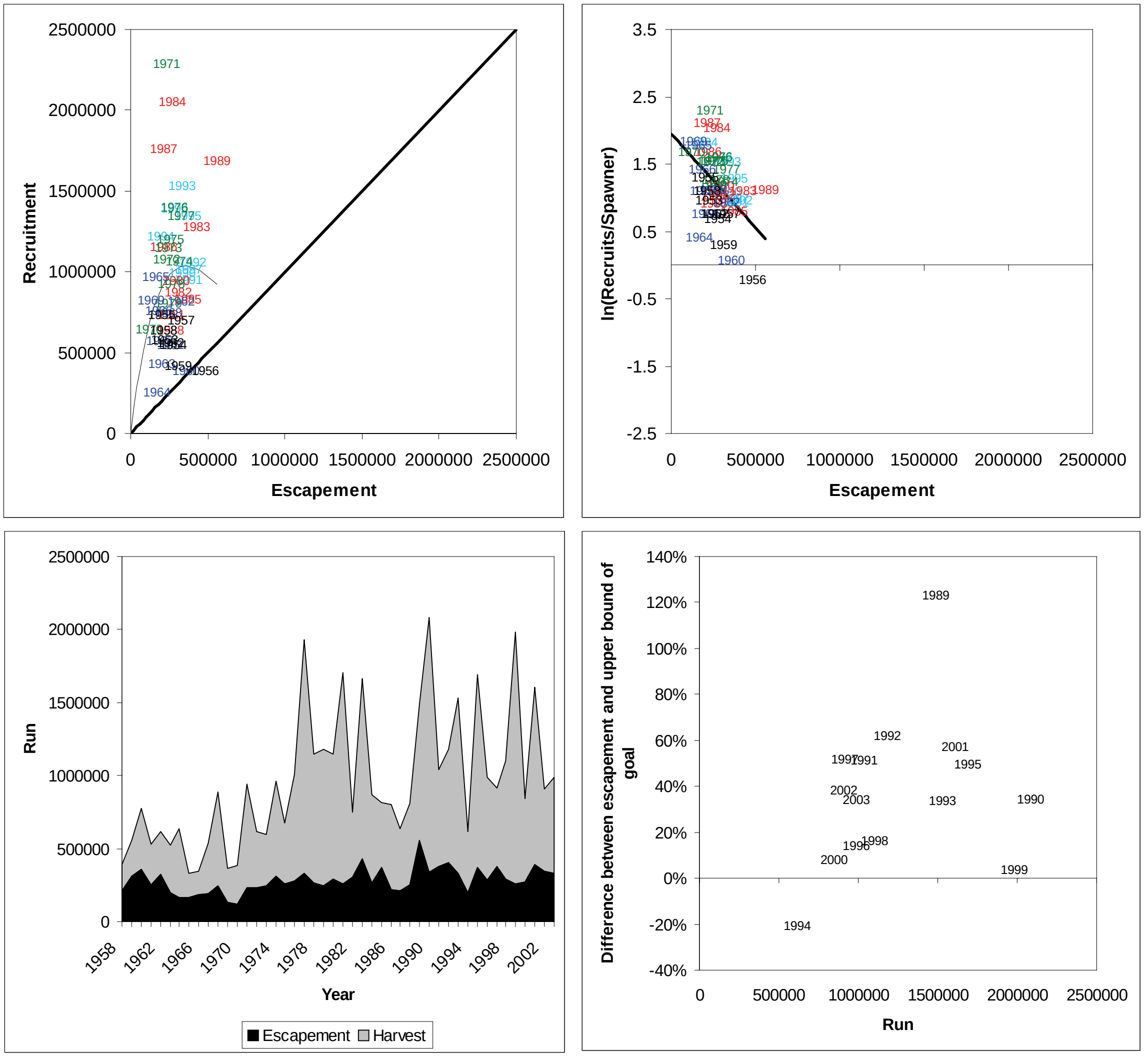
Appendix B28.–Ricker stock-recruitment relation (top panels) and fishery performance data (bottom panels) for the 1990-1997 brood years and 1996-2003 run years for the Buskin stock.



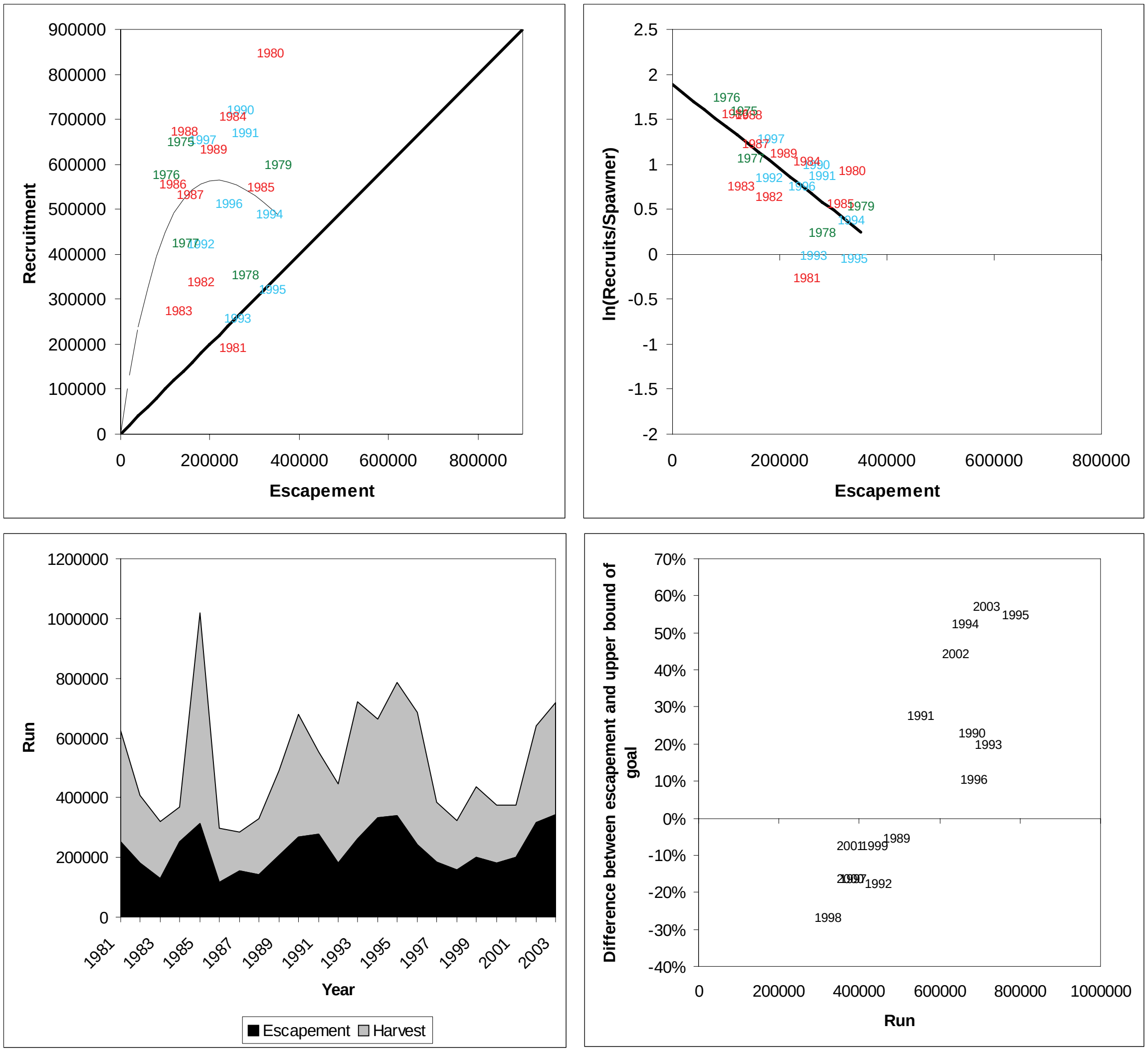
Appendix B29.–Ricker stock-recruitment relation (top panels) and fishery performance data (bottom panels) for the 1982-1997 brood years and 1988-2004 run years for the Afognak stock. Bottom right panel depicts run data from the most recent 15 years (1990-2004).



