Exxon Valdez Oil Spill
State/Federal Natural Resource Damage Assessment Final Report

Run Reconstruction and Life-History Model

Fish/Shellfish Study Number 28
Final Report

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Geiger, H.J., B.G. Bue, S. Sharr, A.C. Wertheimer, and T. Mark Willette. *in press*. A life history approach to estimating the damage to Prince William Sound pink salmon from the *Exxon Valdez* oil spill. *In* S.D. Rice et al. [eds.]. *Exxon Valdez* Oil Spill Symposium Proceedings. American Fisheries Society Symposium 18:0000-0000.

Templin, W.D., J.S. Collie, and T.J. Quinn II. *in press*. Run reconstruction of the wild pink salmon fishery in Prince William Sound, 1990 - 1991. *In* S.D. Rice et al. [eds.]. *Exxon Valdez* Oil Spill Symposium Proceedings. American Fisheries Society Symposium 18:0000-0000.

Templin, W.D. 1995. Reconstruction of wild pink salmon (*Oncorhynchus gorbuscha*) runs in Prince William Sound, Alaska. M.S. Thesis. University of Alaska Fairbanks.

Templin, W.D., J.S. Collie, T.J. Quinn II., and H.J. Geiger. *in prep*. A run reconstruction model with stochastic movement for a series of mixed-stock salmon fisheries.

Abstract: The *Exxon Valdez* oil spill resulted in contamination of juvenile pink salmon (*Oncorhynchus gorbuscha*) habitat, including freshwater spawning areas in southwestern Prince William Sound (PWS). We estimated the loss of returning wild adult pink salmon in 1990-1992, and speculated about this loss in 1993-1994. From the 1988 brood year (1990 returns) approximately 2 million wild adult pink salmon (28% of potential 1990 production) failed to return due to oil mortality, primarily due to lack of growth during the critical nearshore life stage. From the 1989 and 1990 brood years (1991 and 1992 returns) 60 and 70 thousand adults failed to return, 7% of potential production. The primary cause of death was direct poisoning in the embryo stage of development. These studies have low statistical power to detect oil spill effects in the pre- and post- emergent fry and ocean life stages, therefore the true extent of the injury may be understated. The egg-mortality levels increased in the oiled areas in the 1991 and 1992 brood years. We also report on a run-reconstruction model, a deterministic model that assumed Markovian transition probabilities for the migration of each individual stock. Our most important finding is that of excessive harvest rates on pink salmon stocks in the northern and northwestern part of PWS.

Key Words: Compensentory mortality, harvest rates, life history, pink salmon, Prince William Sound, radio tagging, run reconstruction.

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EXECUTIVE SUMMARY

The 1989 *Exxon Valdez* oil spill resulted in contamination of juvenile pink salmon (*Oncorhynchus gorbuscha*) habitat, including much of the freshwater spawning area in the southwest portion of Prince William Sound. We examined the available evidence collected up to 1992 and estimated the loss of returning wild adult pink salmon to Prince William Sound in 1990, 1991 and 1992, and speculated about the loss in 1993 and 1994. From the 1988 brood year, that returned in 1990, we estimated somewhat less than 2 million wild adult pink salmon failed to return because of mortality attributable to the oil spill. This was approximately 28% of the potential production in the southwestern part of Prince William Sound in 1990. The mortality in the 1988 brood year was primarily due to lack of growth during the critical nearshore life stage. From the 1989 and 1990 brood years, that returned in 1991 and 1992, we estimated that 60 and 70 thousand adults failed to return due to oil mortality — less than 7% of the potential production in the southwestern part of the Sound. In these years, the most important detected cause of death was direct poisoning of salmon in the embryo stage of development. All of our estimates were based on only the statistically detectable mortality effects. These studies have low statistical power to detect oil spill effects in the preemergent fry, postemergent fry, and ocean life stages. Consequently, our estimate may have understated the true extent of the injury. Following the 1990 brood year, we expected egg-mortality levels in oiled areas to nearly equal control levels. The egg-mortality levels increased in the oiled areas in the 1991 and 1992 brood years. Other authors speculated that these increases were due to genetic damage resulting from parents incubating in the oiled substrate. Assuming the genetic damage hypothesis is correct, at the time of our original analysis in July of 1993, we expected 240 and 80 thousand wild adult pink salmon would fail to return in 1993 and 1994 due to oil spill effects.

We also report on a run-reconstruction model and run-reconstruction results. The final model was a deterministic model that differs from previous run-reconstruction models in that it assumed Markovian transition probabilities for the migration of each individual stock. Our most important finding is that of excessive harvest rates on pink salmon stocks in the northern and northwestern part of Prince William Sound. These stocks were largely unaffected by the oil spill, but they have recently been suffering escapement shortfalls. These observations have important management implications, but are unrelated to the oil spill.

INTRODUCTION

In the weeks following the oil spill, the Alaska Department of Fish and Game and the National Marine Fisheries Service initiated several studies to (1) develop improved estimates of pink salmon (*Oncorhynchus gorbuscha*) escapement for pre- and post-spill years, (2) measure egg (embryo) survival, (3) measure fry survival, (4) observe the nearshore condition and distribution of fry in Prince William Sound, (5) measure hatchery and wild salmon survival in the saltwater environment, and (6) survey the pink salmon habitat affected by the oil spill. Prince William Sound is divided into nine fishing districts, which serve to define stocks for the purposes of fisheries management (Figure 1). Because of the path of the oil, fish spawning or rearing in the Southwest Fishing District (District 226), were of particular concern. Below, we will bring the results of these studies together, and look at the information available up to 1992; our goal is to answer the question, "just what was the effect of the *Exxon Valdez* oil spill on the important wild pink salmon resource in Prince William Sound?"

On the advice of outside reviewers, we initiated a project to estimate the productivities and harvest rates of pink salmon stocks for as many years as possible. This latter effort came to be known as the run-reconstruction project, after the description found in Starr and Hilborn (1988). At the time the project was initiated, reconstructing the runs was thought be important not only for estimating injury, but particularly as a management tool to help managers see how to lower harvest rates on damaged stocks to prevent further declines. This project turned out to be more difficult than we first imagined. We lacked specific knowledge of pink salmon migration through Prince William Sound to final spawning locations. We examined historical tagging data and conducted a limited radiotagging study in 1992 to gain insight into migration movement, but we still had only a superficial understanding of the migration dynamics. We now know that the reduction in pink salmon productivities caused by the oil spill is probably far below the level we can resolve with the run-reconstruction methods. Even so, this project has produced valuable information on harvest rates and demonstrated that harvest rates have been too high on stocks that have declined in recent years.

Pink salmon populations in Prince William Sound are not static. Powerful forces that may have affected them in recent years include the 1964 Alaskan earthquake, an increasingly intense commercial fishery, tremendous increases in hatchery production, and the *Exxon Valdez* oil spill. The 1964 earthquake severely damaged some stocks and eliminated many runs entirely (Roys 1971). In the mid 1980s, large runs of hatchery-produced pink salmon began to equal and then far outnumber the wild salmon (Eggers et al. *in press*). Hatchery stocks are an important input to the commercial fishing industry, but from an ecological perspective, they are entirely different from the wild salmon. In this report we focus on the wild salmon that play an important part in the Prince William Sound ecosystem and an important economic role in the Prince William Sound fishing industry.

The size of pink salmon runs to Prince William Sound has fluctuated wildly (Figure 2) in response to unobserved phenomena in the freshwater and marine environments. With this much background variability, even extremely large damage would be entirely undetectable using before-and-after comparisons of any function of population size. To gain statistical power we focused on the affected life-history stages, looking for differences in life-history statistics between groups of fish classified as oiled and unoiled in the same year. We refer to this summary of life-stage comparisons as the life-history model. Note that we will be using *revised* escapement estimates (available from Dan Sharp, Alaska Department of Fish and Game, Cordova, Alaska) that differ considerably from previous estimates. The revised estimates are larger and are based on improved measurements of observer bias, and stream life.

We followed the 1988 brood year by estimating parental escapement, survival to emergence, and survival to emigration in 1989. We measured growth and survival of coded wire tag groups as they migrated through the oil in the nearshore environment in the spring of 1989, and measured their final return numbers in 1990. We then continued with the odd-year line: following the 1989 brood year as they incubated in the oiled and unoiled streams of Prince William Sound, migrated in the relatively unoiled nearshore areas in 1990, and returned in 1991. The 1990 through 1992 brood years were followed in a similar manner up to the summer of 1992. At each life stage for the 1988 through 1992 brood years we summarized evidence that the presence of oil reduced survival, and evidence that a survival reduction was translated to reduced survival at the adult life stage. Figure 3 illustrates the life-history pattern for pink salmon, showing the life stages, and points where oil detectably reduced survival in wild pink salmon.

The oil spill could have reduced survival at an early juvenile life stage, yet the final return of adult salmon could have remained unaffected because of *compensatory mortality*: mortality that increases when density is high and decreases when density is low. In her review of the pink salmon literature, Alexandersdottir (1987) cited Heard's (1978) work in Sashin Creek in Southeast Alaska in 1967 and Donnelly's (1983) work in Kodiak and concluded that compensatory mortality was linked to an overabundance of spawners and that density-dependent survival could be a factor from spawning to outmigration.

If compensatory mortality effects are negligible at a particular life stage and at all subsequent life stages, then estimating the effects of the oil spill could be straightforward: the estimated proportional loss of production could simply be the measured decrease in estimated survival at that life stage. Alternatively, if compensatory mechanisms exist, the loss of production from the oil spill would be overestimated by assuming oil-induced mortality translates directly into reduced adult production. We examined the available evidence that compensatory mortality could be caused by oil-induced loss of production.

The effect of the *Exxon Valdez* oil spill on any important part of the biota will never be exactly known. Unfortunately, the failure to precisely measure injury from the oil spill is sometimes confused with justification for concluding the injury is nonexistent. Similarly, the ability to statistically detect some aspect of injury is sometimes confused with significance in a larger biological sense. Rather than perform a statistical test of the hypothesis that pink salmon populations were completely unchanged by the oil spill, we viewed our responsibility as identifying the *biologically* — not *statistically* — important sources of mortality, and providing the most reasonable estimates of the magnitude of loss, in units of adult salmon, consistent with the information available to us.

OBJECTIVES

1. Develop a conceptual framework for estimating population level injury of wild pink salmon populations in Prince William Sound caused by the *Exxon Valdez* oil spill.

2. Develop a conceptual framework for estimating salmon production and harvest rates in 1990 and 1991 in the commercial fishing districts of Prince William Sound.

PART I — LIFE-HISTORY MODEL OF LOSS OF ADULT ANIMALS

METHODS

Life History and Population Dynamics

Let y_{t+2} represent the subsequent Prince William Sound wild pink salmon production in year $t+2$ from an escapement of x_t spawners in brood year t. Let s_t represent the random variable that summarizes survival and fecundity. This is commonly called return-per-spawner, and is usually expressed as some function of previous escapement (e.g., Ricker 1975). We are interested in the life-history steps underlying the return-per-spawner when escapement has been restricted to approximately what managers consider optimal. Formally, the process is described by

$$y_{t+2} = s_t x_t \ . \tag{1.1}$$

In year $t+2$, Prince William Sound salmon management attempts to harvest all of the return except a fixed escapement goal, x_{goal}. Due to management error, the actual escapement is x_{t+2}, and the process repeats itself.

In years when the oil spill reduced survival, let p_t be the fraction of the total number of eggs from brood year t that were potentially affected by oil sometime in their life. Let s'_t be the return-per-spawner that reflects a reduction due to the oil spill, including the effects of compensatory mortality.

In years when a fraction of the potential production is reduced by an oil-spill effect, we assume production is given by

$$y_{t+2} = [(1-p_t)s_t + p_t s'_t\ ]x_t \ . \tag{1.2}$$

Note the quantity $(1-p_t)$ is the fraction of eggs unaffected by oil, and s_t is the return-per-spawner, so that $(1-p_t)s_t x_t$ denotes the production from unoiled streams; similarly, $p_t s'_t x_t$ denotes the production from oiled streams, and production from both sources equals the total production.

In actual practice, managers observe $\hat{x}_t$, a function of x_t, where the function describes observational error. Similarly, $\hat{y}_{t+2}$ denotes the estimated total run that consists of the catch, which is approximately known, and the estimated escapement.

To estimate parameters, we first assume no strong compensatory mortality mechanisms, or at least no compensatory mortality after the affected life stage. Without reference to stochastic models, we estimate parameters in equations (1.1) and (1.2) algebraically, assuming that s'_t is approximately equal to s_t multiplied by the estimated reduction in survival.

Letting r_t denote the product of reduction in survival at each affected life stage, estimates of s'_t and s_t are found as follows by replacing elements in equation (1.2) with their estimates and solving,

$$\hat{s}_t' = \hat{s}_t \hat{r}_t \,, \tag{1.3}$$

and then from (1.2),

$$\hat{s}_t = \frac{\hat{y}_{t+2}}{\hat{x}_t}\left((1-\hat{p}_t)+\hat{p}_t\hat{r}_t\right)^{-1} .$$

Production, expressed in units of adult salmon that would have returned had there been no oil spill, is then estimated by

$$\hat{y}_{no\,oil,t+2} = \hat{s}_t\hat{x}_t \,,$$

and the estimated loss in brood year *t*, at the adult population level, is given by

$$\hat{L}_t = \hat{y}_{no\,oil,t+2} - \hat{y}_{t+2} \,.$$

To estimate typical values of s_t, for the purpose of projecting future production from the 1991 and 1992 escapements, we considered the median recruits-per-spawner from 1963 to 1987. Information on the steps that lead to s_t from the pink salmon literature was used to provide additional justification for this estimate. Five stochastic steps lead to the return-per-spawner value, s_t: (1) the fraction of the run consisting of females, denoted Fem_t ; (2) the average fecundity per female, denoted, Fec_t ; (3) the fraction of the potential egg deposition that is actually deposited, denoted Dep_t ; (4) the survival from eggs deposited to emergence, denoted Seg_t ; and (5) the marine survival, denoted Smr_t. The overall return-per-spawner, s_t, is simply the product of each of these stochastic outcomes:

$$s_t = Fem_t \bullet Fec_t \bullet Dep_t \bullet Seg_t \bullet Smr_t \,.$$

The Fraction of Potential Egg Deposition in Oiled Streams

Estimates of the fraction of eggs in oiled streams were obtained by estimating the fraction of streams affected by oil and adjusting for the relative egg density in oiled streams. We assumed that only streams in the Southwest Fishing District were affected, ignoring some oiling on Montague Island and elsewhere.