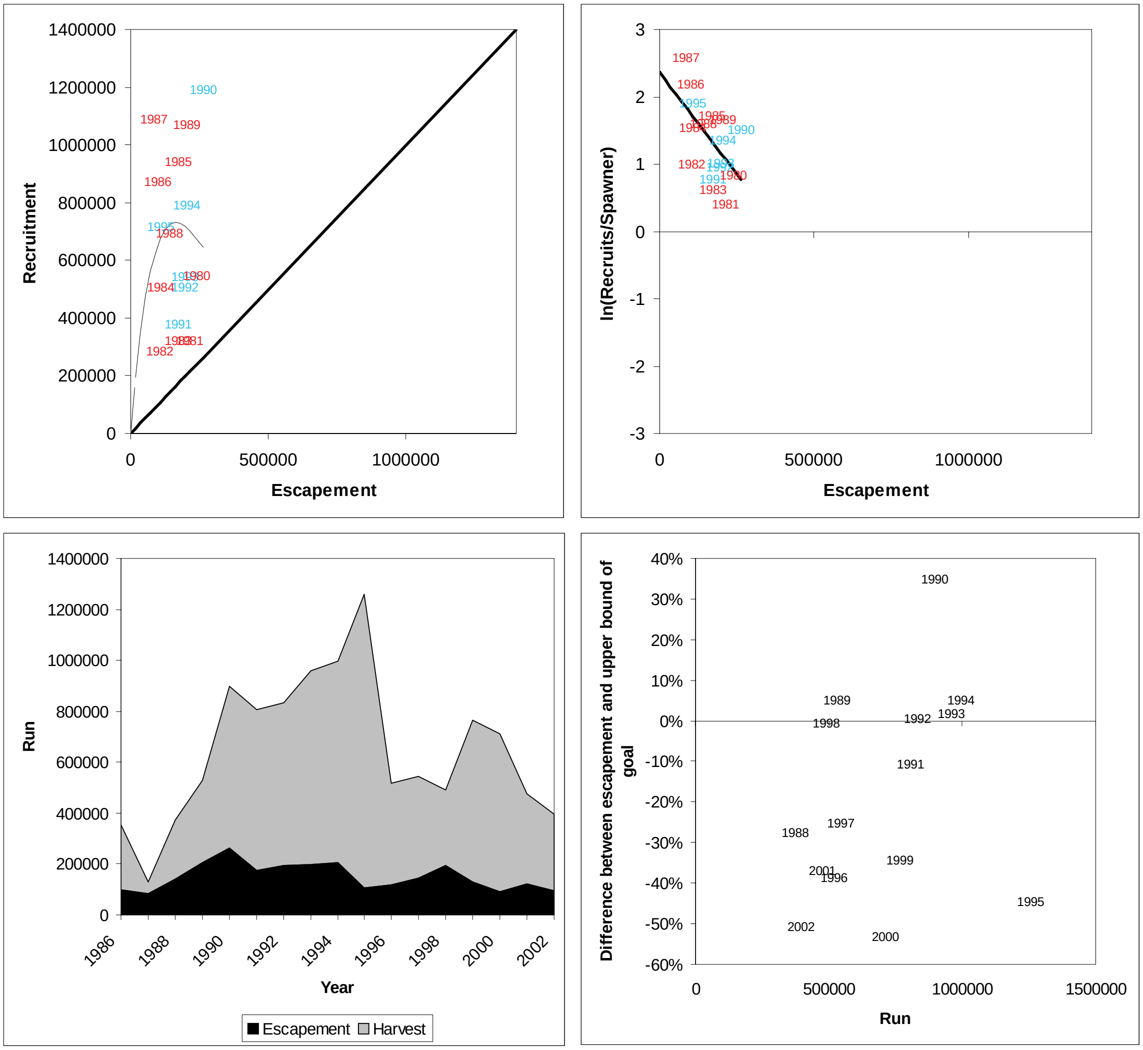
Appendix B30.–Ricker stock-recruitment relation (top panels) and fishery performance data (bottom panels) for the 1952-1997 brood years and 1958-2003 run years for the Chignik ER stock. Bottom right panel depicts run data from the most recent 15 years (1989-2003).



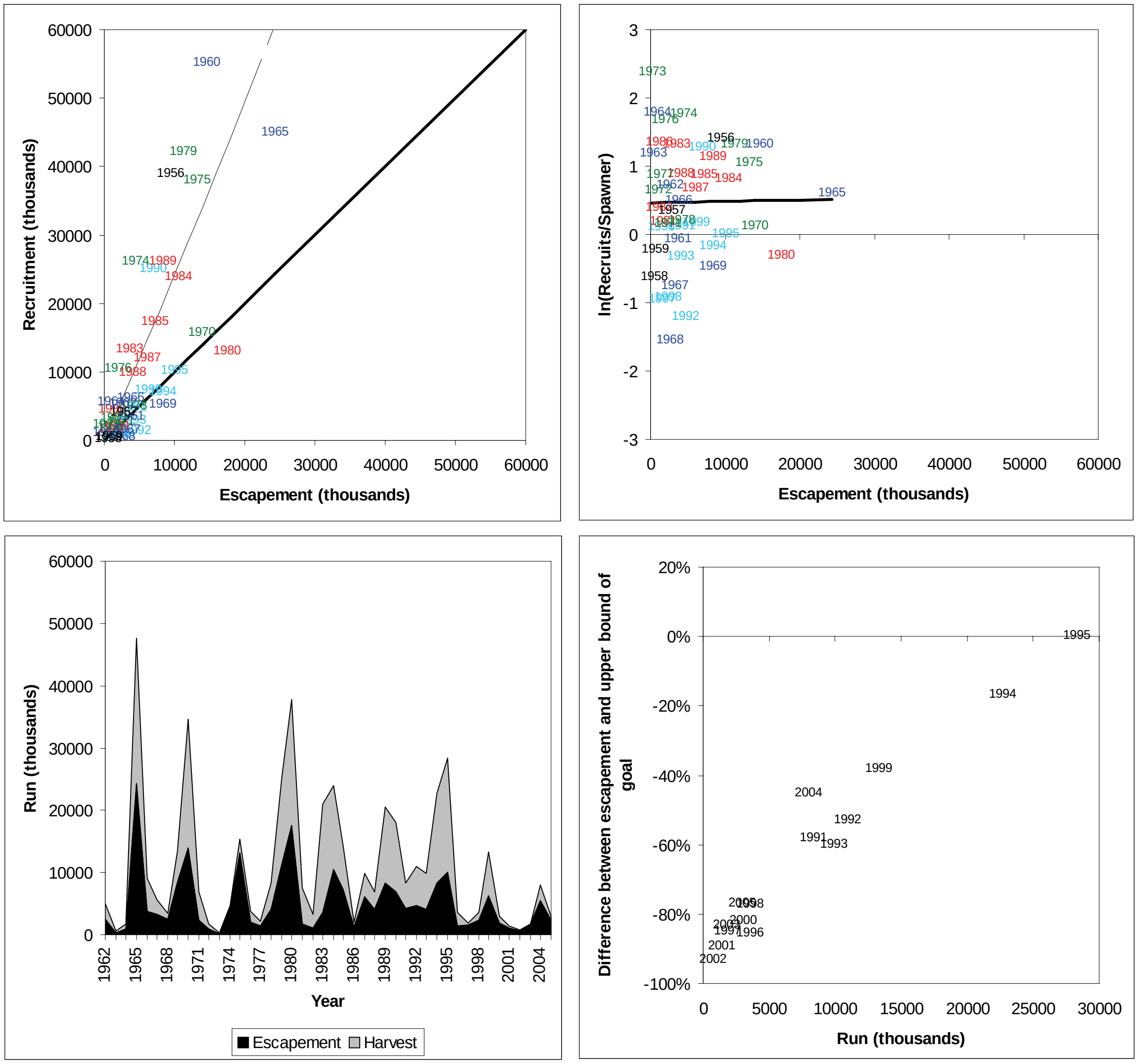
Appendix B31.–Ricker stock-recruitment relation (top panels) and fishery performance data (bottom panels) for the 1952-1997 brood years and 1958-2003 run years for the Chignik LR stock. Bottom right panel depicts run data from the most recent 15 years (1989-2003).