To estimate the fraction of pink salmon spawning streams affected by oil, we needed a sample of streams with information on oiling level and egg density. In 1991 the aerial survey of spawning escapement was expanded to include a representative sample of oiled and control streams. To determine which streams in the 1991 aerial survey were affected by oil, we referred to Middleton et al. (1992), personal field observations, and conversations with other observers. In general, if a stream was classified as "*Heavy*" through "*Very Light*" in Middleton et al., we considered it an oiled stream. In cases where Middleton et al. disagreed with our own field observation, we relied on our observations. The peak spawner density from this survey was used as a proxy for the egg density in each stream in the survey. To estimate the fraction of the potential egg deposition in the Southwest Fishing District that incubated in oiled streams, we calculated the weighted average of the proportion of streams classified as oiled in the 1991 survey, using the peak aerial escapement count in the 1991 aerial survey as a weight. Then, to estimate the fraction of the entire potential egg deposition in the whole Sound that was affected by oil, we multiplied this weighted average by the fraction of the entire escapement in the Southwest Fishing District.

Oil-Induced Mortality in the Freshwater Stage

Let m_k be the underlying mortality rate of juveniles, at some life stage, with oiling level k. If this is the only affected life stage, then the proportional reduction in survival at this life stage, defined as r above, is found by

$$r = \frac{(1-m_{oil})}{(1-m_{unoil})} .$$

To estimate r, we substituted the unweighted estimated average mortality in the embryos using data described in Sharr et al. (1994a, 1994d). Average mortality was not weighted by total eggs deposited at each tidal stage because estimates of total eggs deposited by tidal stage were unavailable to us.

The Fraction Exposed in the Early Marine Stage

The fraction of eggs that could eventually be affected by exposure to oil in any life stage through the early marine life stage was the most difficult parameter to estimate. In the end, we simply used the estimated fraction of the 1988 escapement in the Southwest Fishing District, knowing that fry that emerged anywhere in the Southwest Fishing District in 1989 were a short distance from exposure once they emigrated into the marine environment. We know from Willette et al. (1995) that some fish from unoiled areas emigrated to oiled marine areas and vice versa.

RESULTS

Willette et al. (1995) estimated that fry from unoiled areas that reared in oiled nearshore environments in 1989 experienced a marine survival of 72% of their unoiled potential based on coded wire tagging studies at the Wallace H. Noerenberg Hatchery.

Our estimates of the proportional reduction in survival of oiled eggs relative to control eggs, together with estimates of overall embryo-stage mortality for oiled and unoiled streams, are provided in Table 1. We estimated that survival from egg deposition to the fry stage was 92% of its potential in oiled areas for the 1989 brood year and 88% of its potential for the 1990 brood year. Sharr et al. (1994a) found statistically detectable excess mortalities in the eyed-embryo stage, which they attributed to oil-spill effects, but failed to find statistically detectable effects in the preemergent fry stage of development. Statistically detectable elevated mortalities were also noted by Sharr et al. (1994a, 1994d) between oiled and unoiled sites for the 1991 and 1992 brood years.

We estimated the fraction of pink salmon spawning streams contaminated with oil to be 31% of all spawning streams in the Southwest Fishing District. Unoiled streams had larger average peak escapement counts than oiled streams, meaning that 31% is expected to overstate the proportion of eggs affected in the Southwest Fishing District. When we used peak spawner density from the 1991 aerial escapement survey as a proxy for egg density, as described above, an estimated 20% of the potential egg deposition in the Southwest Fishing District was associated with streams classified as oiled. But when we used escapement information to estimate the fraction of potential egg deposition in the entire Sound potentially affected by oil during the freshwater stage, the estimate never exceeded 6% of the eggs (Table 2).

Estimated Adult Salmon that Failed to Return

In 1990 total production of wild pink salmon was estimated to be 18.40 million from an escapement of 4.99 million in the 1988 brood year. We assumed that 32% of the potential 1988 brood year were exposed to oil effects by using the proportional escapement in the Southwest Fishing District, as described above. Based on the observed reduction of marine survival of coded-wire-tagged fish from Willette et al. (1995), we estimated the proportional reduction in survival to be 72%, as described above. Substituting these estimates for the appropriate quantities in equation (1.2) yields

$$18.40 = ((1 - 0.32)s_{1988} + 0.32\,(s_{1988}\;0.72))\;4.99\,.$$

Solving for s_{1988} produced an estimated return-per-spawner in the absence of oil of 4.06. Applying this return-per-spawner to the 1988 escapement produced an estimate of 20.26 million adults that would have returned in the absence of oil. By subtraction, the estimated loss of adult pink salmon in 1990 was approximately 1.86 million. Key statistics and results for the 1988 through 1991 brood years are provided in Table 2. Using the same reasoning, we estimated the loss of adult pink salmon to be approximately 60 thousand for the 1989 brood year and 70 thousand for the 1990 brood year.

Compensatory Mortality

We found no evidence that compensatory-mortality mechanisms operate on the scale of variation induced by oil spill effects. Figure 4 shows the new stock-recruitment history using the revised estimates of escapement (available from Dan Sharp, Alaska Department of Fish and Game, Cordova, Alaska). Although compensatory-mortality mechanisms may control production in Prince William Sound at escapement extremes — such as when escapement reaches 20 million — for the important brood years of 1988, 1989, and 1990, the escapement remained very near what managers have traditionally considered optimum (the escapement goal in the old *index units* can be found in Geiger and Savikko [1991]; an escapement goal has not been formulated in units of the *revised* escapement estimates).

To see if compensatory mortality was operating in the embryo stage of development we examined estimated egg survival, up to the time the survey was conducted, as a function of observed egg density for 1989, 1990, and 1991. Although some slight compensatory mortality might have occurred as densities exceed 2,500 eggs per unit of surface area (0.186 m^2) in the lower tidal stages in 1989, no strong compensation was observed. We were unable to detect a relationship between egg density and the empirical logit (Agresti 1990) of egg survival (analysis of covariance, *P-val* = 0.31) after adjusting for year, tidal stage, and oiling level.

If oil-induced mortality is strongly compensated for in the preemergent fry stage, then the proportion of live fry would be strongly related, with negative slope, to the proportion of live eggs. Figures 5a-c show this relationship for the 1989 through 1991 fry-dig studies. These graphs show considerable mortality and variation in mortality from site to site, yet the measured mortality is low in the fry stage, irrespective of the mortality between egg deposition and fry stage. Thus, no compensatory mortality was seen in this life stage.

To look for compensatory mortality in the marine life stages, we examined Prince William Sound pink salmon hatchery production as a function of fry released (from Eggers et al. [*in press*], and recent estimates from Prince William Sound hatchery operators). This relationship is shown in Figure 6. The number of fry emigrating from freshwater systems shows a strong, linear relationship to the number of returning adults, within the range of 0 to approximately 600 million hatchery fry. The slope of a smooth line through these data is approximately 5% — a reasonable average survival for pink salmon (Heard 1991). These data indicate no compensatory-survival mechanisms in the marine life stages.

In summary, we found no evidence that oil-induced mortality in either the freshwater or the marine environment would be compensated for by density-dependent mechanisms in Prince William Sound pink salmon populations.

Typical Life-History Values and the 1991 and 1992 Brood Years

The annual return-per-spawner is a random variable in equation (1.1). This random variable results from the realization of five previous stochastic steps, as described above. Table 3 shows our best estimate of typical values for life-history parameters at each of the steps from various sources in the pink salmon literature, and from post-spill unpublished coded-wire tagging studies of wild pink salmon (data available from the Alaska Department of Fish and Game, Cordova, Alaska). These estimates led us to the conclusion that typically about 1.65 recruits-per-spawner are generated from an escapement near the optimum level.

Using the revised estimates of escapement, the median return-per-spawner from the 1963 to 1987 brood years was 1.79. To ensure this statistic represents years with moderate to low escapement, brood years with an escapement in excess of 10 million spawners were excluded, yet the median return-per-spawner remained unchanged.

The life-history parameters from Table 3 led to a similar picture of the typical return-per-spawner values that recently have been observed in Prince William Sound. However, this image is quite different from the one based on previous escapement estimates (Heard 1991; Eggers et al. *in press*), where the typical return-per-spawner is thought to be closer to 4.0. In the absence of oil spill effects, we assumed 1.79 returns-per-spawner is a typical value for projecting future production, at the time this report was originally prepared in June 1993. The projected returns for the 1991 and 1992 brood years were 17.3 million and 4.9 million, in the absence of oil-spill effects. If the estimated egg-stage-survival ratio between oiled and control areas represents persistent oil spill effects, the projected return is reduced by approximately 240 thousand for the 1991 brood year and 80 thousand for the 1992 brood year.

DISCUSSION

Our studies indicated that a detectable number of wild adult pink salmon failed to return in 1990 because of oil-induced mortality caused by the *Exxon Valdez* oil spill. We estimated this loss at more that a million adult pink salmon. This loss may represent over a quarter of the potential production in the Southwest Fishing District. Unless we considerably underestimated the injuries in the 1989 and 1990 brood years, the loss of adult salmon was measurable, but small relative to other human-induced mortality, such as that caused by the commercial fishery. We concluded that missing adult pink salmon from these brood years was less than 10% of the potential wild production in the Southwest Fishing District and less than 2% of the potential wild production in the entire Sound.

The commercial harvest in 1990 was a poor indicator of the effects the oil spill had on the wild pink salmon resource in the affected areas of Prince William Sound. Survival of the 1988 brood year was strengthened by favorable environmental conditions throughout the Sound. More importantly, the size of the harvest of wild salmon was eclipsed by the harvest of hatchery-produced salmon, which provide a wholly different ecological role in Prince William Sound. The total catch of salmon in Prince William Sound increased throughout the 1980s because of increasing hatchery production. In 1989 fry from the 1988 brood year of wild salmon were joined by 507 million hatchery fry (Sharr et al. 1994b), the second largest release of pink salmon fry in Prince William Sound at the time.

Even though the salmon hatcheries largely masked the effect of oil on the wild salmon resource that returned in 1990, the oil had a detectable effect on the hatchery resource as well (Willette et al. 1995). Of the total 507 million hatchery-produced pink salmon fry released in 1989, 160 million fry were from the Armin F. Koernig Hatchery (Sharr et al. 1994b), which sits just off the path of the oil in the southwestern portion of the Sound. Using the same reasoning we used for the wild stocks, the potential loss of the hatchery resource in 1990 is in units of millions of adults salmon. The overall estimated survival for the 1988 brood year, which returned in 1990, was 4.24% for the Armin F. Koernig Hatchery. The survival at the Wallace H. Noerenberg Hatchery, a similar hatchery, but further from the path of the oil, had an estimated survival of 8.49% (Sharr et al. 1994b) — approximately twice as large. The estimated survivals in years without an oil influence for the Armin F. Koernig and Wallace H. Noerenberg Hatcheries were 6.8% and 8.8%, respectively, in 1987 (Peltz and Geiger 1990); 4.52% and 4.99%, respectively, in 1991 (Sharr et al. 1994b); and 2.08% and 0.94%, respectively, in 1992 (Sharr et al. 1995). Although not compelling in themselves, these data do not conflict with presumed large numbers of missing adult salmon that would have returned to the Armin F. Koernig Hatchery in 1990.

We concluded there were detectable numbers of missing wild adult salmon that would have returned in 1991 and 1992 from the 1989 and 1990 brood years. The primary reason for the loss was decreased embryo-stage survival. The presence of oil is known to elevate egg-stage mortality (Moles et al. 1987). This appears to have happened in the contaminated streams in Prince William Sound, yet relatively few streams were oiled — approximately 31% of the streams, by our criteria, in that part of Prince William Sound most affected by oil. The oiled streams tended to be north-facing, in the southwestern area of the Sound, and had a lower density of spawners when the stream densities were observed in 1991.

Moderate errors in the spawner density in these streams, moderate errors in the number of streams oiled, or even moderate errors in the ratio of survival in oiled and unoiled streams would not have affected our larger conclusions about the result of egg-stage damage in the 1989 through 1992 brood years: the number of lost adult salmon probably was far fewer than 10% of the potential adult production in the Southwest Fishing District, and less than a few percent of the potential production in the entire Sound.

The most serious criticism of these estimates is that our assumed fraction of fish exposed in the nearshore environment was little more than a guess. From Willette et al. (1995) we got a glimpse of how dramatic a change in overall survival the oil could have caused in this life stage. Most authors believe the most critical period for pink salmon survival is when the fish first enter the marine environment (e.g. Alexandersdottir 1987, Heard 1991), and that growth is essential for survival in the near shore areas (Parker 1962a, 1962b, 1964, 1965, 1968, 1971). Moles and Rice (1983) showed petroleum can affect growth at this life stage, and similar effects have been seen in other salmonids (Vignier et al. 1992; Woodward et al. 1981). Because of the extent the marine environment was oiled, a great number of fish were potentially affected. Even without an exact count of the number of fish exposed, we can conclude the greatest potential for damage to wild pink salmon, resulting from the *Exxon Valdez* oil spill came from their exposure to oil in the critical nearshore environment.

The second most serious criticism of this study is that we may have missed large, delayed mortality in the marine life stage in brood years after 1988, and may have missed mortality in the fry stages in all brood years. Direct examination of preemergent fry in oiled streams by Wiedmer et al. (*in press*) showed damage in individual animals. Unfortunately, Wiedmer et al. provided no quantitative assessment.

The most important, unanswered question about pink salmon in relation to this study is why did the estimated egg-stage mortality not converge to control levels — but instead, become more dissimilar in 1991 and 1992? The egg-stage effects we have been attributing to the oil spill could simply have reflected natural differences in sites. Sharr et al. (1994a) explain why we feel this is unlikely; they speculated that the difference may be due to genetic damage. This hypothesis seems reasonable, but untested.

PART II — THE RUN-RECONSTRUCTION MODEL

METHODS

Overview of Methods

To reconstruct the return migration of wild pink salmon through the fishery in Prince William Sound, we make the following assumptions: (1) each salmon belongs to a stock, (2) fish of each stock migrate purposefully to their stream of origin to spawn, and (3) once in the Sound, salmon movement is described by a Markov process (Taylor and Karlin, 1984); that is, the movement of a fish in a given stock is solely determined by its location on a given day. The reconstruction begins on the last day a pink salmon remains alive in a stream in the Sound and moves by daily steps backward in time to the day the first pink salmon enters the Sound from the Gulf of Alaska.

The stocks are defined by escapement within management district boundaries that were set in the 1960s based on similarities between the spawning populations (Figures 1 and 7). The Unakwik (229) and Eshamy (225) districts contain small pink salmon spawning populations and are pooled with their respective geographically adjacent districts: Northern (222) and Southwest (226). This consolidation leads to a model that considers seven stocks as they traverse seven fishery districts.

The model reconstructs the history of each stock as it traverses the salmon fishery by accumulating fish in a series of pools as they pass through the Sound: one pool for the Gulf of Alaska and seven pools of migrating fish, one in each district. Catch and escapement are removed from these pools and migration is modeled by moving salmon between pools. By keeping track of the fish as they pass through these pools, the model develops stock-specific information on the harvest rates, run sizes and distributions in space and time.

The model is deterministic and assumes there is no observation error in the data, which is similar to models presented by Starr and Hilborn (1988) and Mundy et al. (1993). We model migration between fishing districts as a Markov process for the following reasons: (1) computer programming is simpler, (2) fish are allowed to move at varying rates, (3) sensitivity analysis of the migration assumptions is simpler, and (4) using transition probabilities backward in time functionally creates an increase in the speed of migration as the season progresses, as shown below.

Capital letters indicate values accumulated (pooled) across strata: time, stock, district. Underlined variables are vectors over the missing subscript. Bold letters indicate matrices and

Greek letters indicate rates, proportions, or estimated parameters. Each variable may be accompanied by the following subscripts:

t = day of the year $\qquad t = 1,2,3,\ldots,365$
n = stock $\qquad n = 1,2,3,\ldots,7$
d = district $\qquad d = 1,2,3,\ldots,7$

The variables used in the model have the following definitions:

y = number of fish escaping the fishery
s = number of fish entering the stream pool
τ = number of days a fish spends in the mouth pool
c = stock-specific catch
C = observed catch
ρ = harvest rate
P = number of fish in harvestable pool before catch
P^* = number of fish in harvestable pool after catch
Θ = matrix of migration probabilities
$\mathbf{I}$ = identity matrix
$\mathbf{U}$ = diagonal matrix with elements ρ

The escapement data consisted of aerial counts of the number of fish alive in the streams observed, but the reconstruction required information on the daily arrival of fish to the streams. Assuming that all fish survive for a set number of days in freshwater (the stream life), and using the historical distributions of fish in the stream for odd and even years, we distributed the total escapement of each stock according to a discrete, normal timing curve.

Run-Reconstruction Model

Salmon hold at the mouth of the stream for a number of days before ascending to the spawning gravel (Heard 1991). Because fishing is not allowed within 1,000 yards of stream mouths, these fish are no longer part of the harvestable pool and are considered a part of the escapement pool. Assuming that all salmon hold for τ days before entering the stream, the number of stock n salmon escaping the fishery, y_{tnd} , is

$$y_{tnd} = s_{t+\tau,nd} .$$

The escapement of a stock in all seven districts can be written as the 7x1 vector, $\underline{y}_{tn}$. Under the definition that a stock consists of all the fish that spawn within a district, the only non-zero element of $\underline{y}_{tn}$ is the nth element corresponding to the district stock n escapes in. We set all τ

= 5 days as a best estimate of the average time spent at the mouth (Sam Sharr, Alaska Department of Fish and Game, personal communication).

The fishery in recent years has been concentrated in regions where pink salmon stocks mix as they migrate through the Sound. Because there is currently no evidence of differential harvest of the stocks, all stocks within a pool of migrating salmon are assumed to be equally available to the fishing gear. Thus, the relative contribution of each stock to the observed catch was equal to its relative abundance in the migratory pool,

$$c_{tnd} = C_{td} \frac{P_{tnd}}{\sum_n P_{tnd}} . \tag{2.1}$$

The harvest of wild salmon was estimated by removing estimates of the catch of hatchery fish as described in Sharr et al. (1994b; 1994c; 1995).

It follows from equation (2.1) that the daily fraction of available fish removed in the harvest, the harvest rate ρ_{td}, from that migratory pool can be calculated as

$$\rho_{td} = \frac{c_{tnd}}{P_{tnd}} = \frac{C_{td}}{\sum_n P_{tnd}} . \tag{2.2}$$

We assumed that a salmon's return migration through Prince William Sound is unidirectional and follows the pathways in Figure 7. Computationally, this movement is controlled by the migration matrix Θ_n (θ_{ij} is the probability that a given fish comes from district j during the previous 24 hours, given that it is in district i; Tables 4a - g). The diagonal elements of Θ_n are the probabilities that fish stay in the same area and are calculated as $1\text{-}p^{-1}$, where p is the average number of days that a salmon spends in that district. Alternatively, p^{-1} can be thought of as the probability of a successful transition. Each θ_{ij} was estimated from the results of a pink salmon radio tagging experiment in 1992. Entry to the fishery from the Gulf of Alaska is subsumed into this matrix. Thus, all matrices and vectors have dimensions 8x8 and 8x1, respectively. Columns sum to 1.0 so that fish neither disappear nor appear after entering the migration.

The pools of migrating fish are central to the reconstruction method. It is in these pools that harvest, escapement, and migration interact to produce the spatial and temporal distributions of salmon. The daily size of the pool is a function of inputs and outputs. Because the model works backward in time, catch, escapement, and emigration are inputs, and immigration (from other districts or the Gulf of Alaska) is the output. On any given day, the order of events is arbitrarily assumed to be catch and escapement, then migration. Pool abundance is determined at the very beginning of the day prior to catch, escapement, and migration. We express this with an equation governing the size of the migratory pool backward in time,

$$\underline{P}_{tn} = \Theta_n \, \underline{P}_{t+1,n} + \underline{c}_{tn} + \underline{y}_{tn} \, . \tag{2.3}$$

The left-hand side of equation (2.3) is the abundance in the migratory pools at the beginning of day t and the right-hand side is the abundance in the migratory pools at the beginning of the following day $(t+1)$ moved according to the migration matrix with the catch and the escapement on day t added.

Notice that estimating c_{tnd} requires knowledge of P_{tnd}, which, in turn, depends on the estimated value of c_{tnd}. We bypassed this problem by noting the harvest rate ρ_{td} was the same for all stocks. By rearranging equation (2.2), substituting into equation (2.3), and defining $\mathbf{U}_t$ to be a diagonal square matrix with elements ρ_{td}, we developed the recursive pool-size equation

$$(\mathbf{I} - \mathbf{U}_t) \, \underline{P}_{tn} = \Theta_n \, \underline{P}_{t+1,n} + \underline{y}_{tn} \, ,$$

as an intermediate step to developing the final form of the recursive pool-size equation

$$\underline{P}_{tn} = (\mathbf{I} - \mathbf{U}_t)^{-1} \, [\Theta_n \, \underline{P}_{t+1,n} + \underline{y}_{tn}] \, . \tag{2.4}$$

Because we want information on the stock-specific catches c_{tnd}, which are not explicitly computed by equation (2.4), we added an extra computational step. We defined the 7x1 vector $\underline{P}^*_{tn}$ as the number of salmon remaining in each migratory pool after catch is removed, i.e.,

$$\underline{P}^*_{tn} = \Theta_n \, \underline{P}_{t+1,n} + \underline{y}_{tn} \, ,$$

We then computed $\underline{c}_{tn}$ as

$$\underline{c}_{tn} = \underline{P}_{tn} - \underline{P}^*_{tn} \, .$$

The total run size of each stock, R_n , is computed as

$$R_n = \Sigma_d \underline{1}' \underline{c}_{tn} + \Sigma_d \underline{1}' \underline{y}_{tn} = \Sigma_d \Sigma_t \, c_{tnd} + \Sigma_d \Sigma_t \, y_{tnd} \, ,$$

where $\underline{1}'$ is the transpose of a 365×1 vector of ones. Also of interest is the seasonal harvest rate experienced by each stock ρ_n,

$$\rho_n = \frac{\Sigma_d \Sigma_t \, c_{tnd}}{R_n} \, .$$

Escapement Inputs to the Run Reconstruction

More than 800 streams that line the coast of Prince William Sound provide spawning sites for pink salmon. Most are small and have barriers to upstream movement within 1/4 mile of the mouth; much of the spawning occurs near the stream mouth. Of the total number of streams, 211 are used by area managers to construct indices of the entire escapement (Pirtle 1977) by means of periodic aerial estimates of abundance. Index streams account for about 85% of the total escapement. During a season each index stream is observed from the air about ten times and on each survey an estimate is made of the total number of salmon in the stream, at the mouth, and in the bay near the stream mouth. Although an attempt is made to fly each stream weekly, vagaries in weather and funding may disrupt the schedule, limiting the available data.

A fish-day is defined as one fish alive in the stream for one day. This unit plays a central role in estimating the escapement. Total fish-days can be estimated by interpolating between actual weekly observations of abundance. The numbers of fish in a stream can be estimated by accounting for a survival component. For example, two fish-days might be the result of two salmon in the stream for one day, or one salmon in the stream for two days. A salmon typically survives longer than one day in freshwater, so the estimate of total fish-days must be adjusted by the average lifespan — called *the stream life* — of a salmon in the stream. Because total fish-days are estimated by accumulating and interpolating, this is called the *area-under-the-curve estimate* of escapement. See English et al. (1992) and Johnson and Barrett (1988) for more details.

Working from the assumption that the adjusted escapement data are without error, the reconstruction moves backward in time from the day the last salmon moves into the stream to the day the first fish enters the fishery. Because the run reconstruction operates with daily time steps, daily escapement is an input to the model. Therefore, a method was developed to estimate the daily stream entries from weekly observations of fish in streams.

Data that were available to us in an accessible form included: (1) daily average percentage of fish-days pooled by district for the odd- and even-year lines, (2) estimated total escapement by district for each year, and (3) estimated number of fish-days by district for each year. The estimated typical escapement timing of individual stocks was derived from the average daily percents of the total escapement by district. While averaged data do not reflect yearly variation in escapement timing, there is evidence that the timing of escapement is a descriptive characteristic of a stock (Rugolo, 1984).

The procedure to estimate the number of fish in a stream by the area-under-the-curve method from periodic counts is similar to the method described by Mundy and Mathisen (1981) to estimate daily and annual abundance from periodic catch observations. Given the stream-observation curve and the stream life, they estimated the size, shape, and timing of the distribution of fish arriving at the stream that would best explain the observations. By adapting this method to fit the available information, the daily entries of salmon to the streams of each district were estimated by determining the shape and timing of the daily percentage of total district-wide escapement entry distribution that resulted in the best fit to the average daily percentage of total fish-days distribution for that district and cycle-year.

For the purposes of this discussion, *stream* refers to all streams in a district, unless otherwise noted, and estimated values are indicated with a *hat* or carrot symbol (^). The following is our notation for this process:

λ_d = stream life of stock *d*
A_d = total number of fish-days of stock *d* in index streams
E_d = total escapement of stock *d* to index streams
b_t = entry of fish to the stream pool on day *t*
β_t = daily entry proportion into the stream pool on day *t*
S_t = number of fish in stream pool on day *t*
h_t = number of fish that die on day *t*
σ_d = standard deviation of stream entry date for stock *d*
μ_d = mean day of stream entry to all streams for stock *d*
Ξ_d = total escapement to all streams for stock *d*
κ_t = estimated scaled daily entry
π_t = observed daily proportion of total fish-days
$\hat{\pi}_t$ = predicted daily proportion of total fish-days

The underlying model assumes that the number of fish in the stream is equal to the cumulative arrivals minus the cumulative deaths. From this assumption, the number of fish in the stream on day *t* is equal to the number of fish alive in the stream on day *t*-1, plus the fish that enter on day *t* minus the fish that die on day *t*:

$$S_t = b_t + S_{t-1} - h_t . \tag{3.1}$$

Assuming all salmon in a district survive in freshwater for exactly λ days and that stocks are delineated by district boundaries, a stock-specific stream life, λ_d, can be estimated. Stream life has been empirically estimated for several of the index streams (Sam Sharr, Alaska Department of Fish and Game, Cordova, Alaska, unpublished data), and the resulting estimates have been applied to all the other streams according to similarities in stream type. We estimated the district-wide stream life as an average of the stream lives in index streams weighted by the size of the escapement to each index stream. Using the total number of fish-days, $A_d = \sum_i A_{id}$, spent in the index streams *i* in district *d* and the estimated total escapement,

$E_d = \sum_i E_{id}$, for those index streams, the district-specific average stream life, λ_d , is calculated as

$$\lambda_d = \frac{A_d}{E_d} . \tag{3.2}$$

The number of fish-days in each index stream, A_i , is a function of streamlife, λ_i, and escapement, E_i , for that stream, i.e., $A_i = \lambda_i E_i$.. Then, the stock-specific stream life from equation (3.2) is a weighted average, weighted by the escapement to each of the n streams in the district:

$$\lambda_d = \frac{\sum_i^n \lambda_i E_i}{\sum_i^n E_i} = \frac{\sum_i^n \lambda_i E_i}{n\bar{E}} = \frac{\sum_i^n \lambda_i \frac{E_i}{\bar{E}}}{n} .$$

The estimated total annual pink salmon escapements to the index streams in each district, A_d , were provided by Sam Sharr, Alaska Department of Fish and Game, Cordova, Alaska (unpublished data).