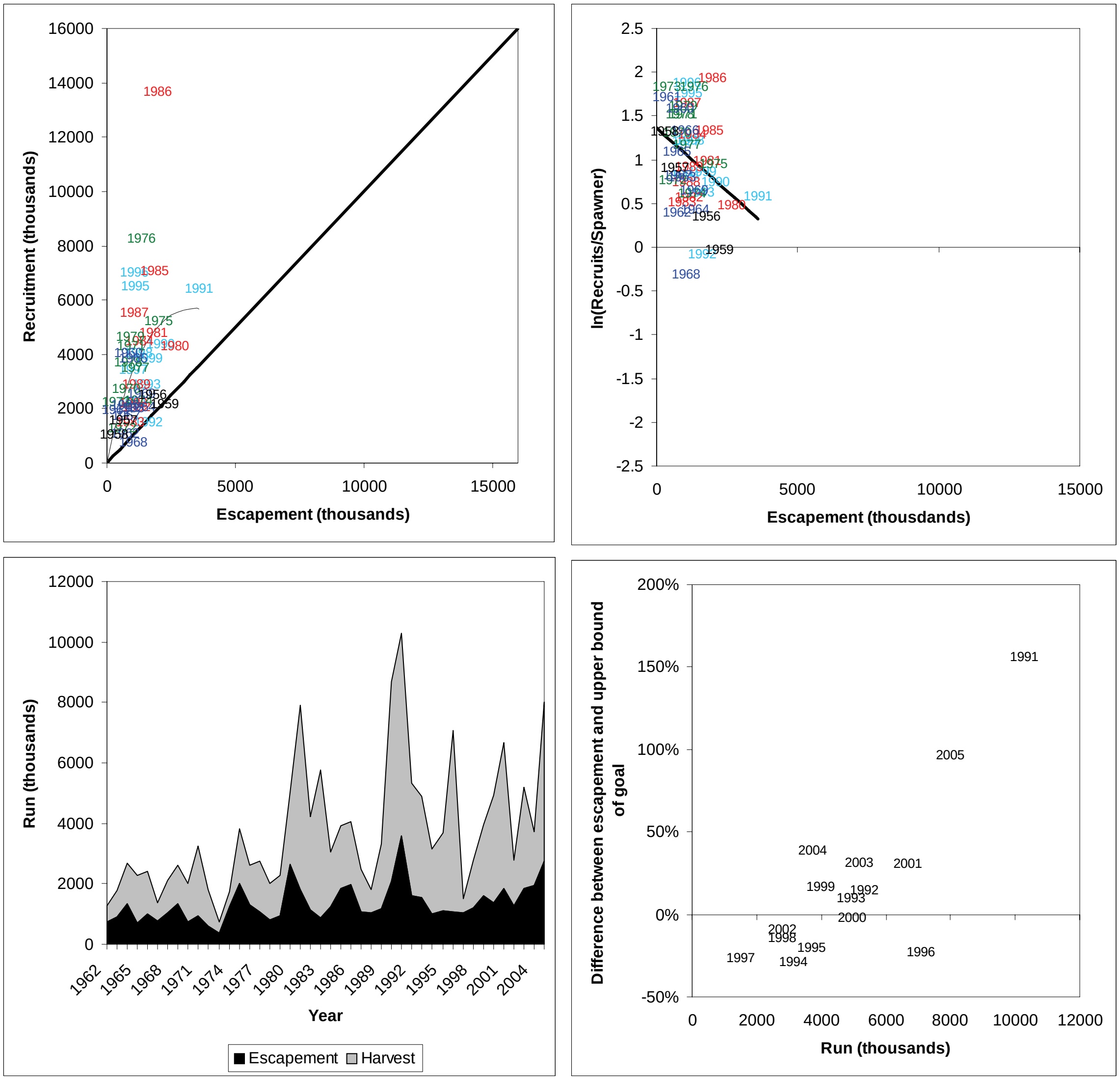
Appendix B 32.–Ricker stock-recruitment relation (top panels) and fishery performance data (bottom panels) for the 1975-1997 brood years and 1975-2003 run years for the Nelson stock. Bottom right panel depicts run data from the most recent 15 years (1989-2003).



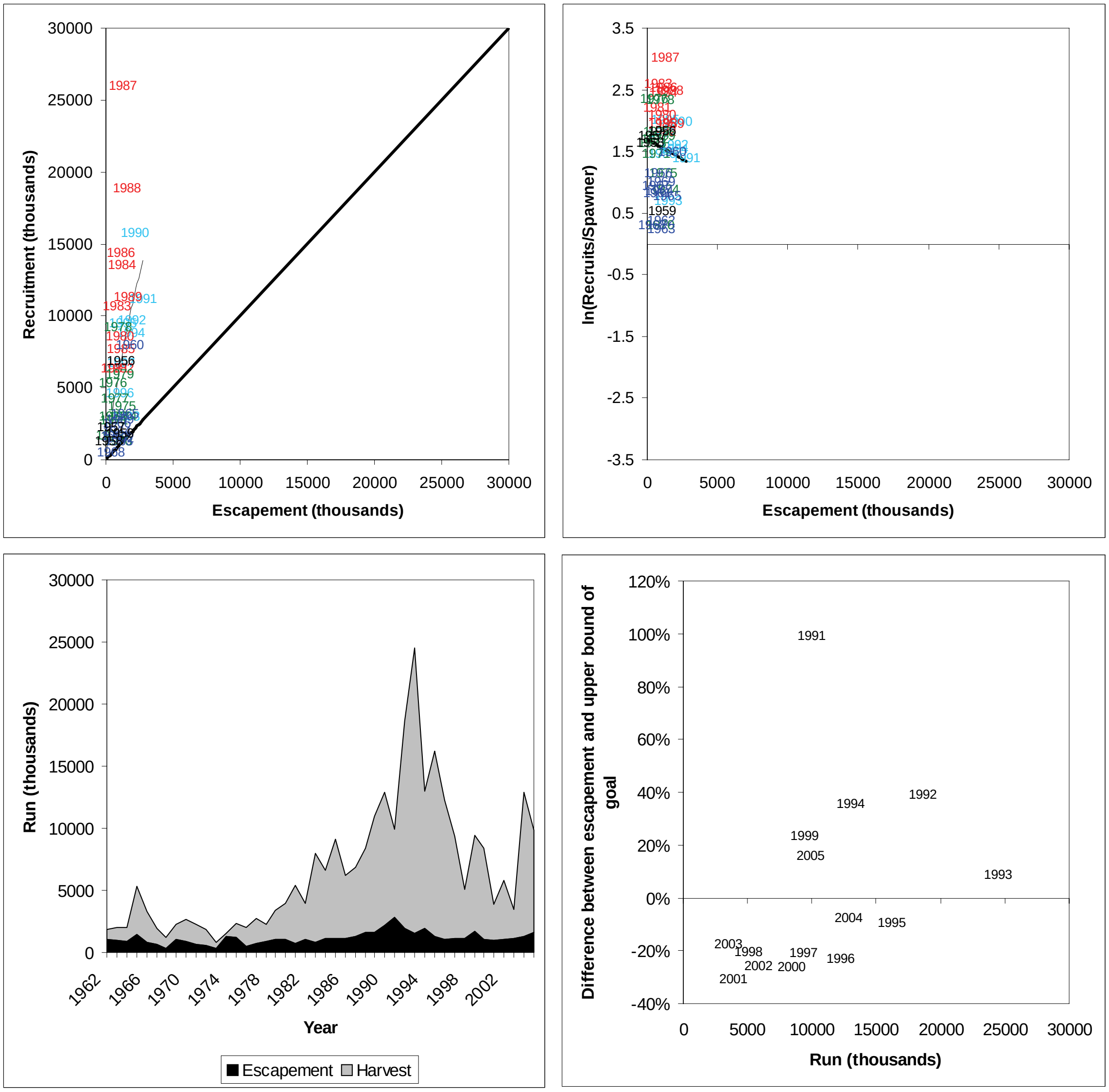
Appendix B33.–Ricker stock-recruitment relation (top panels) and fishery performance data (bottom panels) for the 1980-1995 brood years and 1980-2003 run years for the Bear LR stock. Bottom right panel depicts run data from the most recent 15 years (1989-2003).



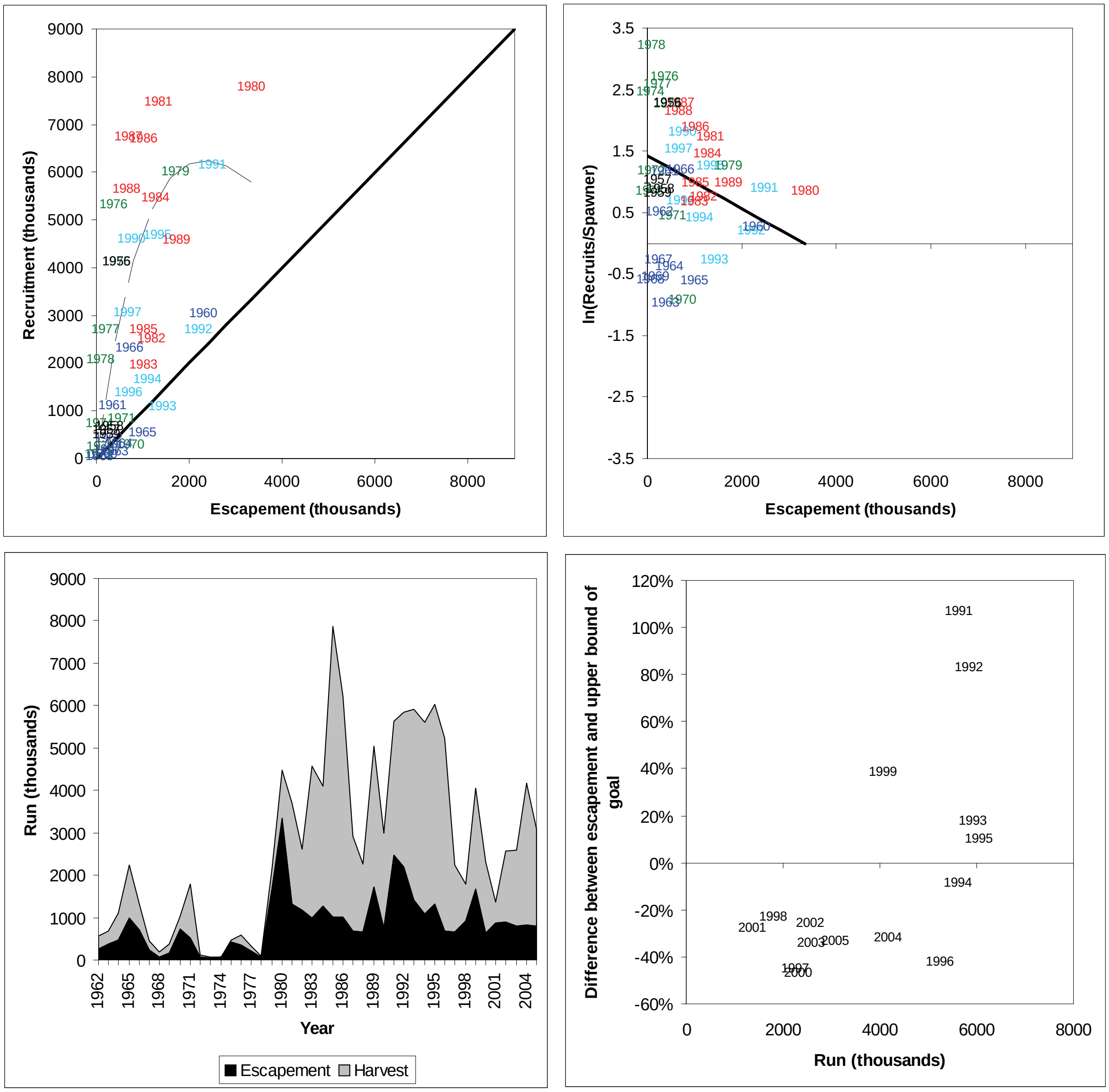
Appendix B34.–Ricker stock-recruitment relation (top panels) and fishery performance data (bottom panels) for the 1956-1999 brood years and 1962-2005 run years for the Kvichak stock. Bottom right panel depicts run data from the most recent 15 years (1991-2005).