The daily entry of salmon is assumed to be approximately normally distributed with a mean day of entry μ, a standard deviation of σ, and a known total escapement Ξ. Normality is assumed for statistical reasons, because only two parameters (μ and σ) must be estimated, and because historic average distributions of stream entry are approximately normal. The estimated daily arrival of salmon to the stream, $\hat{b}$, is approximated with the following equation:

$$\hat{b}_t = \frac{\Xi}{\hat{\sigma}\sqrt{2\pi}} e^{-\frac{(t-\hat{\mu})^2}{2\hat{\sigma}^2}} . \tag{3.3}$$

The π in the denominator of equation (3.3) represents the number pi.

The estimation process begins by computing an entry curve from initial estimates of μ and σ; Ξ is assumed to be known and does not change during the estimation process. Because the observed stream counts are in percentages of the total and in units of fish-days, the daily entry is similarly scaled and divided by the estimated stream life to be in the same units. The estimated daily entry proportion, β_t , is estimated from $\hat{b}_t$ as

$$\hat{\beta}_t = \frac{\hat{b}_t}{\Xi \hat{\lambda}} .$$

Because a salmon is assumed to only survive λ days in the stream, the number of deaths on day t, h_t, can be expressed as its equivalent, $b_{t-\lambda}$, the number of fish entering λ days earlier. Equation (3.1) can be rewritten as

$$\hat{\pi}_t = \hat{\beta}_t + \hat{\pi}_{t-1} - \hat{\beta}_{t-\lambda}$$

to compute the estimated daily percent of total fish-days in the stream, $\hat{\pi}_t$, resulting from the estimated distribution of daily percent of total entry to the stream, $\hat{\beta}_t$.

The parameter estimates $\hat{\mu}$ and $\hat{\sigma}$ are those that minimize the sum of the squared errors (SSQ) between the log-observed daily proportion, $\ln(\pi_t)$, and the log-predicted daily proportion, $\ln(\hat{\pi}_t)$, of the fish-days in the streams of the district:

$$SSQ = \sum_t [\ln(\frac{\hat{\pi}_t}{\pi_t})]^2 .$$

Error is assumed to be multiplicative as the individual values of π_t range over several magnitudes. Assuming a lognormal error structure coerces the estimator to fit the tails as well as the peak. Once the mean and the standard deviation of date of entry ($\hat{\mu}$ and $\hat{\sigma}$) are estimated, estimating the daily number of fish entering the escapement in a district is straightforward using equation (3.3).

Daily arrivals were estimated for each of the nine districts for the years 1989-1992. Where necessary, districts were combined by summing the number arriving each day in each district. In all cases the algorithm successfully produced estimates of the stream-entry distributions. For example, see Figure 8 for the estimated distribution of the daily percent of total fish-days in the stream, $\hat{\pi}_t$, and the observed daily percent of total fish-days in the stream, π_t, for the Northwestern District (224) in 1989. After estimating the temporal distribution of entry to the streams, $\hat{b}_t$, the relationship between the daily entry of fish to the streams and the resulting number of fish that may be observed in the streams for the Northwestern District (224) in 1989 is given in Figure 9. The latter curve is the estimated π_t distribution scaled to thousands of fish.

Radio Tagging

In 1992 pink salmon were tagged at three locations within Prince William Sound along hypothesized migration routes: (1) near Point Elrington and in Latouche Passage at the point most pink salmon enter the Sound, (2) along the eastern shore of Culross Island, and (3) along the southern shore of Glacier Island. Fish were captured either with 4-3/4 mesh, 50-fathom gillnets hung in the "Coghill configuration," or with seines by means of short-term charters of boats in the commercial fleet. When gillnets were used, technicians immediately cut the webbing of the gillnet and placed the fish into a tote that contained clean saltwater.

Tagging methods were similar to those described in Barton (1992). If the fish looked healthy and unharmed, the fish was tagged, but if the technicians saw any evidence of bleeding from the gills, the fish was released untagged. The tag was attached just below the dorsal fin with two Petersen needles twisted together; the Petersen needles were attached to the radio tag with epoxy glue and nylon tie straps. The date, time, technicians, location, and tag number were recorded and the fish was released. The procedure for seine-caught fish was the same, except no webbing was cut and the fish were not examined carefully for bleeding from the gills.

The tags and receivers were supplied by Lotek Engineering of Ontario. The receiver was a Lotek SRX 400 with CODE LOG operating firmware. The tags measured approximately 15 mm by 42mm and weighed the equivalent of 10.5 grams in the water. We acquired 200 tags on four frequencies (149.64, 149.66, 149.68, and 149.70 MHz), with 50 individually digitally coded tags per frequency. One tag was placed in approximately 2 meters of freshwater below the airplane dock in Eyak Lake to serve as a positive control at the beginning and end of each survey flight.

We initiated a tag recovery program using posters and flyers; we attended fishermen's organization meetings; and most importantly we offered reward hats and tee shirts. The hats were offered in a variety of styles, from plain black to Hawaiian print design, all bearing the distinctive tagging study logo.

We used a Bellanca Scout airplane which generally flew at a speed of 70 knots and at an altitude of 500 feet. Two four-element Yagi antenna were attached to the wing struts following the advice of an engineer from Lotek Engineering who visited the project.

As the plane flew along the survey course, a technician and pilot listened for the characteristic "chirping" sound of the tag through the airplane's intercom system. The transmitter scanned each frequency for 2.5 seconds so that all four frequencies were scanned every 10 seconds. As the plane flew over significant spawning streams, the technician recorded a unique stream number and the time. The plane's location was generally recorded every 1 to 8 minutes, so that the location was known within approximately 10 nautical miles for any particular minute. When the technician or the pilot heard a tag "chirp," the pilot maneuvered the plane to determine the direction by means of the loudness of the "chirping." The technician attempted to decode the tag, switching the receiver out of scan mode and into decode mode. The data-logging feature of the receiver recorded the unique tag number and exact time a tag was detected. When the technician decoded the tag, the tag number, the stream number, and the time were recorded. The receiver was then placed back into scan mode and the survey continued.

RESULTS

Radio Tagging

We assumed that pink salmon migration is unidirectional (Figure 7). Alternate pathways exist for Districts 221 and 223, but fish were not allowed to reverse direction in the model. The pathways were consistent with the radio tagging and historical tagging data, except that we ignored some reverse migration pathways that had been demonstrated with tagging. Most notable were migration of fish from the Northwestern District (224) to the Southwest District (226).

Next, we calculated distances between points selected in each district and the Gulf of Alaska (Table 5). We shortened the distance from the point we chose to represent the Gulf of Alaska to the Southeastern District (228) because this distance included travel past the Southwest District through the Gulf of Alaska. Next, we calculated the average transit time between districts based on distance and average swimming speed. We used the overall average swimming speed for consistency.

Migration matrices were constructed in the backward direction since the reconstruction starts with escapement and worked backward through Prince William Sound. The migration probability was $1/p$ where p is the average transit time to the next district. The probability of remaining in the district was $1-1/p$. Where multiple pathways existed a proportion of the migrants is sent in each direction; p was estimated by the mean travel time to the alternative districts, weighted by the proportion going each way. The results of these calculations are the set of migration matrices listed in Tables 4a - g.

One potential problem was that the exponential "decay" of fish out of a district resulted in long-tailed movement distributions. Since we were working backwards, the tail was for fish moving out to the Gulf of Alaska. In fact, the effect on the run reconstruction was that later entrants to Prince William Sound moved more quickly to their district of origin, which was consistent with our understanding of salmon migration.

The overall mean rate of travel was 4.67 miles per day (mpd). This number was used to construct the migration matrices.

The distribution of swimming speeds was very asymmetrical. We classified the travel times by 2 mpd categories to obtain a frequency distribution that fit with a gamma distribution reasonably well.

The results of the entire tagging study are provided in Table 6. This table shows tag location, time and place of harvest of the tagged fish, if available, and time and place of freshwater radio detection, if available.

Run Reconstruction

The 1989 stock-specific results from the reconstruction are found in Table 7a. The estimated total run sizes for each stock ranged from 417,000 for the Northwestern stock (224) to 4.2 million for the Eastern stock (221). Estimated harvest rates were low for most stocks, ranging from 0% for the Montague stock (227) to the extremely high value of 87% for the Coghill stock (223). The stocks with the highest estimated harvest rates were the Eastern stock (221), the Northern stock (222), and the Coghill stock (223). The Northwest stock (224), Southwest stock (226), and Montague stock (227) experienced low harvest rates in 1989. This was because the southwestern and southcentral areas of the Sound were closed to most commercial fishing due to oil in the water and on the beaches. Catches in the Southwest District (226) in 1989 were from harvests in hatchery terminal areas. Portions of the northwestern Sound (Districts 222, 223, and 224) were also closed at times during the season, and fishing effort in the Southeast District (228) was minimal (Geiger and Savikko 1990). The high harvest rate on the Coghill stock (223) should have been expected, since much of the fishing effort in the Sound had been concentrated in a few unoiled areas in Districts 222 and 223.

In 1990 the estimated stock-specific run sizes (Table 7b) ranged from 486,000 for the Montague stock (227) to 7.3 million for the Eastern stock (221). The estimated harvest rates ranged from 1% for the Southeast stock (228) to 89% for the Coghill stock (223). The 1990 return year had excellent runs of wild stocks (3.9 returns-per-spawner) as well as abundant hatchery returns. Harvest rates on all but the southeastern stocks (227 and 228) were high and the estimated sound-wide harvest rate was 68%. The estimated harvest rate on the Coghill stock (223) was an exceptional 89%; the model estimated the return-per-spawner in excess of 10 fish for this stock.

In 1991 the estimated stock-specific run sizes (Table 7c) ranged from 686,000 for the Northeastern stock (224) to 6.6 million for the Southwest stock (226). Because wild-stock escapements were low for the first part of the season, fishing was curtailed along the migratory pathways. When the adult salmon finally returned late in the season, the Southwest District (226) was opened for longer periods than usual to take advantage of the abundant salmon. This pattern of fishing allowed the Northern and Eastern stocks (221 and 222) to escape much of the fishing effort, which was reflected in lower estimated harvest rates. Returns in 1991 were good, with a sound-wide estimated return-per-spawner of 2.4.

In 1992 the estimated run size for each stock (Table 7d) ranged from 169,000 for the Coghill stock (223) to 1.5 million for the Eastern stock (221). The return of pink salmon to the Sound in 1992 was extremely low: Escapements did not exceed 60% of the desired goal for any stock but the Southwest stock (226) and stocks in the northwestern part of the Sound (222, 223, and 224) received less than 40% of their target escapement levels. Poor wild-stock escapements caused fishing to be confined to hatchery terminal harvest areas for the last half of the season and harvest rates were low, ranging from 0% (stocks 227 and 228) to 57% (stock 223) and the estimated sound-wide harvest rate was 38%. Stocks from the northern districts experienced the highest harvest rates, probably due to the many fisheries they must traverse during migration. Stock-specific returns-per-spawner estimates during 1992 were low, ranging from 0.26 (228) to 1.3 (222) and the sound-wide return-per-spawner was estimated to be 0.71. The poor return is reflected in the estimated survival rates of 1.5% to 1.7% for hatchery-stock pink salmon (Geiger and Savikko 1993).

Estimated seasonal harvest rates and return-per-spawner values were not evenly distributed among the stocks during the four seasons reconstructed. Stocks that traversed more fisheries or constituted a large portion of the migratory pool during periods of large catches tended to have higher harvest rates. For example, the Coghill stock (223) is subject to harvest in four fishing districts (Figure 7) — Districts 222, 223, 224 and 226. The Eastern stock (221) migrates through six districts (Figure 7) — Districts 221, 222, 223, 224, 226 and 228 — but its earlier time of migration allows it to miss much of the harvest pressure in Districts 222, 223, 224 and 226.

We explored the model's sensitivity to migration speed and run timing as a possible source of misallocation of salmon to the Coghill stock (223). Due to the mechanics of the reconstruction, we expected changes in the relative composition of the pools of harvestable fish to affect the resulting distribution of harvest among stocks. The reconstruction program was rerun twice, with the escapement-entry timing of the Coghill stock alternately shifted 10 days earlier and later to shift its temporal distribution within each of the fisheries it traversed. We also expected changes in the transition rates of stock 223 to affect an individual fish's vulnerability by changing its rate of travel. Two more runs, with our original migration rate for stock 223 doubled, then halved, were computed to test the effects of error in the transition rates.

Figure 10 shows the effect of changes in migration timing and migration speed of the Coghill stock (223) in 1990. Earlier migration moves many of the Coghill-stock salmon through the fishery prior to the period of harvest, reducing their probability of capture, and consequently the estimated harvest rate on the stock. Later migration increases the estimated harvest rate on the Coghill stock because the peak of the stock's abundance coincides with the peak of harvest effort. Faster migration decreases the availability of an individual Coghill-stock fish, which reduces the harvest rate, while slower migration has the opposite effect. In all cases, changes in stock 223's harvest rate are inversely reflected in the estimated harvest rate on stocks 221 and 222, indicating that the allocation of some of the salmon to stocks 221, 222 and 223 is dependent on assumptions about migration. This exercise demonstrated how errors in assumed migration timing or migration speeds affected the run-reconstruction estimates. This also helped explain how the mixed-stock fishery affected the actual stocks.

DISCUSSION

One of the major findings of the reconstruction of the 1989 through 1992 runs of wild pink salmon in Prince William Sound was that some stocks are experiencing very high harvest rates over the course of the season. This finding may seem obvious, but this is the first time a quantitative analysis of stock-specific harvest history has been possible in Prince William Sound, and this finding helps explain the downward trend in escapement in districts unaffected by the *Exxon Valdez* oil spill.

The relative magnitudes of harvest pressure are similar among regional groups of stocks. In all four years, the southeastern stocks (227 and 228) had the lowest reconstructed harvest rates in the Sound; the northern stocks (221, 222, and 223) generally experienced harvest pressures greater than the sound-wide average; and the Southwest stock (226) experienced moderate seasonal harvest rates that were generally lower than the sound-wide harvest rate.

The regional pattern in stock-specific harvest rates reflects the obvious fact that the intensity of harvest pressure experienced by a stock is related to the number and intensity of fisheries it must traverse during the season. The southeastern stocks experience only the fishery in the district to which they return (Figures 1 and 7). Little or no fishing effort is expended in these districts, thus they have low seasonal harvest rates. The Southwest stock (226) migrates directly to its home district, usually the most intense mixed-stock fishery in the Sound. For the years when fishing in District 226 was restricted (1989 and 1992), harvest rates were low. In 1990 intense fishing in District 226 increased the harvest rate for both stocks 226 and 224. In 1991 poor wild-stock escapements delayed fishing until late in the season, allowing the Northwest stock (224) to cross the district with little fishing pressure. Due to a dramatic influx of pink salmon late in the season, managers opened more of the migratory pathways to fishing whereby harvest pressure on all stocks present subsequently increased. The northern stocks must travel through more districts and thus encounter more fishing effort than do stocks from other regions. Although the Eastern stock (221) traverses one more district than the Northern or Coghill stocks (222 and 223), it has the lowest estimated harvest rate of the three. This is due to the Eastern stock (221) missing much of the fishing effort due to an earlier migration timing.

The return-per-spawner estimates show the same regional trends seen in the harvest rates. Except for the Coghill stock (223) in 1989, 1990, and 1991, the return-per-spawner estimates are generally consistent with values in Table 3. The southeastern stocks are generally the least productive, followed by the southwestern stocks. The northern stocks are the most productive in the Sound, and except for the odd-year line of the Eastern stock (221), show productivities well above the sound-wide estimate. This pattern of productivity might be explained by several factors: (1) the streams in the southern districts are more exposed to the harsh winter weather of the Gulf of Alaska than the interior streams, (2) rain-fed island streams are subject to greater variability in stream flow than mainland streams fed by snow melt, and (3) western streams are generally shorter and steeper than eastern streams and provide lower-quality spawning habitat.

The high productivity attributed to the Coghill stock (223) might be the result of too much of the catch being allocated to this stock by the reconstruction. If so, the salmon that are mistakenly attributed to the Coghill stock (223) are most likely from the Eastern and Northern stocks (221 and 222) because these stocks share similar pathways and timing during migration. Small errors in catch allocation would have a large, relative effect on the estimated Coghill stock productivity because of the stock's small size. In 1992, when fishing was restricted and harvests were low, the return-per-spawner for the Coghill stock was 1.10, lower than the estimated productivity of 1.31 for the Northern stock (222).

The weakest part of the method is our understanding of the migration behavior of wild pink salmon in the Sound. Our assumed migration pathways perhaps are not flexible enough to account for the fish sometimes overshooting and reversing direction along migration pathways as our tag study showed. Wandering and probing behavior that pink salmon have been observed to exhibit before actual homing (Heard 1991) are not reflected in our model because we have little specific information on these actions. Starr and Hilborn (1988) discuss the necessity for good migration information when reconstructing a mixed-stock fishery because of the possibility of misallocating harvest when migration behavior is misspecified.

Our model does have features that capture biological realism not found in other run-reconstruction models. Movement backward in time allows the average residence time in the Sound to change over the course of the season. To show what we mean, the cumulative percent-of-total entry to the Sound was compared with the cumulative percent-of-total entry to the streams for the Montague stock (227) in 1990. This stock was selected for several reasons: (1) it experienced very little harvest in 1990, (2) it traverses only one district (227), and (3) it does not interact with other stocks. Thus, the results for this stock are solely the result of the stream-entry distribution as input and the probability of transition to the Gulf of Alaska. In Figure 11 the left most curve denotes entry and the other denotes exit — the difference between the two curves in the horizontal direction is the residence time. At the point where 25% of this stock had entered the Sound, the residence time was 16 days. The difference narrowed to 13 days by the time 75% of the stock had entered the Sound. So the model presupposes a change in residence time of 3 days from the mid-early portion of the run to the mid-late part of the run. Similar reductions in average residence time were computed for all other stocks as well.

The most important result from the reconstructions is the indication that the northern stocks — which have been experiencing chronic escapement shortfalls — are experiencing the most intense harvest pressure of all the stocks in the Sound.

CONCLUSIONS FROM PARTS I AND II

The greatest damage to Prince William Sound pink salmon resulting from the *Exxon Valdez* oil spill seems to have come from exposure to petroleum in the critical nearshore environment. We estimated that the number of lost adult pink salmon in the 1990 return was in units of millions. If this estimate is nearly correct, the largest and most important source of injury is the one we least understand.

Injury in the egg life stage was demonstrated for the 1989 and 1990 brood years. Moderate errors in the estimated spawner density, moderate errors in the number of streams oiled, or even moderate errors in the ratio of survival in oiled and unoiled streams would not have affected the larger conclusions about the result of egg-stage damage in the 1989 through 1992 brood years: the lost adult salmon probably was at most 10% of the potential adult production in the Southwest Fishing District.

The most important, unanswered question about pink salmon is why did the estimated egg-stage mortality not converge to control levels, but indeed become more dissimilar in 1991 and 1992? The effects we have been attributing to the oil spill could simply be natural differences in sites. The genetic-damage hypothesis put forward by Sharr et al. (1994a) seems a reasonable, if untested, explanation to us, but this explanation is far from unequivocal.

The run-reconstruction results did not support a hypothesis of extensive and lasting oil-induced damage. However, this study pointed out a pattern of alarmingly high harvest rates in the northwestern part of Prince William Sound, especially on Coghill-stock pink salmon. This area of the Sound has experienced escapement shortfalls for a number of years, going back into the 1980s (Geiger et al. 1992; Geiger 1993). We have not attempted to quantify the number of adults that have failed to return due to overharvest in a manner similar to the way we reported the oil spill damage. However the effects of overharvest on wild pink salmon might be similar or even greater than the effects of the oil spill.

At best, these estimates give a fuzzy picture of the actual effects of the oil spill had on the wild pink salmon resources in Prince William Sound. Taking the uncertainty into consideration, these estimates are perhaps best used to gauge the order of magnitude of the injury for each brood year. Unless we have considerably underestimated the injuries in the 1989 and subsequent brood years — which is a real possibility — the most interesting feature of the 1989 and later brood years is how small the damages were to wild pink salmon populations in Prince William Sound. In the 1988 brood year, the greatest potential for damage coincided with a year of excellent environmental conditions that may have strongly counteracted the effects of oil. Had this spill occurred in a year like 1991, which saw very poor marine survival, the effect of the oil spill on pink salmon in Prince William Sound could have been quite different.

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Table 1. Estimated overall egg-stage mortalities from oiled sites and control sites in Prince William Sound, with estimated percentage reduction in survival in oiled areas, by brood year. The estimates are based on weighted averages of mortalities by tide stage found in Sharr et al. (1994a) and Sharr et al. (1994d) with weights formed from estimated egg densities.

Year	Oiled Sites	Control Sites	Survival in Oiled Areas as Percent of Potential Survival
1989	0.174	0.104	92%
1990	0.295	0.195	88%
1991	0.433	0.221	73%
1992	0.450	0.250	73%

Table 2. Estimates of oil-spill induced losses of adult production with other important statistics for brood years 1988, 1989, and 1990; the expected future losses for brood years 1991 and 1992 are based on the assumption the genetic damage hypothesis is correct. Losses are expressed in units of million adults that fail to return two years following the brood year. The estimated return-per-spawner is the estimate for what would have been possible without the oil spill. Estimated production is for all of Prince William Sound.

Brood-Year	Soundwide Escapement (millions)	Southwest District Escapement (millions)	Subsequent Production (millions)	Return-per Spawner Coef. (*s*)	Affected PED (*p*)	Estimated Survival Redn.(*r*)	Estimated Production Without Oil	Estimated Lost of Adults (millions)
1988	4.99	1.61	18.40	4.06	0.32	0.72	20.26	1.86
1989	6.89	1.91	16.58	2.41	0.06	0.92	16.6	0.06
1990	6.18	1.77	4.5	0.74	0.06	0.88	4.6	0.07
1991	9.66	2.21	---	(1.79)[1]	0.05	0.73	17.3	0.2[2]
1992	2.71	0.81	---	(1.79)	0.06	0.73	4.9	0.08[2]

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[1] Assumed based on typical life-history parameters from previous years.

[2] Assuming differences between oil spill sites and control sites are due to persistent genetic damage past the 1990 broodyear.

Table 3. Life history survival and fecundity values from the pink salmon literature. Let *Fem* be the fraction of the run consisting of females, *Fec* the average fecundity per female, *Dep* is the fraction of the potential egg deposition that is actually deposited, *Seg* is the survival from eggs to emergence, *Smr* is the marine survival, and $s_t = Fem_t\, Fec_t\, Dep_t\, Seg_t\, Smr_t$. is the return-per-spawner.

Lifehistory Stage	Conversion			Next Stage	Typical Value	Source
Escapement	times	*Fem*	=	Females;	$Fem \approx 0.5$	Assumed
Females	times	*Fec*	=	PED[3];	$Fec \approx 1875$	Heard(1991)
PED	times	*Dep*	=	AED[4];	$Dep \approx 0.44$	Heard(1991)
AED	times	*Seg*	=	Fry;	$Seg \approx 0.20$	Estimated by eye from Ignell's (1988) data
Fry	times	*Smr*	=	Adults;	$Smr \approx 0.02$	Sharr et al. (1995)
Escapement	times	*s*	=	Adults;	$s \approx 1.65$	By multiplication

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[3] Potential Egg Deposition.

[4] Actual Egg Deposition.

Tables 4a through 4g. Estimated transition rates for each stock in the run reconstruction model.

Table 4 a. Estimated transition rates used in run reconstruction for stock 221.

					District *j*				
		221	222	223	224	226	227	228	Gulf
	221	0.80	0	0	0	0	0	0	0
	222	0.17	0.89	0	0	0	0	0	0
	223	0	0	0	0	0	0	0	0
District *i*	224	0	0	0	0	0	0	0	0
	226	0	0.11	0	0	0.89	0	0	0
	227	0	0	0	0	0	0	0	0
	228	0.03	0	0	0	0	0	0.87	0
	Gulf	0	0	0	0	0.11	0	0.13	1.00

Table 4 b. Estimated transition rates used in run reconstruction for stock 222.

					District *j*				
		221	222	223	224	226	227	228	Gulf
	221	0	0	0	0	0	0	0	0
	222	0	0.89	0	0	0	0	0	0
	223	0	0	0	0	0	0	0	0
District *i*	224	0	0	0	0	0	0	0	0
	226	0	0.11	0	0	0.89	0	0	0
	227	0	0	0	0	0	0	0	0
	228	0	0	0	0	0	0	0	0
	Gulf	0	0	0	0	0.11	0	0	1.00

Table 4 c. Estimated transition rates used in run reconstruction for stock 223.

					District *j*				
		221	222	223	224	226	227	228	Gulf
	221	0	0	0	0	0	0	0	0
	222	0	0.89	0.09	0	0	0	0	0
	223	0	0	0.81	0	0	0	0	0
District *i*	224	0	0	0.10	0.75	0	0	0	0
	226	0	0.11	0	0.25	0.89	0	0	0
	227	0	0	0	0	0	0	0	0
	228	0	0	0	0	0	0	0	0
	Gulf	0	0	0	0	0.11	0	0	1.00

Table 4 d. Estimated transition rates used in run reconstruction for stock 224.

					District *j*				
		221	222	223	224	226	227	228	Gulf
	221	0	0	0	0	0	0	0	0
	222	0	0	0	0	0	0	0	0
	223	0	0	0	0	0	0	0	0
District *i*	224	0	0	0	0.86	0	0	0	0
	226	0	0	0	0.14	0.89	0	0	0
	227	0	0	0	0	0	0	0	0
	228	0	0	0	0	0	0	0	0
	Gulf	0	0	0	0	0.11	0	0	1.00

Tables 4a through 4g (cont.) . Estimated transition rates for each stock in the run reconstruction model.

Table 4 e. Estimated transition rates used in run reconstruction for stock 226.

					District *j*				
		221	222	223	224	226	227	228	Gulf
	221	0	0	0	0	0	0	0	0
	222	0	0	0	0	0	0	0	0
	223	0	0	0	0	0	0	0	0
District *i*	224	0	0	0	0	0	0	0	0
	226	0	0	0	0	0.89	0	0	0
	227	0	0	0	0	0	0	0	0
	228	0	0	0	0	0	0	0	0
	Gulf	0	0	0	0	0.11	0	0	1.00

Table 4 f. Estimated transition rates used in run reconstruction for stock 227.

					District *j*				
		221	222	223	224	226	227	228	Gulf
	221	0	0	0	0	0	0	0	0
	222	0	0	0	0	0	0	0	0
	223	0	0	0	0	0	0	0	0
District *i*	224	0	0	0	0	0	0	0	0
	226	0	0	0	0	0	0	0	0
	227	0	0	0	0	0	0.90	0	0
	228	0	0	0	0	0	0	0	0
	Gulf	0	0	0	0	0	0.10	0	1.00

Table 4 g. Estimated transition rates used in run reconstruction for stock 228.