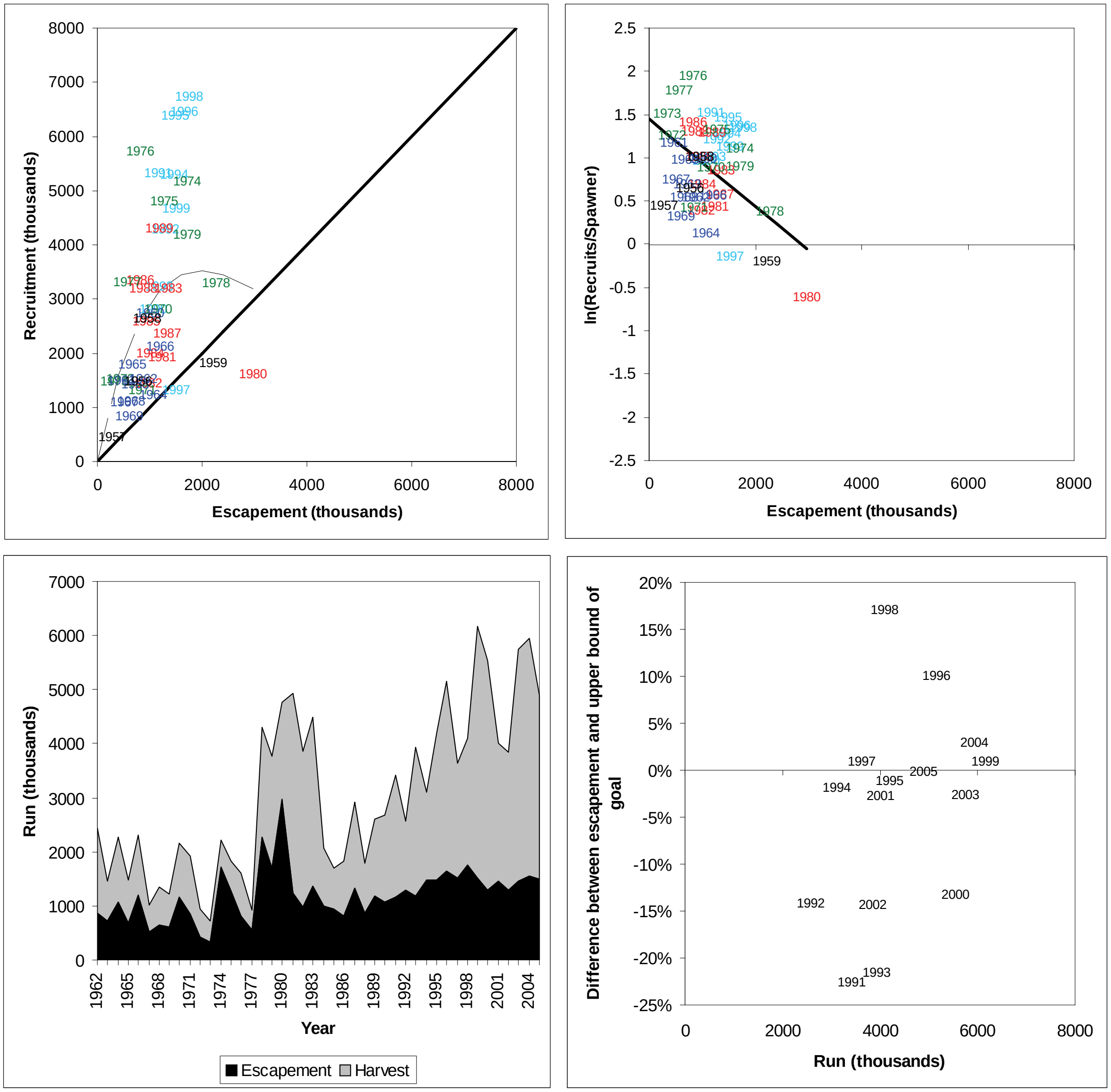
Appendix B35.–Ricker stock-recruitment relation (top panels) and fishery performance data (bottom panels) for the 1956-1999 brood years and 1962-2005 run years for the Naknek stock. Bottom right panel depicts run data from the most recent 15 years (1991-2005).



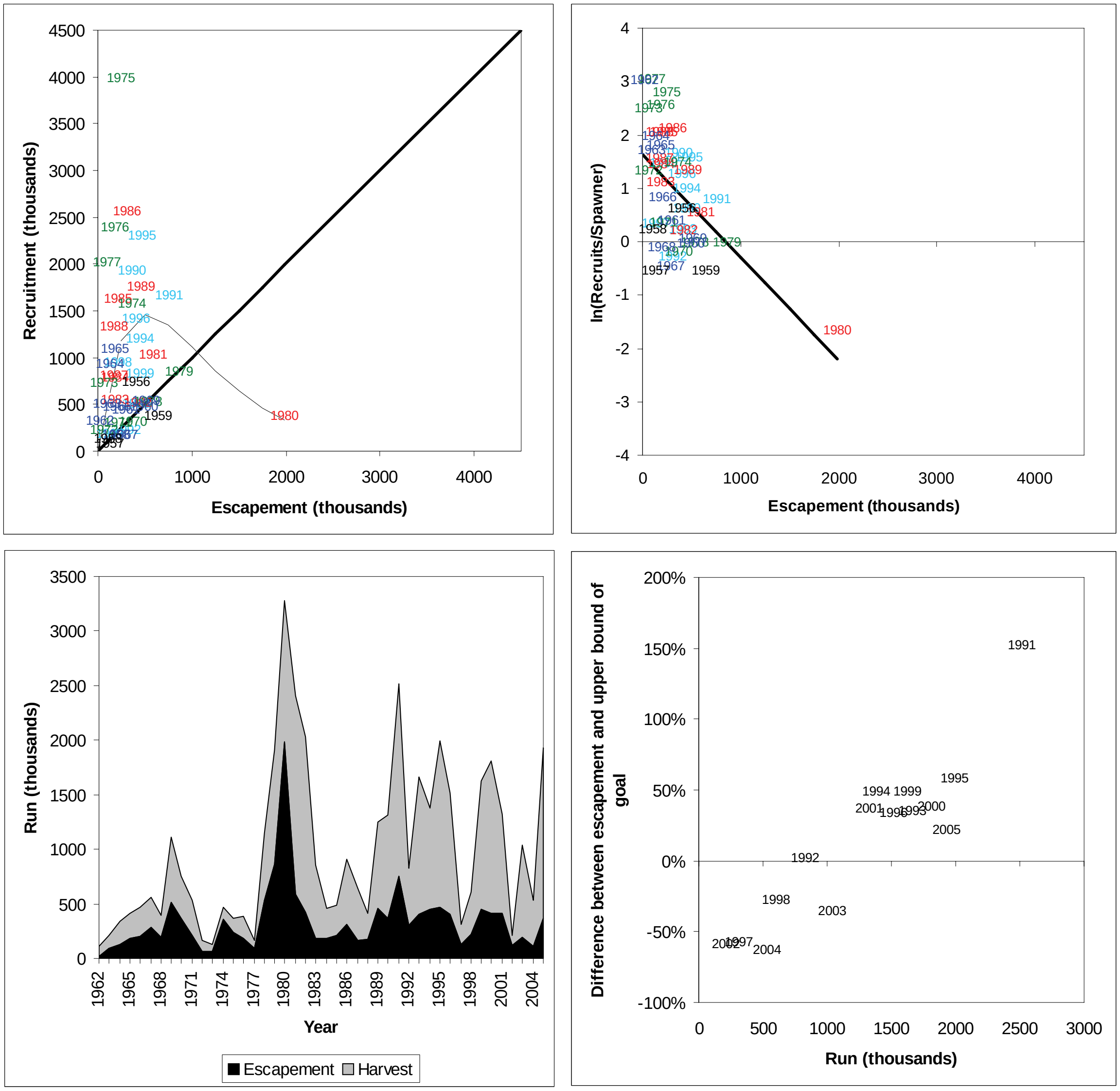
Appendix B36.–Ricker stock-recruitment relation (top panels) and fishery performance data (bottom panels) for the 1956-1997 brood years and 1962-2005 run years for the Egegik stock. Bottom right panel depicts run data from the most recent 15 years (1991-2005).



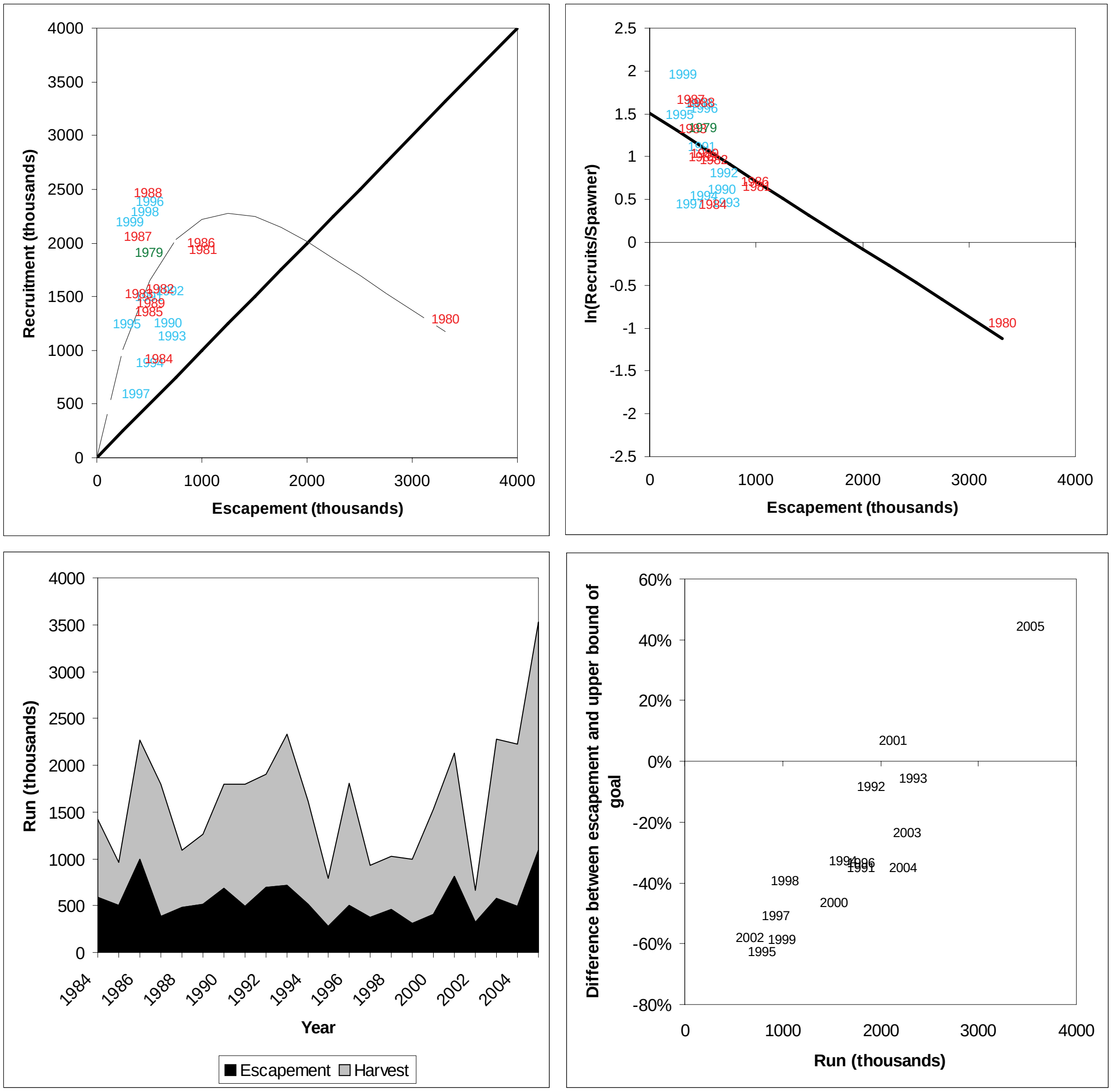
Appendix B37.–Ricker stock-recruitment relation (top panels) and fishery performance data (bottom panels) for the 1956-1997 brood years and 1962-2005 run years for the Ugashik stock. Bottom right panel depicts run data from the most recent 15 years (1991-2005).



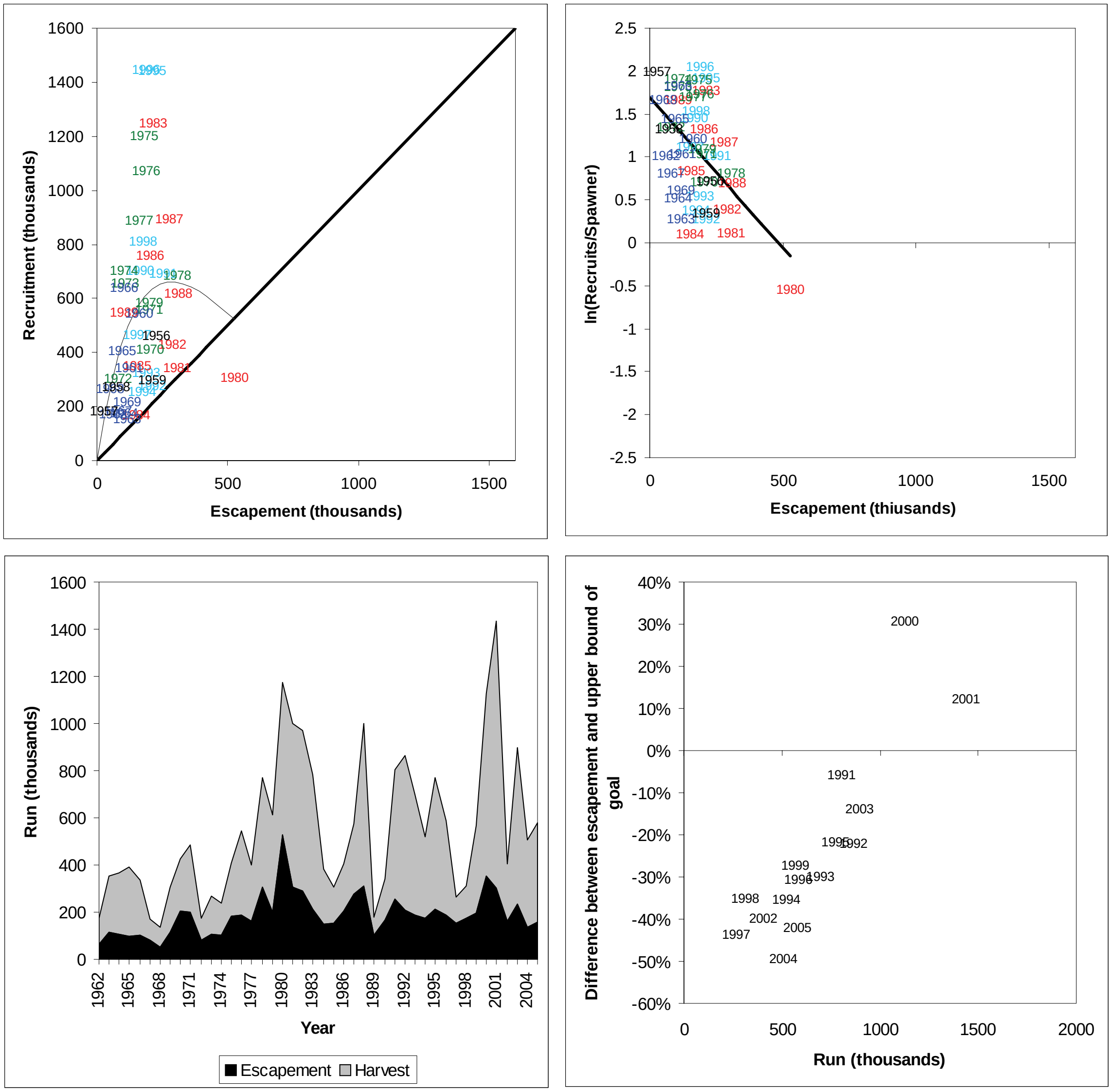
Appendix B38.–Ricker stock-recruitment relation (top panels) and fishery performance data (bottom panels) for the 1956-1999 brood years and 1962-2005 run years for the Wood stock. Bottom right panel depicts run data from the most recent 15 years (1991-2005).