					District *j*				
		221	222	223	224	226	227	228	Gulf
	221	0	0	0	0	0	0	0	0
	222	0	0	0	0	0	0	0	0
	223	0	0	0	0	0	0	0	0
District *i*	224	0	0	0	0	0	0	0	0
	226	0	0	0	0	0	0	0	0
	227	0	0	0	0	0	0	0	0
	228	0	0	0	0	0	0	0.87	0
	Gulf	0	0	0	0	0	0	0.13	1.00

Table 5. Migration pathways and distances between Prince William Sound districts.

FROM - TO	DISTANCE (MILES)	AVERAGE TIME (DAYS)	RANGE OF RADIOTAG TIMES (DAYS)
Gulf - 226	41.4	8.87	7.50
Gulf - 227	49.1	10.51	
Gulf - 228	35.0	7.49	
228 - 221	23.1	4.95	
226 - 224	33.5	7.17	6.16
226 - 222	43.5	9.31	6.16 - 7.13
224 - 223	16.1	3.45	7.60
222 - 223	33.4	7.15	7.6
222 - 221	24.3	5.20	5.20 - 17.22

Table 6. Tagging release and recapture data for the 1992 radio tagging study. Stream designations available from the ADF&G, Cordova Alaska.

Tagging District	Channel	Code	Application Date	Commercial Capture Date	Time Between Captures (Days)	Capture Location	1st Flight Detection	Time to Detection (Days)	Detection Location
226	17	1	23-Jun						
226	17	2	24-Jun						
226	17	3	24-Jun	5-Jul	11	Dist. 221-61, Found at Processor			
226	17	4	24-Jun						
226	17	5	24-Jun	7-Jul	13	VFDA Octagon, Seiner, 221-61			
226	17	6	24-Jun	26-Jun	2	Outside of Main Bay, Gillnet, 225-20			
226	17	7	24-Jun						
226	17	8	24-Jun						
226	17	9	24-Jun						
226	17	10	24-Jun				1-Aug	38	Found in Valdez Stream.
226	17	11	30-Jun	14-Jul	14	Valdez Tanker Term., Seiner, 221-61	13-Jul	13	Stream 145
226	17	12	30-Jun						
226	17	13	30-Jun	7-Jul	7	Goldmine, Seiner, 221-61			
226	17	14	1-Jul	13-Jul	12	On a Tender	13-Jul	12	Tag from tender. Stream 656
226	17	15	1-Jul						
226	17	16	1-Jul						
226	17	17	1-Jul						
226	17	18	1-Jul						
226	17	19	13-Jul						
226	17	20	1-Jul						
226	17	21	1-Jul	5-Jul	4	Goldbeach, 221-61, Found in cannery.			
226	17	22	7-Jul				24-Jul	17	Stream 655
226	17	23	7-Jul	3-Aug	27	VFDA Brood Pond, 221-61			
226	17	24							
226	17	25	7-Jul				24-Jul	17	Stream 603
226	17	26	13-Jul						
226	17	27	7-Jul						
226	17	28	7-Jul						
226	17	29	7-Jul						
226	17	30	7-Jul	17-Jul	10	Potato Pt. Seine opener #2, 221-50	24-Jul	17	Stream 603
226	17	31	7-Jul				31-Jul	24	Stream 603
226	17	32	7-Jul	11-Jul	4	Entrance to Jack Bay, Seiner, 221-50			
226	17	33	7-Jul						
226	17	34	13-Jul						
226	17	35	13-Jul						
	17	36	Not used						
226	17	37	12-Jul						
226	17	38	12-Jul						

Table 6. (Cont.)

Tagging District	Channel	Code	Application Date	Commercial Capture Date	Time Between Captures (Days)	Capture Location	1st Flight Detection	Time to Detection (Days)	Detection Location
226	17	39	12-Jul						
226	17	40	13-Jul						
222	17	41	8-Jul	17-Jul	9	VFDA SHA Cost Recovery harvest, 221-61			
222	17	42	8-Jul	16-Jul	8	Gold Creek Mine, Seine opener #2, 221-61			
222	17	43	8-Jul	17-Jul	9	VFDA SHA Cost Recovery harvest, 221-61			
222	17	44	8-Jul						
222	17	45	8-Jul						
222	17	46	8-Jul						
222	17	47	8-Jul				22-Aug	45	Stream 142
222	17	48	8-Jul				27-Jul	19	Stream 137
222	17	49	8-Jul	14-Jul	6	VFDA SHA Cost Recovery harvest, 221-61			
222	17	50	8-Jul						
222	18	1	20-Jul						
222	18	2	20-Jul				8-Aug	19	Stream 99
222	18	3	20-Jul						
222	18	4	20-Jul						
222	18	5	20-Jul				27-Jul	7	Stream 153
222	18	6	20-Jul						
222	18	7	20-Jul						
222	18	8	20-Jul						
222	18	9	20-Jul						
222	18	10	20-Jul						
226	18	11	19-Jul				31-Jul	12	Stream 637 since 7/24
226	18	12	25-Jul						
226	18	13	25-Jul	3-Aug	9	Unakwik, Payday Pt., Seine, 222-20			
226	18	14	25-Jul	27-Jul	2	AFK SHA, 226-62			
226	18	15	25-Jul						
226	18	16	25-Jul						
226	18	17	25-Jul				13-Aug	19	Esther Hatchery
226	18	18	25-Jul						
226	18	19	25-Jul	3-Aug	9	Seiner, 222-22			
226	18	20	25-Jul	6-Aug	12	Seiner at Fox Farm, 226-51			
224	18	21	16-Jul				24-Jul	8	Stream 676
224	18	22	16-Jul				31-Jul	15	Stream 665
224	18	23	16-Jul						
224	18	24	16-Jul						
224	18	25	16-Jul				18-Aug	33	Stream 451

Table 6. (Cont.)

Tagging District	Channel	Code	Application Date	Commercial Capture Date	Time Between Captures (Days)	Capture Location	1st Flight Detection	Time to Detection (Days)	Detection Location
224	18	26	16-Jul						
224	18	27	16-Jul						
224	18	28	16-Jul				7-Aug	22	Stream 301
224	18	29	24-Jul				7-Aug	14	Stream 458 mouth
224	18	30	16-Jul	17-Jul	1	Nellie Juan Light, GN, 225-10			
224	18	31	16-Jul	31-Jul	15	Port San Juan, 226-62			
224	18	32	24-Jul						
224	18	33	24-Jul						
224	18	34	24-Jul				13-Aug	20	Esther Hatchery
224	18	35	24-Jul				29-Jul	5	Stream 476
224	18	36	24-Jul	28-Jul	4	Esther Hatchery, 222-40	29-Jul	5	Esther Hatchery
224	18	37	24-Jul						
224	18	38	24-Jul						
224	18	39	24-Jul				13-Aug	20	Esther Hatchery
224	18	40	24-Jul						
226	18	41	30-Jul	5-Aug	6	Seiner opening #7, Dist. 226-40			
226	18	42	13-Jul						
226	18	43	13-Jul						
226	18	44	30-Jul						
226	18	45	30-Jul						
226	18	46	30-Jul	14-Aug	15	Seiner SW Dist., Crab Bay, 226-61			
226	18	47	30-Jul				16-Aug	17	Boat near Bishop rock
226	18	48	28-Jul			No Information			
226	18	49	30-Jul				13-Aug	14	Esther Hatchery
226	18	50	30-Jul						
222	19	1	20-Jul						
222	19	2	20-Jul	31-Jul		Ester			
222	19	3	20-Jul						
222	19	4	20-Jul	1-Aug	12	Cannery Creek net pen, 222-21			
222	19	5	20-Jul						
222	19	6	20-Jul						
222	19	7	27-Jul						
222	19	8	20-Jul						
222	19	9	20-Jul	30-Jul	10	Cannery Creek net pen, 222-21	27-Jul	7	East of Cannery Creek
222	19	10	20-Jul						
222	19	11	20-Jul				22-Aug	33	Stream129
226	19	12	27-Jul						

Table 6. (Cont.)

Tagging District	Channel	Code	Application Date	Commercial Capture Date	Time Between Captures (Days)	Capture Location	1st Flight Detection	Time to Detection (Days)	Detection Location
224	19	50	6-Aug			Esther Subdistrict, 223-40			
226	20	1	19-Aug	21-Aug	2	2 mi. S. Bishop Rk,Seine, 226-60			
226	20	2	19-Aug	23-Aug	4	Sawmill Bay, 226-62			
226	20	3	19-Aug						
226	20	4	19-Aug	24-Aug		Evans Point	27-Aug	8	On Boat near Shelter Bay
226	20	5	19-Aug				27-Aug	8	AFK Hatchery
226	20	6	19-Aug						
226	20	7	19-Aug						
226	20	8	19-Aug						
226	20	9	19-Aug						
224	20	10	25-Aug						
224	20	11	25-Aug						
224	20	12	25-Aug						
224	20	13	25-Aug				8-Sep	14	Falls Bay - On Boat
224	20	14	25-Aug						
	20	15 Not used							
224	20	16	25-Aug						
224	20	17	25-Aug						
224	20	18	25-Aug	1-Sep		Ester			
224	20	19	25-Aug	27-Aug	2	Lake Bay, Esther, 223-40	3-Sep	9	Esther Hatchery
224	20	20	25-Aug						
226	20	21	22-Aug				27-Aug	5	AFK Hatchery
226	20	22	22-Aug						
226	20	23	22-Aug	27-Aug	5	AFK Netpens, 226-61			
226	20	24	22-Aug				27-Aug	5	Stream 676
226	20	25	22-Aug				28-Aug	6	Esther Hatchery
226	20	26	22-Aug				1-Sep	10	Stream 636
226	20	27	22-Aug				22-Sep	31	Stream 681
226	20	28	22-Aug				7-Sep	16	Stream 16368
226	20	29	22-Aug						
226	20	30	2-Sep	6-Sep	4	Main Bay, set net, 225-21			
226	20	31	2-Sep						
226	20	32	2-Sep				28-Sep	26	Bainbridge Pt. (No Stream #)
226	20	33	2-Sep				7-Sep	5	Stream 661
226	20	34	2-Sep						
226	20	35	2-Sep						
226	20	36	2-Sep						

Table 6. (Cont.)

Tagging District	Channel	Code	Application Date	Commercial Capture Date	Time Between Captures (Days)	Capture Location	1st Flight Detection	Time to Detection (Days)	Detection Location
226	19	13	27-Jul	29-Jul	2	Cannery Creek net pen, 222-21			
226	19	14	27-Jul	3-Aug	7	Cannery Creek net pen, 222-21			
226	19	15	27-Jul						
226	19	16	27-Jul	6-Aug	10	Seiner in Unakwik, 222-20	7-Aug	11	Cannery Creek
226	19	17	27-Jul	2-Aug	6	AFK SHA, Seiner, 226-62			
226	19	18	27-Jul	3-Aug	7	Cannery Creek, 222-22			
226	19	19	27-Jul						
226	19	20	27-Jul						
226	19	21	7-Aug	9-Aug	2	Seine opener #7.SW Dist. 226			
226	19	22	7-Aug	8-Aug	1	Outer LaTouche Is., Seiner, 226-			
226	19	23	7-Aug	15-Aug	8	Crab Bay, Seiner, 226-61			
226	19	24	7-Aug				16-Aug	9	Stream 666
226	19	25	7-Aug						
226	19	26	8-Aug	11-Aug	3	AFK SHA. Seiner, 226-62	16-Aug	8	AFK Hatchery
226	19	27	8-Aug	27-Aug	19	AFK Netpen, 226-62			
226	19	28	8-Aug				16-Aug	8	Stream 744
226	19	29	8-Aug						
224	19	30	29-Jul	30-Jul	1	Esther Pass E. Marker, 223-40	13-Aug	15	Island Bay (on boat)
224	19	31	29-Jul				13-Aug	15	Esther Hatchery
226	19	32	8-Aug						
224	19	33	29-Jul						
224	19	34	29-Jul	3-Aug	5	Evans Is., Shelter Bay, 226-40			
224	19	35	29-Jul						
224	19	36	29-Jul	30-Jul	1	Hodgkins Pt. Esther, Seiner, 223-40			
224	19	37	29-Jul				13-Aug	15	Esther Hatchery
224	19	38	29-Jul	1-Aug	3	Esther Hatchery, 223-40			
224	19	39	29-Jul						
224	19	40	29-Jul				13-Aug	15	Stream 480
224	19	41	6-Aug				28-Aug	22	Esther Hatchery
224	19	42	6-Aug	7-Aug	1	Esther SHA, seine, 223-40			
224	19	43	6-Aug				13-Aug	7	Esther Hatchery
224	19	44	6-Aug						
224	19	45	6-Aug	21-Aug	15	Main Bay set net, 225-21			
224	19	46	6-Aug						
224	19	47	6-Aug	12-Aug	6	Eshamy Bay Gill net, 225-30			
224	19	48	6-Aug				13-Aug	7	Esther Hatchery
224	19	49	6-Aug				8-Sep	33	Esther Hatchery

Table 6. (Cont.)

Tagging District	Channel	Code	Application Date	Commercial Capture Date	Time Between Captures (Days)	Capture Location	1st Flight Detection	Time to Detection (Days)	Detection Location
226	20	37	2-Sep						
	20	38	Not used						
226	20	39	19-Aug	27-Aug	8	Seiner, 226-60			
224	20	40	14-Aug	20-Aug	6	Pt. Culross, seiner, 223-40			
224	20	41	14-Aug						
224	20	42	14-Aug				18-Aug	4	Esther Hatchery
224	20	43	14-Aug						
224	20	44	14-Aug	21-Aug		Ester			
224	20	45	14-Aug	14-Aug	0	Found in processor, Eshamy or Esther?			
224	20	46	14-Aug				18-Aug	4	Esther Hatchery
224	20	47	14-Aug						
224	20	48	14-Aug						
224	20	49	14-Aug						
226	20	50	2-Sep	9-Sep		Ester			

Tables 7a -d Stock-specific run reconstruction statistics of interest for 1989 to 1992 return years. Escapement, harvest, and run size are in units of thousand fish.