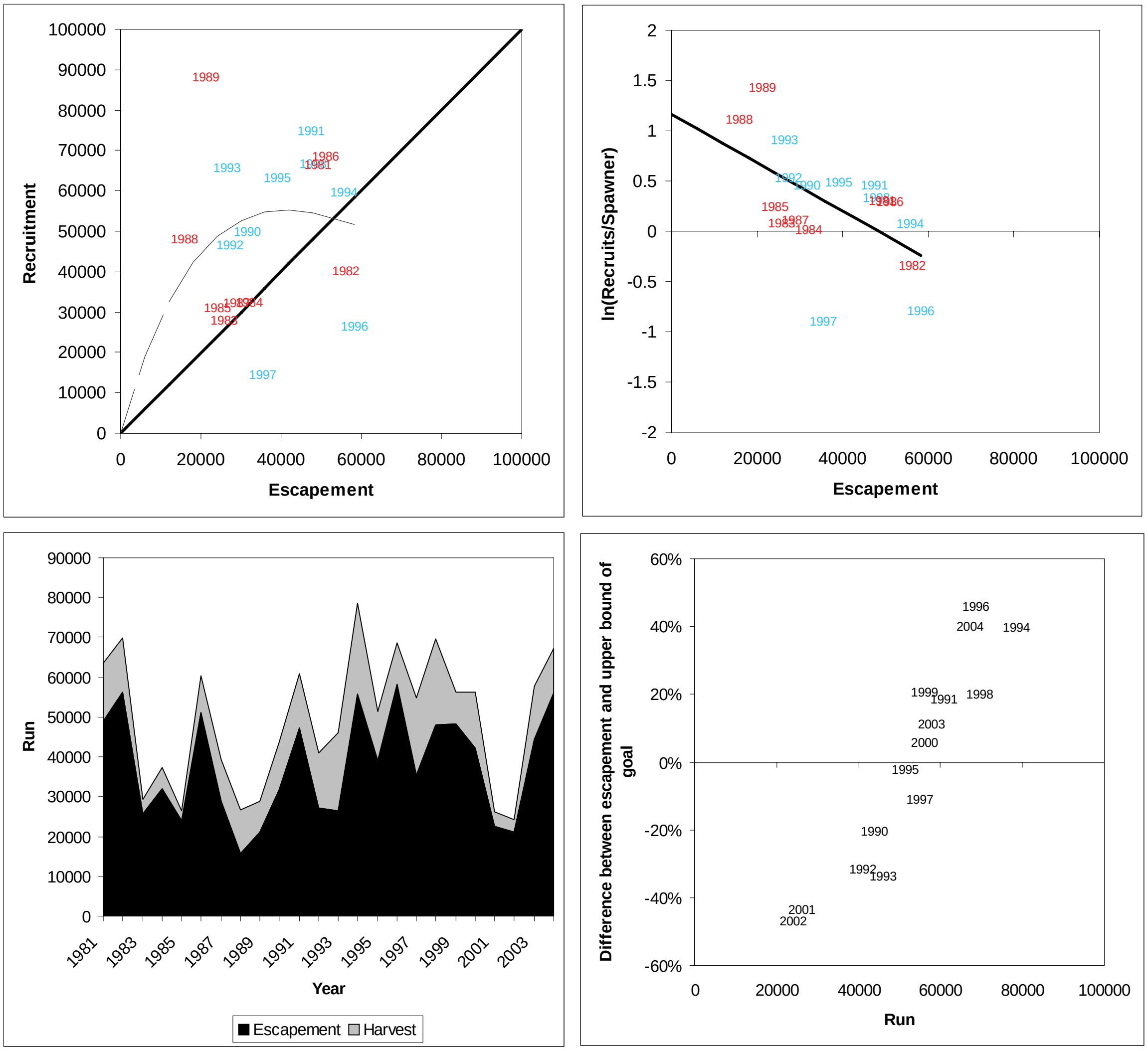
Appendix B39.–Ricker stock-recruitment relation (top panels) and fishery performance data (bottom panels) for the 1956-1999 brood years and 1962-2005 run years for the Igushik stock. Bottom right panel depicts run data from the most recent 15 years (1991-2005).



Appendix B40.–Ricker stock-recruitment relation (top panels) and fishery performance data (bottom panels) for the 1979-1999 brood years and 1984-2005 run years for the Nushagak stock. Bottom right panel depicts run data from the most recent 15 years (1991-2005).



Appendix B41.–Ricker stock-recruitment relation (top panels) and fishery performance data (bottom panels) for the 1956-1998 brood years and 1962-2005 run years for the Togiak stock. Bottom right panel depicts run data from the most recent 15 years (1991-2005).



Appendix B42.–Ricker stock-recruitment relation (top panels) and fishery performance data (bottom panels) for the 1981-1998 brood years and 1981-2004 run years for the Middle Fork Goodnews stock. Bottom right panel depicts run data from the most recent 15 years (1990-2004).

APPENDIX C
Stock-Recruitment Analyses

Appendix C1.–Parameter estimates (NPCV's in parentheses; NPCV's ≤ 0.250 in bold) for the Ricker SLR model of sockeye salmon stocks in the Southeast and Yakutat areas of Alaska.

Stock	Assessment[a]	Brood years	$\ln\alpha'$	β	σ_ε	S_{EQ}	S_{MSY}	μ_{MSY}
Chilkat	Weir/M-R	19	**1.878**	7.851E-6	**0.441**	**239,156**	**88,147**	**0.692**
			(0.110)	(0.274)	**(0.139)**	**(0.187)**	**(0.216)**	**(0.071)**
Chilkoot	Weir/M-R	19	NE[b]	NE	NE	NE	NE	NE
Italio	Peak aerial	26	0.865	4.717E-5	**0.914**	**18,329**	**8,055**	0.380
			(0.316)	(0.378)	**(0.106)**	**(0.232)**	**(0.240)**	(0.272)
Situk	Weir	22	**1.379**	**1.089E-5**	**0.356**	**128,231**	**51,578**	**0.562**
			(0.122)	**(0.175)**	**(0.122)**	**(0.080)**	**(0.098)**	**(0.092)**
Redoubt	Weir	15	**2.149**	4.302E-5	**1.137**	**49,969**	17,466	**0.751**
			(0.178)	(0.333)	**(0.191)**	**(0.213)**	(0.252)	**(0.105)**
East Alsek-Doame	Peak aerial	26	**1.457**	9.794E-6	**0.660**	148,811	59,223	**0.580**
			(0.228)	(0.569)	**(0.106)**	(0.390)	(0.444)	**(0.169)**
Klukshu	Weir	21	**1.391**	**6.192E-5**	**0.444**	**22,462**	**9,044**	**0.560**
			(0.183)	**(0.249)**	**(0.142)**	**(0.100)**	**(0.127)**	**(0.139)**
Lost	Peak foot	14	**1.847**	**2.790E-4**	**0.432**	**6,619**	**2,454**	**0.685**
			(0.132)	**(0.197)**	**(0.160)**	**(0.089)**	**(0.121)**	**(0.086)**
Akwe	Peak aerial	13	**1.460**	4.958E-5	**0.565**	**29,454**	**11,716**	**0.581**
			(0.189)	(0.292)	**(0.199)**	**(0.184)**	**(0.200)**	**(0.142)**
Speel	Weir	14	**2.845**	**1.110E-4**	**1.044**	**25,616**	**7,707**	**0.856**
			(0.180)	**(0.205)**	**(0.213)**	**(0.158)**	**(0.168)**	**(0.066)**
McDonald	Foot survey	17	**0.826**	7.499E-7	0.561	1,101,205	486,947	**0.365**
			(0.219)	(0.926)	(0.256)	(0.809)	(0.845)	**(0.183)**

[a] M-R = mark-recapture estimate.

[b] NE = no estimate was possible.

Appendix C2.–Parameter estimates (NPCV’s in parentheses; NPCV’s ≤ 0.250 in bold) for the Ricker SLR model of sockeye salmon stocks in the Prince William Sound area of Alaska.

Stock	Assessment	Brood years	$\ln\alpha'$	β	σ_{ε}	S_{EQ}	S_{MSY}	μ_{MSY}
Eshamy	Weir	27	**2.260**	**3.889E-5**	**0.727**	**58,111**	**19,863**	**0.772**
			(0.110)	**(0.226)**	**(0.140)**	**(0.165)**	**(0.191)**	**(0.060)**
Coghill	Weir	37	**2.297**	1.311E-5	**1.053**	**175,143**	**59,413**	**0.779**
			(0.125)	(0.261)	**(0.125)**	**(0.200)**	**(0.223)**	**(0.067)**
Copper	Sonar	39	**1.681**	1.036E-6	**0.415**	**1,622,767**	620,383	**0.643**
			(0.107)	(0.339)	**(0.127)**	**(0.241)**	(0.272)	**(0.074)**

Appendix C3.–Parameter estimates (NPCV's in parentheses; NPCV's ≤ 0.250 in bold) for the Ricker SLR model of sockeye salmon stocks in the Upper Cook Inlet area of Alaska.

Stock	Assessment	Brood years	$\ln\alpha'$	β	σ_ε	S_{EQ}	S_{MSY}	μ_{MSY}
Kenai	Sonar	32	**2.113**	5.834E-7	**0.520**	3,621,660	1,275,213	**0.744**
			(0.080)	(0.461)	**(0.118)**	(0.424)	(0.449)	**(0.046)**
Kasilof	Sonar	31	**2.131**	**3.157E-6**	**0.355**	**675,211**	**236,867**	**0.748**
			(0.062)	**(0.207)**	**(0.146)**	**(0.157)**	**(0.178)**	**(0.036)**
Crescent	Sonar	31	**1.585**	1.361E-5	**0.546**	**116,461**	**45,313**	**0.617**
			(0.159)	(0.269)	**(0.092)**	**(0.137)**	**(0.169)**	**(0.114)**
Russian ER	Weir	33	**1.176**	5.252E-6	**0.781**	223,844	93,502	**0.491**
			(0.164)	(0.807)	**(0.141)**	(0.764)	(0.799)	**(0.129)**

Appendix C4.–Parameter estimates (NPCV’s in parentheses; NPCV’s ≤ 0.250 in bold) for the Ricker SLR model of sockeye salmon stocks in the Kodiak, Chignik, and Alaska Peninsula areas of Alaska.

Stock	Assessment	Brood years	lnα’	β	σ_ε	S_{EQ}	S_{MSY}	μ_{MSY}
Nelson	Weir	23	**1.968**	**4.660E-6**	**0.405**	**422,374**	**152,992**	**0.713**
			(0.125)	**(0.227)**	**(0.160)**	**(0.112)**	**(0.153)**	**(0.077)**
Bear LR	Weir	16	**2.491**	6.068E-6	**0.509**	**410,506**	133,669	**0.811**
			(0.163)	(0.379)	**(0.138)**	**(0.242)**	(0.318)	**(0.076)**
Chignik ER	Weir	46	**1.265**	3.676E-7	**0.592**	3,441,344	1,415,908	**0.521**
			(0.127)	(0.773)	**(0.103)**	(0.742)	(0.769)	**(0.098)**
Chignik LR	Weir	46	**1.984**	2.502E-6	**0.463**	**792,767**	**286,305**	**0.716**
			(0.114)	(0.307)	**(0.103)**	**(0.207)**	**(0.246)**	**(0.070)**
Karluk ER	Weir	16	**1.870**	**4.655E-6**	**0.346**	**401,757**	**148,289**	**0.690**
			(0.162)	**(0.243)**	**(0.175)**	**(0.097)**	**(0.147)**	**(0.105)**
Karluk LR	Weir	16	**2.074**	**2.693E-6**	**0.507**	**770,164**	**273,255**	**0.736**
			(0.131)	**(0.198)**	**(0.165)**	**(0.107)**	**(0.139)**	**(0.078)**
Ayakulik	Weir	33	**1.063**	7.186E-7	**0.702**	1,478,967	629,452	**0.452**
			(0.179)	(0.700)	**(0.129)**	(0.622)	(0.646)	**(0.146)**
Upper Station ER	Weir	29	**1.113**	5.003E-6	**0.689**	222,410	93,880	**0.470**
			(0.188)	(0.629)	**(0.117)**	(0.522)	(0.545)	**(0.153)**
Upper Station LR	Weir	29	**1.611**	2.201E-6	**0.651**	732,141	283,490	**0.624**
			(0.146)	(0.529)	**(0.133)**	(0.435)	(0.468)	**(0.104)**
Frazer	Weir	30	**2.122**	**5.277E-6**	**0.916**	**402,117**	**141,325**	**0.746**
			(0.124)	**(0.229)**	**(0.149)**	**(0.166)**	**(0.185)**	**(0.072)**
Saltery	Weir	21	**1.654**	**2.749E-5**	**0.627**	**60,181**	**23,121**	**0.636**
			(0.160)	**(0.215)**	**(0.147)**	**(0.101)**	**(0.124)**	**(0.113)**
Buskin	Weir	8	1.979	1.086E-4	0.436	**18,219**	6,585	**0.715**
			(0.333)	(0.529)	(0.492)	**(0.209)**	(0.332)	**(0.207)**
Afognak	Weir	16	1.874	1.930E-5	**0.723**	**97,101**	**35,811**	**0.691**
			(0.266)	(0.305)	**(0.136)**	**(0.105)**	**(0.152)**	**(0.173)**

Appendix C5.–Parameter estimates (NPCV’s in parentheses; NPCV’s ≤ 0.250 in bold) for the Ricker SLR model of sockeye salmon stocks in the Bristol Bay area of Alaska.

Stock	Assessment	Brood years	$\ln\alpha'$	β	σ_ε	S_{EQ}	S_{MSY}	μ_{MSY}
Kvichak	Tower	44	**0.794**	NE[a]	**0.883**	NE	NE	**0.353**
			(0.175)		**(0.099)**			**(0.149)**
Naknek	Tower	44	**1.502**	2.903E-7	**0.527**	5,173,774	2,042,960	**0.593**
			(0.114)	(0.433)	**(0.108)**	(0.343)	(0.372)	**(0.084)**
Egegik	Tower	42	**1.670**	NE	**0.708**	NE	NE	**0.640**
			(0.083)		**(0.088)**			**(0.052)**
Ugashik	Tower	42	**1.670**	1.769E-7	**1.040**	9,437,393	3,615,720	**0.640**
			(0.129)	(0.767)	**(0.098)**	(0.753)	(0.780)	**(0.089)**
Wood	Tower	44	**1.410**	3.634E-7	**0.497**	3,880,891	1,557,326	**0.566**
			(0.121)	(0.377)	**(0.078)**	(0.286)	(0.311)	**(0.091)**
Igushik	Tower	44	**2.028**	**1.922E-6**	**0.897**	**1,055,001**	**377,765**	**0.726**
			(0.102)	**(0.230)**	**(0.088)**	**(0.171)**	**(0.189)**	**(0.062)**
Nushagak	Sonar	21	**1.590**	**7.916E-7**	**0.410**	**2,009,201**	**780,914**	**0.618**
			(0.080)	**(0.180)**	**(0.135)**	**(0.131)**	**(0.141)**	**(0.057)**
Togiak	Tower	43	**1.842**	3.506E-6	**0.546**	**525,452**	**194,973**	**0.683**
			(0.099)	(0.266)	**(0.086)**	**(0.186)**	**(0.212)**	**(0.065)**

[a] NE = no estimate possible.

Appendix C6.–Parameter estimates (NPCV's in parentheses; NPCV's ≤ 0.250 in bold) for the Ricker SLR model of sockeye salmon stocks in the Kuskokwim area of Alaska.

Stock	Assessment	Brood years	$\ln\alpha'$	β	σ_{ε}	S_{EQ}	S_{MSY}	μ_{MSY}
MF Goodnews	Weir	18	1.287 (0.256)	2.413E-5 (0.348)	**0.494** **(0.201)**	**53,358** **(0.132)**	**21,870** **(0.171)**	**0.528** **(0.200)**

Appendix C7.–Parameter estimates (NPCV's in parentheses; NPCV's ≤ 0.250 in bold) for the Ricker AR1 model of sockeye salmon stocks in the Southeast and Yakutat areas of Alaska.

Stock	Assessment[a]	Brood years	$\ln\alpha'$	β	ϕ_1	σ_ε	S_{EQ}	S_{MSY}	μ_{MSY}
Chilkat	Weir/M-R	19	**1.893**	7.959E-6	0.377	**0.420**	**237,794**	**87,395**	**0.696**
			(0.128)	(0.277)	(1.043)	**(0.126)**	**(0.197)**	**(0.223)**	**(0.082)**
Chilkoot	Weir/M-R	19	1.469	5.648E-6	0.712	**0.759**	260,105	103,303	0.583
			(0.347)	(0.728)	(0.349)	**(0.212)**	(0.620)	(0.671)	(0.254)
Italio	Peak aerial	26	1.323	**7.937E-5**	**0.831**	**0.535**	16,670	6,791	0.539
			(0.453)	**(0.193)**	**(0.233)**	**(0.128)**	(0.440)	(0.364)	(0.369)
Situk	Weir	22	**1.361**	**1.040E-5**	0.171	**0.360**	**130,884**	**52,970**	**0.551**
			(0.144)	**(0.205)**	(3.863)	**(0.139)**	**(0.099)**	**(0.117)**	**(0.111)**
Redoubt	Weir	15	**2.157**	4.125E-5	0.232	**1.160**	52,299	18,252	**0.753**
			(0.224)	(0.404)	(4.462)	**(0.190)**	(0.290)	(0.321)	**(0.135)**
East Alsek-Doame	Peak aerial	26	**1.535**	1.132E-5	0.591	**0.557**	135,586	53,228	**0.602**
			(0.249)	(0.465)	(0.367)	**(0.102)**	(0.340)	(0.365)	**(0.184)**
Klukshu	Weir	21	**1.364**	**6.005E-5**	0.393	**0.418**	**22,715**	**9,188**	**0.552**
			(0.188)	**(0.234)**	(0.738)	**(0.135)**	**(0.126)**	**(0.136)**	**(0.145)**
Lost	Peak foot	14	ND[b]	ND	ND	ND	ND	ND	ND
Akwe	Peak aerial	13	ND	ND	ND	ND	ND	ND	ND
Speel	Weir	14	**2.845**	**1.054E-4**	-0.262	**1.058**	**26,997**	**8,121**	**0.856**
			(0.202)	**(0.232)**	(0.937)	**(0.235)**	**(0.177)**	**(0.198)**	**(0.074)**
McDonald	Foot survey	17	ND	ND	ND	ND	ND	ND	ND

[a] M-R = mark-recapture estimate.