Table 7a. 1989 stock-specific information from reconstruction.

Stock names :	221	222	223	224	226	227	228	Total
Observed escapement	1850	472	248	374	2104	871	975	6894
Estimated catch	2337	676	1704	42	524	0	53	5337
Estimated stock size	4187	1148	1953	417	2627	871	1028	12231
Estimated harvest rate	0.56	0.59	0.87	0.10	0.20	0.00	0.05	0.44
1987 spawners	2705	570	444	350	1479	779	1050	7377
Returns/spawner	1.55	2.01	4.40	1.19	1.78	1.12	0.98	1.66

Table 7b. 1990 stock-specific information from reconstruction.

Stock names	221	222	223	224	226	227	228	Total
Observed escapement	1558	549	154	451	1913	475	1082	6183
Estimated catch	5749	2276	1313	467	3400	11	10	13226
Estimated stock size	7306	2826	1467	918	5313	486	1092	19409
Estimated harvest rate	0.79	0.81	0.89	0.51	0.64	0.02	0.01	0.68
1988 spawners	1407	615	138	341	1710	315	461	4988
Returns/spawner	5.19	4.60	10.63	2.92	3.11	1.54	2.37	3.89

Table 7c. 1991 stock-specific information from reconstruction .

Stock names :	221	222	223	224	226	227	228	Total
Observed escapement	2319	853	378	525	2406	1384	1794	9659
Estimated catch	1306	624	666	161	4151	0	0	6926
Estimated stock size	3624	1495	1044	686	6557	1384	1794	16585
Estimated harvest rate	0.36	0.43	0.64	0.23	0.63	0.00	0.00	0.42
1989 spawners	1849	472	248	374	2103	870	974	6892
Returns/spawner	1.96	3.17	4.21	1.83	3.12	1.59	1.84	2.41

Table 7d. 1992 stock-specific information from reconstruction.

Stock names :	221	222	223	224	226	227	228	Total
Observed escapement	767	325	73	193	825	249	283	2715
Estimated catch	714	395	96	52	404	0	0	1661
Estimated stock size	1481	720	169	245	1229	249	283	4376
Estimated harvest rate	0.48	0.55	0.57	0.21	0.33	0.00	0.00	0.38
1990 spawners	1558	549	154	451	1913	475	1082	6182
Returns/spawner	0.95	1.31	1.10	0.54	0.64	0.52	0.26	0.71

Tables 8a-d. Estimated total escapement, mean day of escapement, standard deviation of escapement, and mean stream life used to predict stream entry distributions for the reconstruction model.

Table 8a. 1989 district-specific escapement data for pink salmon in Prince William Sound.

District	221	222	223	224	225	226	227	228
Total escapement	1,849	472	248	374	191	1,912	871	974
Mean day of entry	217	218	222	221	235	227	224	220
SD of day of entry	16.6	15.4	12.7	11.6	10.8	10.3	11.0	11.6
Stream life (days)	12.3	11.6	13.0	9.1	6.1	10.2	12.9	12.2

Table 8b. 1990 district-specific escapement data for pink salmon in Prince William Sound.

District	221	222	223	224	225	226	227	228
Total escapement	1,557	549	154	451	141	1,771	475	1,082
Mean day of entry	219	223	219	219	224	220	227	222
SD of day of entry	14.4	12.1	10.6	12.6	9.8	11.7	10.0	10.2
Stream life (days)	10.9	9.0	11.2	9.0	6.4	8.8	11.8	12.8

Table 8 (cont.)

Table 8c. 1991 district-specific escapement data for pink salmon in Prince William Sound.

District	221	222	223	224	225	226	227	228
Total escapement	2,318	853	378	525	195	2,210	1,384	1,794
Mean day of entry	216	219	222	221	236	228	224	219
SD of day of entry	16.5	15.4	12.7	11.5	10.8	10.3	11.0	11.4
Stream life (days)	12.8	11.0	12.8	9.9	4.9	9.4	12.6	14.1

Table 8d. 1992 district-specific escapement data for pink salmon in Prince William Sound.

District	221	222	223	224	225	226	227	228
Total escapement	767	325	73	193	20	805	249	283
Mean day of entry	219	223	219	219	224	220	227	221
SD of day of entry	14.4	12.1	10.6	12.6	9.8	11.7	10.0	10.0
Stream life (days)	11.1	9.5	11.5	9.3	6.5	9.5	11.7	14.7

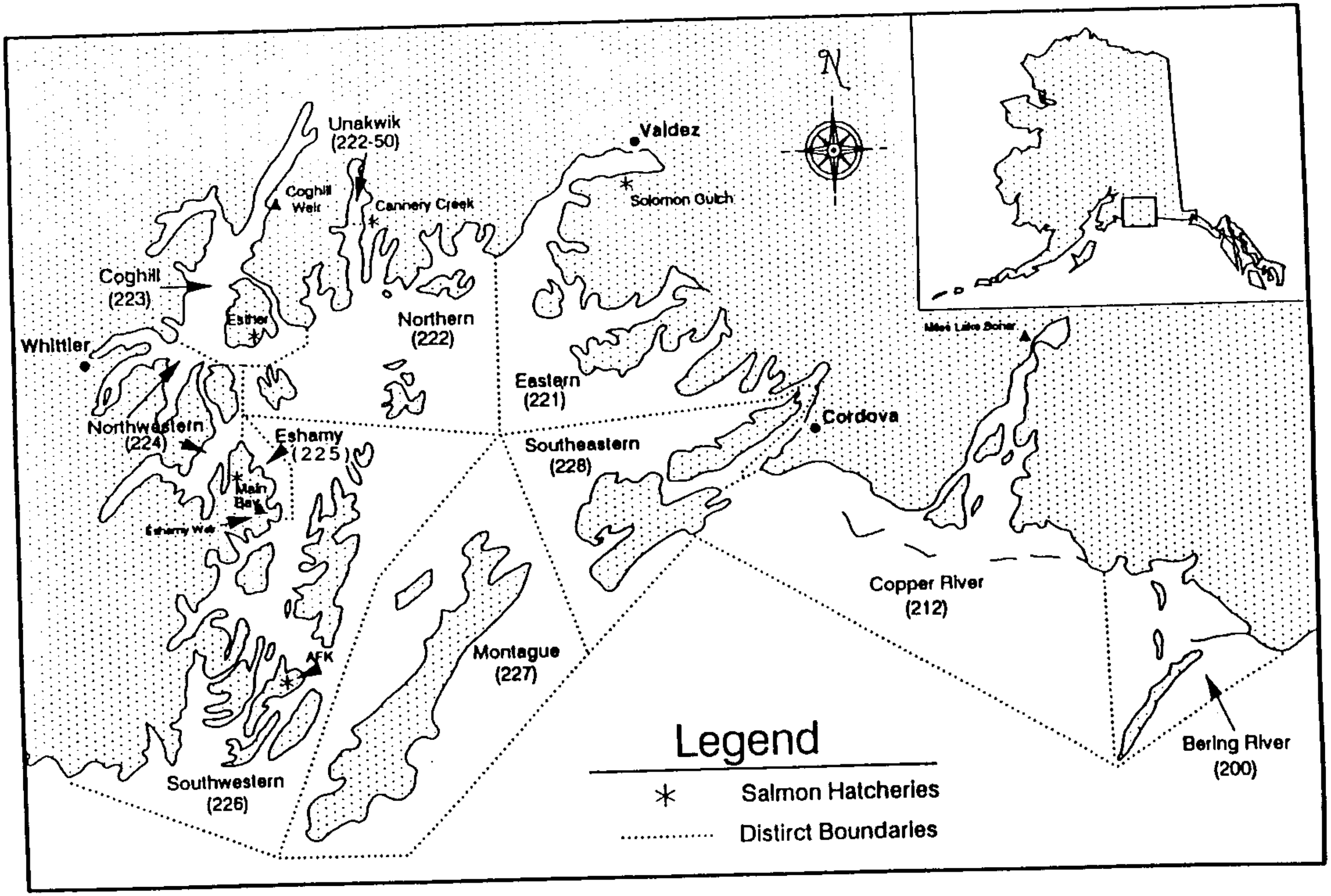

Figure 1. Map of Prince William Sound showing commercial fishing districts and hatchery locations.

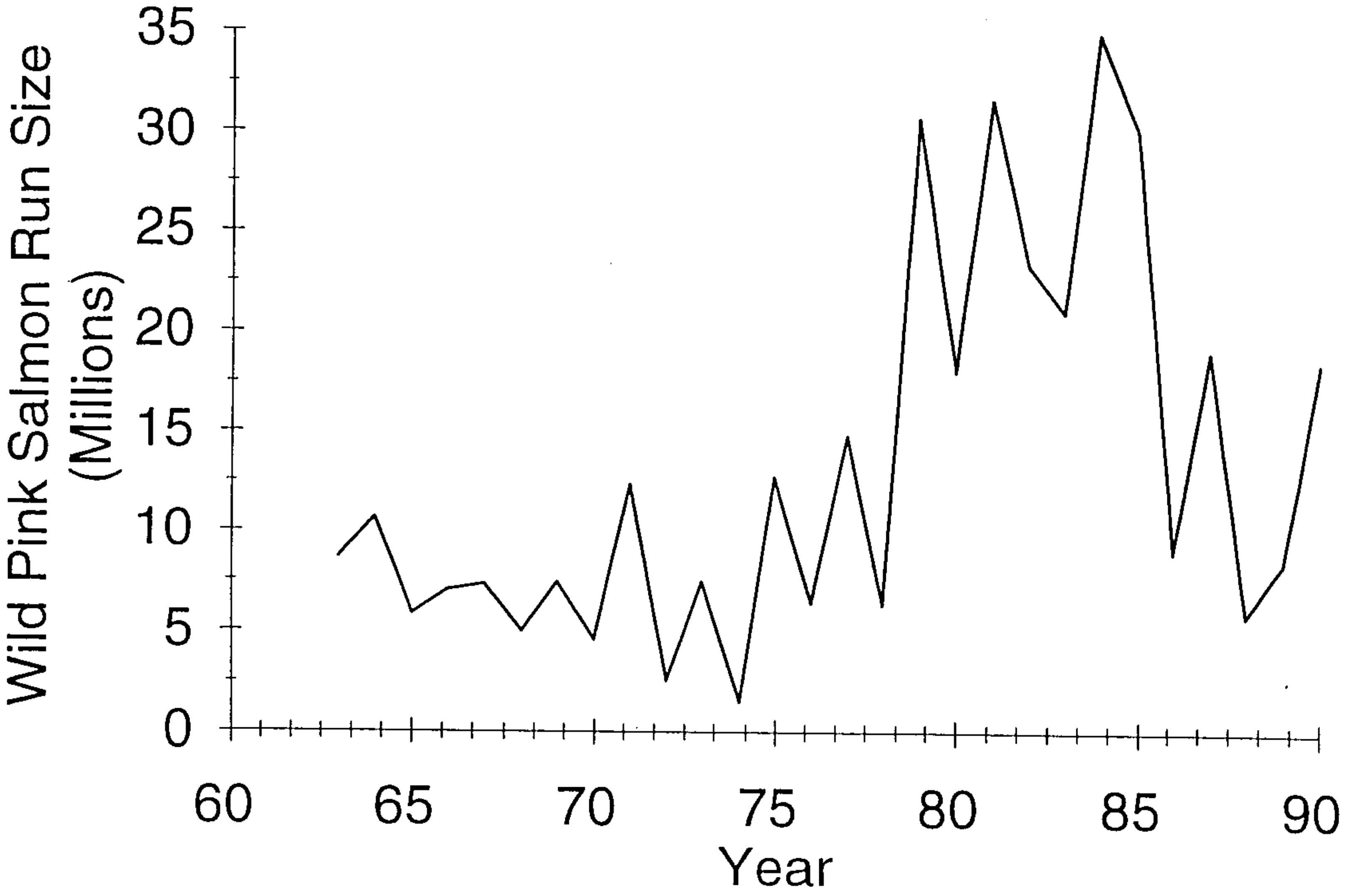

Figure 2. The size of Prince William Sound wild pink salmon runs from 1963 to 1990.