[b] ND = consecutive brood years missing. AR1 model not run.

Appendix C8.–Parameter estimates (NPCV's in parentheses; NPCV's ≤ 0.250 in bold) for the Ricker AR1 model of sockeye salmon stocks in the Prince William Sound area of Alaska.

Stock	Assessment	Brood years	$\ln\alpha'$	β	ϕ_1	σ_ε	S_{EQ}	S_{MSY}	μ_{MSY}
Eshamy	Weir	27	ND[a]	ND	ND	ND	ND	ND	ND
Coghill	Weir	37	**2.257**	1.235E-5	0.341	**1.002**	**182,829**	62,528	**0.772**
			(0.143)	(0.300)	(0.617)	**(0.110)**	**(0.243)**	(0.262)	**(0.079)**
Copper	Weir	39	**1.928**	1.511E-6	0.570	**0.350**	**1,275,428**	**465,612**	**0.704**
			(0.124)	(0.284)	(0.313)	**(0.133)**	**(0.182)**	**(0.217)**	**(0.079)**

[a] ND = consecutive brood years missing. AR1 model not run.

Appendix C9.–Parameter estimates (NPCV’s in parentheses; NPCV’s ≤ 0.250 in bold) for the Ricker AR1 model of sockeye salmon stocks in the Upper Cook Inlet area of Alaska.

Stock	Assessment	Brood years	$\ln\alpha'$	β	ϕ_1	σ_ε	S_{EQ}	S_{MSY}	μ_{MSY}
Kenai	Sonar	32	**1.991**	2.825E-7	0.331	**0.508**	7,048,290	2,541,779	**0.718**
			(0.092)	(0.743)	(0.731)	**(0.115)**	(0.767)	(0.795)	**(0.056)**
Kasilof	Sonar	31	**2.263**	**3.951E-6**	0.597	**0.313**	**572,807**	**195,667**	**0.773**
			(0.083)	**(0.205)**	(0.348)	**(0.165)**	**(0.152)**	**(0.176)**	**(0.044)**
Crescent	Sonar	31	**1.477**	1.206E-5	0.594	**0.449**	**122,480**	**48,580**	**0.586**
			(0.202)	(0.321)	(0.348)	**(0.150)**	**(0.198)**	**(0.223)**	**(0.149)**
Russian ER	Weir	33	**1.124**	3.284E-6	0.177	**0.784**	342,286	144,209	**0.474**
			(0.179)	(0.841)	(1.548)	**(0.147)**	(0.813)	(0.839)	**(0.141)**

Appendix C10.–Parameter estimates (NPCV's in parentheses; NPCV's ≤ 0.250 in bold) for the Ricker AR1 model of sockeye salmon stocks in the Alaska Peninsula, Chignik, and Kodiak areas of Alaska.

Stock	Assessment	Brood years	$\ln\alpha'$	β	ϕ_1	σ_ε	S_{EQ}	S_{MSY}	μ_{MSY}
Nelson	Weir	23	**1.945**	**4.523E-6**	0.129	**0.412**	**430,056**	**156,470**	**0.708**
			(0.135)	**(0.249)**	(6.294)	**(0.185)**	**(0.125)**	**(0.171)**	**(0.085)**
Bear LR	Weir	16	**2.209**	4.294E-6	0.545	**0.443**	514,464	177,685	**0.763**
			(0.175)	(0.458)	(0.700)	**(0.174)**	(0.335)	(0.391)	**(0.096)**
Chignik ER	Weir	46	**1.378**	6.420E-7	0.270	**0.578**	2,146,394	866,174	**0.556**
			(0.146)	(0.672)	(0.676)	**(0.110)**	(0.584)	(0.617)	**(0.110)**
Chignik LR	Weir	46	**2.062**	2.795E-6	0.427	**0.423**	**737,660**	**262,357**	**0.733**
			(0.111)	(0.260)	(0.362)	**(0.106)**	**(0.176)**	**(0.208)**	**(0.066)**
Karluk ER	Weir	16	**1.836**	4.476E-6	0.168	**0.354**	**410,132**	**152,366**	**0.682**
			(0.180)	(0.272)	(33.330)	**(0.199)**	**(0.117)**	**(0.168)**	**(0.118)**
Karluk LR	Weir	16	**1.975**	**2.448E-6**	0.229	**0.515**	**806,566**	**291,799**	**0.714**
			(0.157)	**(0.244)**	(3.490)	**(0.172)**	**(0.139)**	**(0.171)**	**(0.098)**
Ayakulik	Weir	33	**1.019**	6.482E-7	0.503	**0.621**	1,572,039	673,895	**0.437**
			(0.226)	(0.752)	(0.400)	**(0.147)**	(0.703)	(0.718)	**(0.188)**
Upper Station ER	Weir	29	**1.109**	5.239E-6	0.318	**0.669**	211,679	89,407	**0.468**
			(0.234)	(0.657)	(0.846)	**(0.142)**	(0.543)	(0.578)	**(0.190)**
Upper Station LR	Weir	29	**1.434**	1.397E-6	0.561	**0.562**	1,026,952	410,372	**0.573**
			(0.191)	(0.708)	(0.395)	**(0.138)**	(0.643)	(0.671)	**(0.142)**
Frazer	Weir	30	**2.148**	**5.350E-6**	0.083	**0.930**	**401,599**	**140,404**	**0.751**
			(0.132)	**(0.241)**	(9.124)	**(0.156)**	**(0.174)**	**(0.194)**	**(0.076)**
Saltery	Weir	21	**1.650**	**2.725E-5**	-0.251	**0.622**	**60,566**	**23,286**	**0.635**
			(0.155)	**(0.201)**	(0.717)	**(0.164)**	**(0.090)**	**(0.115)**	**(0.109)**
Buskin	Weir	8	1.893	9.926E-5	-0.083	0.476	19,067	7,007	**0.696**
			(0.339)	(0.574)	(0.926)	(0.536)	(0.251)	(0.371)	**(0.216)**
Afognak	Weir	16	1.249	1.219E-5	0.530	**0.695**	102,482	42,281	0.515
			(0.434)	(0.455)	(0.741)	**(0.188)**	(0.268)	(0.279)	(0.334)

Appendix C11.–Parameter estimates (NPCV's in parentheses; NPCV's ≤ 0.250 in bold) for the Ricker AR1 model of sockeye salmon stocks in the Bristol Bay area of Alaska.

Stock	Assessment	Brood years	$\ln\alpha'$	β	ϕ_1	σ_ε	S_{EQ}	S_{MSY}	μ_{MSY}
Kvichak	Tower	44	0.860	NE[a]	0.520	**0.762**	NE	NE	**0.378**
			(0.282)		(0.282)	**(0.108)**			**(0.241)**
Naknek	Tower	44	**1.539**	3.199E-7	0.221	**0.520**	4,810,500	1,887,096	**0.604**
			(0.115)	(0.394)	(0.874)	**(0.109)**	(0.319)	(0.343)	**(0.083)**
Egegik	Tower	42	**1.949**	1.244E-7	**0.650**	**0.545**	15,666,693	5,696,312	**0.709**
			(0.142)	(0.807)	**(0.231)**	**(0.091)**	(0.812)	(0.852)	**(0.086)**
Ugashik	Tower	42	**1.991**	4.315E-7	**0.710**	**0.750**	4,613,891	1,663,994	**0.718**
			(0.223)	(0.390)	**(0.190)**	**(0.098)**	(0.399)	(0.390)	**(0.144)**
Wood	Tower	44	**1.580**	5.074E-7	0.377	**0.471**	**3,113,860**	**1,212,565**	**0.615**
			(0.125)	(0.280)	(0.446)	**(0.099)**	**(0.190)**	**(0.213)**	**(0.089)**
Igushik	Tower	44	**1.948**	**1.701E-6**	0.504	**0.781**	**1,145,073**	**416,411**	**0.708**
			(0.145)	**(0.234)**	(0.312)	**(0.115)**	**(0.204)**	**(0.206)**	**(0.092)**
Nushagak	Sonar	21	1.601	7.950E-7	0.066	0.420	2,013,303	781,090	0.621
			(0.084)	(0.190)	(27.900)	(0.139)	(0.137)	(0.148)	(0.060)
Togiak	Tower	43	**1.894**	3.768E-6	0.286	**0.530**	**502,704**	**184,700**	**0.696**
			(0.111)	(0.266)	(0.666)	**(0.110)**	**(0.184)**	**(0.213)**	**(0.071)**

[a] NE = no estimate was possible.

Appendix C12.–Parameter estimates (NPCV's in parentheses; NPCV's ≤ 0.250 in bold) for the Ricker AR1 model of sockeye salmon stocks in the Kuskokwim area of Alaska.

Stock	Assessment	Brood years	$\ln\alpha'$	β	ϕ_1	σ_ε	S_{EQ}	S_{MSY}	μ_{MSY}
MF	Weir	18	1.149	1.997E-5	0.214	**0.501**	**57,554**	**24,147**	**0.482**
Goodnews			(0.298)	(0.433)	(2.300)	**(0.179)**	**(0.189)**	**(0.229)**	**(0.242)**