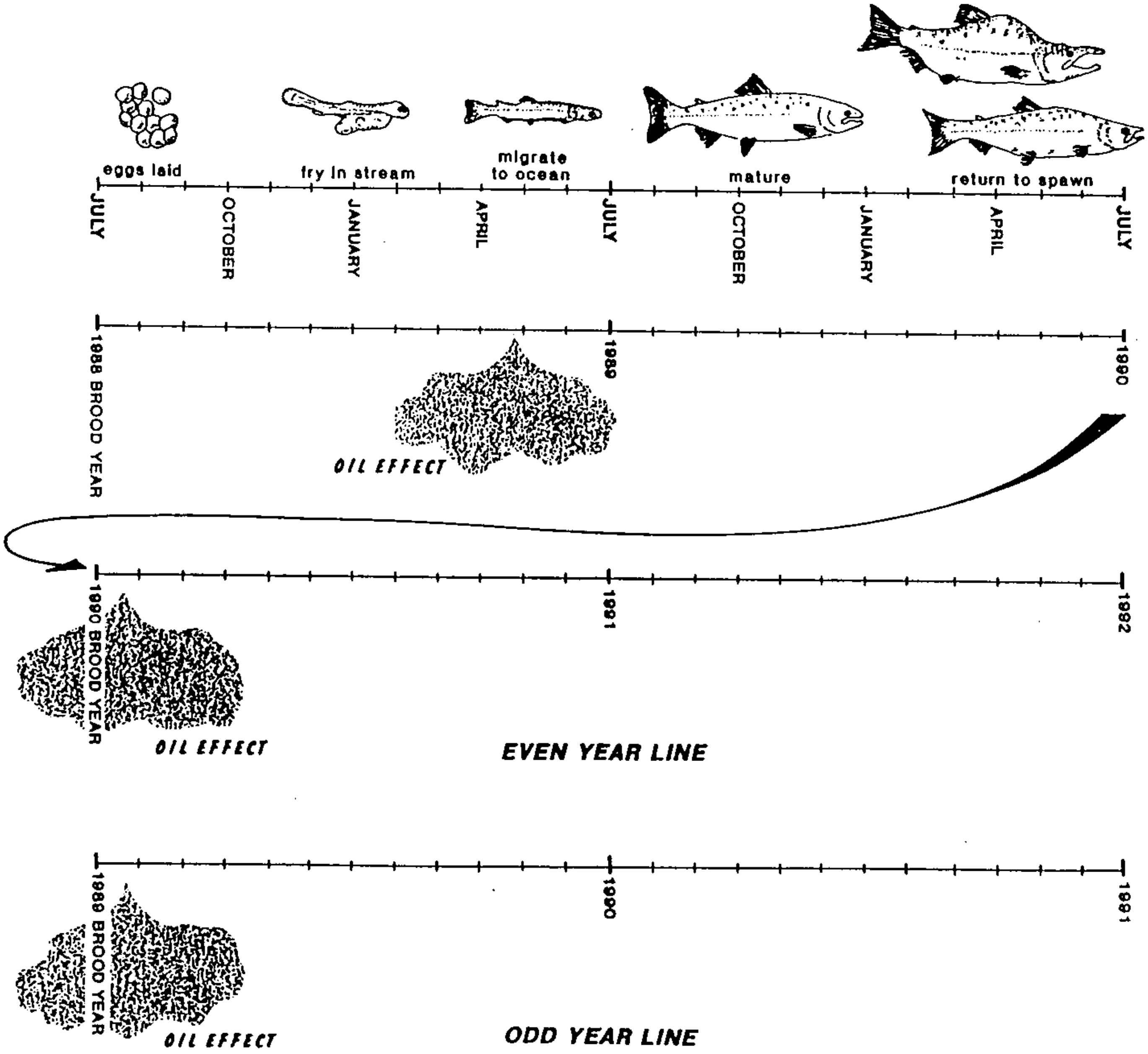

Figure 3. Pink salmon life-history stages. Detectable effects in the odd and even-year lines shown by dark blotchs.

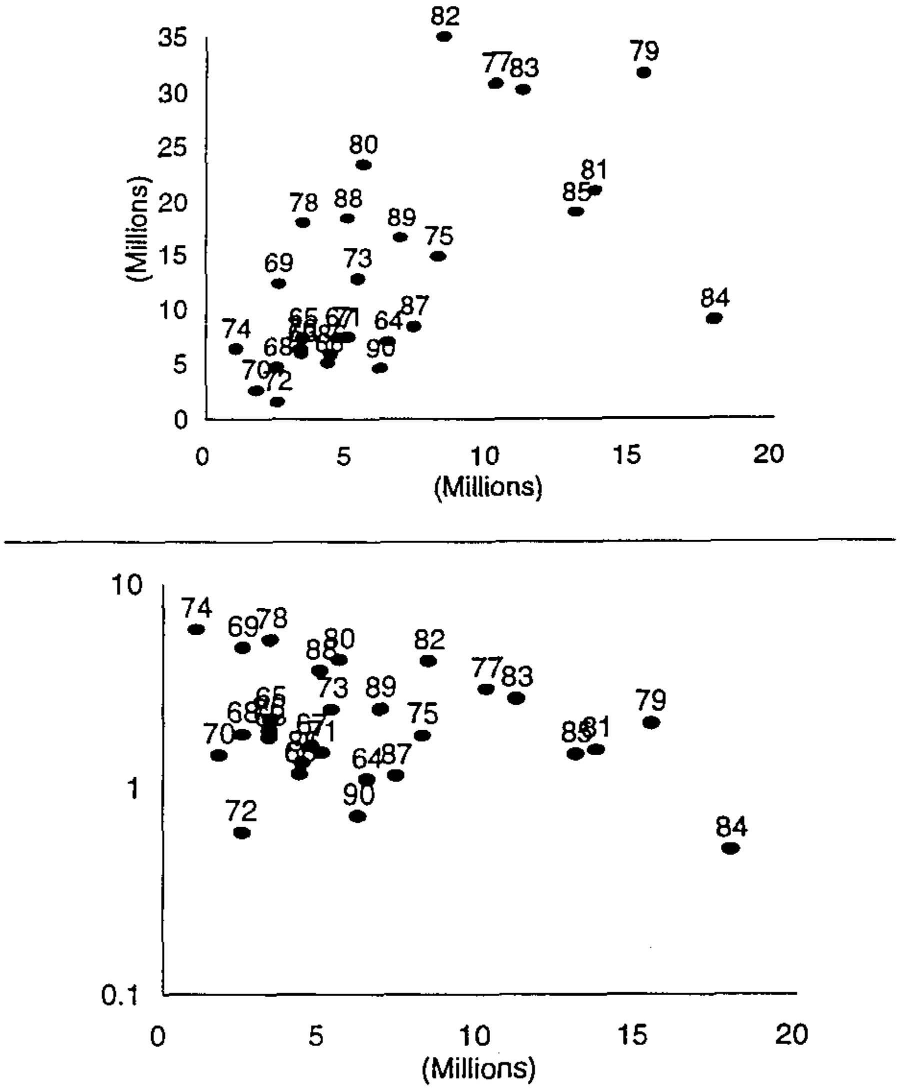

Figure 4. Stock-recruitment history for Prince William Sound pink salmon. The numbers denote the brood year. The top graph shows the total return as a function of parential escapement. The bottom graphic shows the ratio of returns-to-spawners on a log scale as a function of parential escapement.

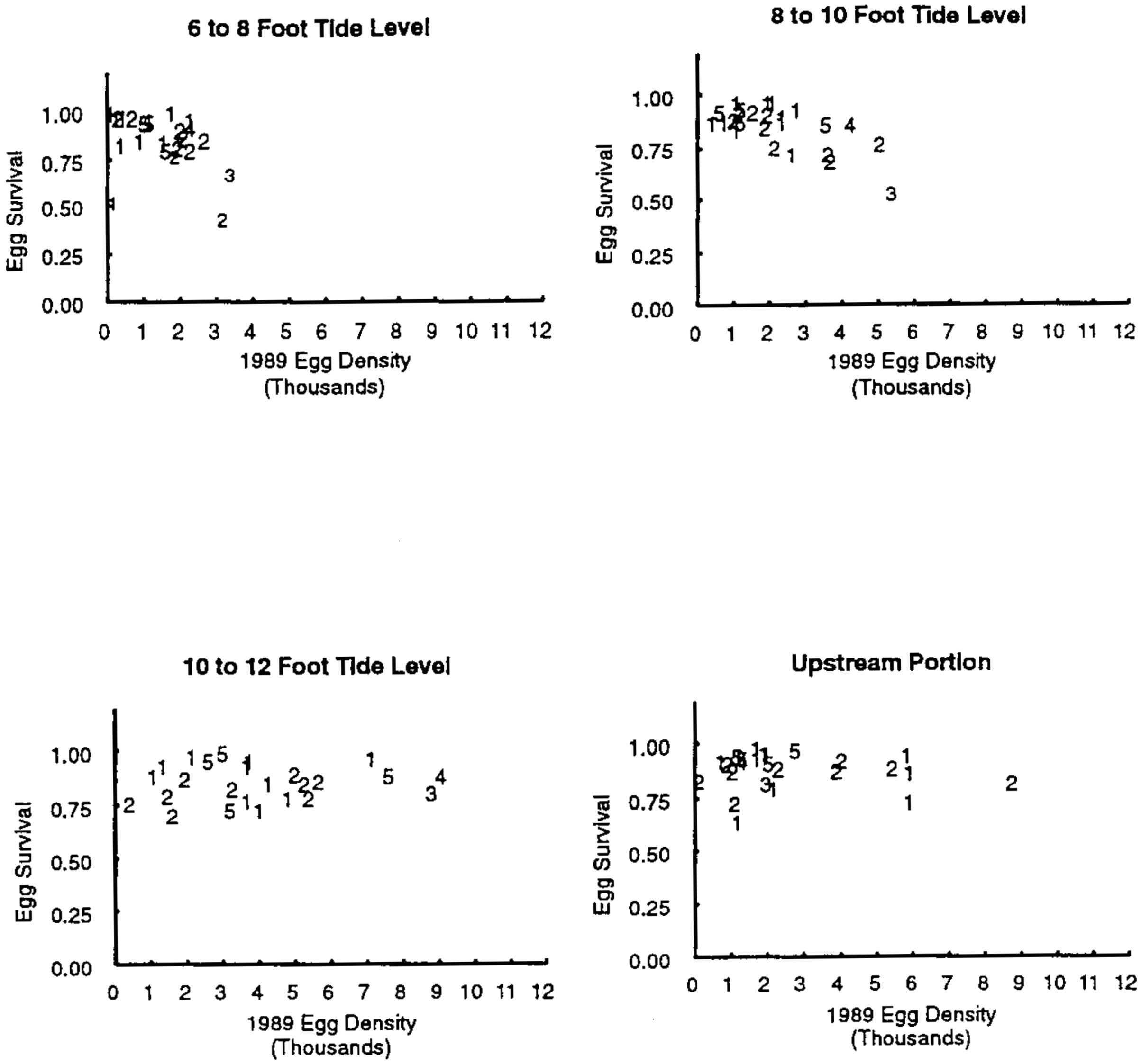

Figure 5a. Observed egg-stage survival as a function of egg density in 1989, by tide stage. The points are shown by the number 1 through 5. These numbers denote the oiling category of this egg dig. The codes are 1 for unoiled, 2 for oiled, 3 through 5 denote streams with some question about their oiling level.

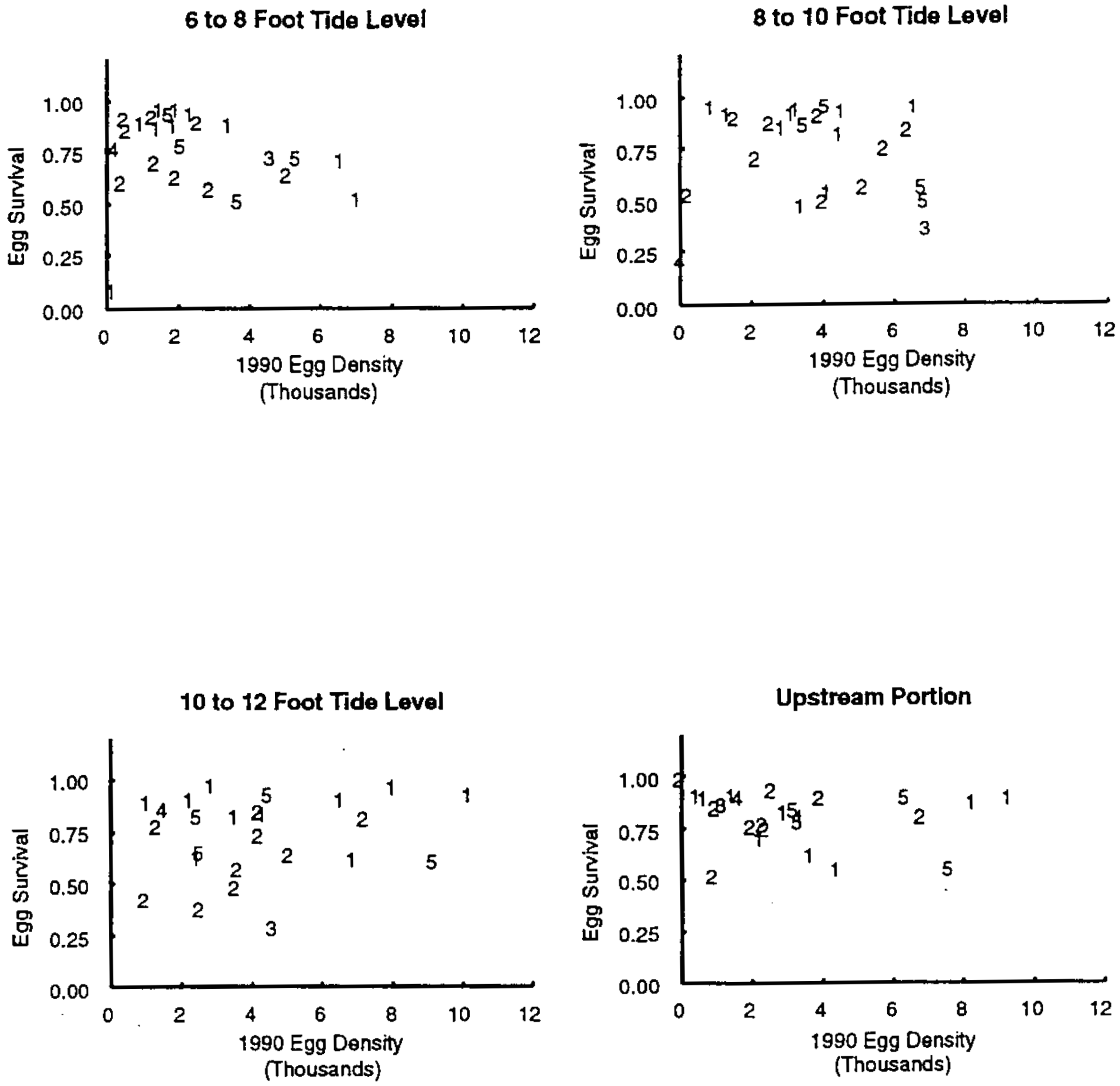

Figure 5b. Observed egg-stage survival as a function of egg density in 1990, by tide stage. The points are shown by the number 1 through 5. These numbers denote the oiling category of this egg dig. The codes are 1 for unoiled, 2 for oiled, 3 through 5 denote streams with some question about their oiling level.

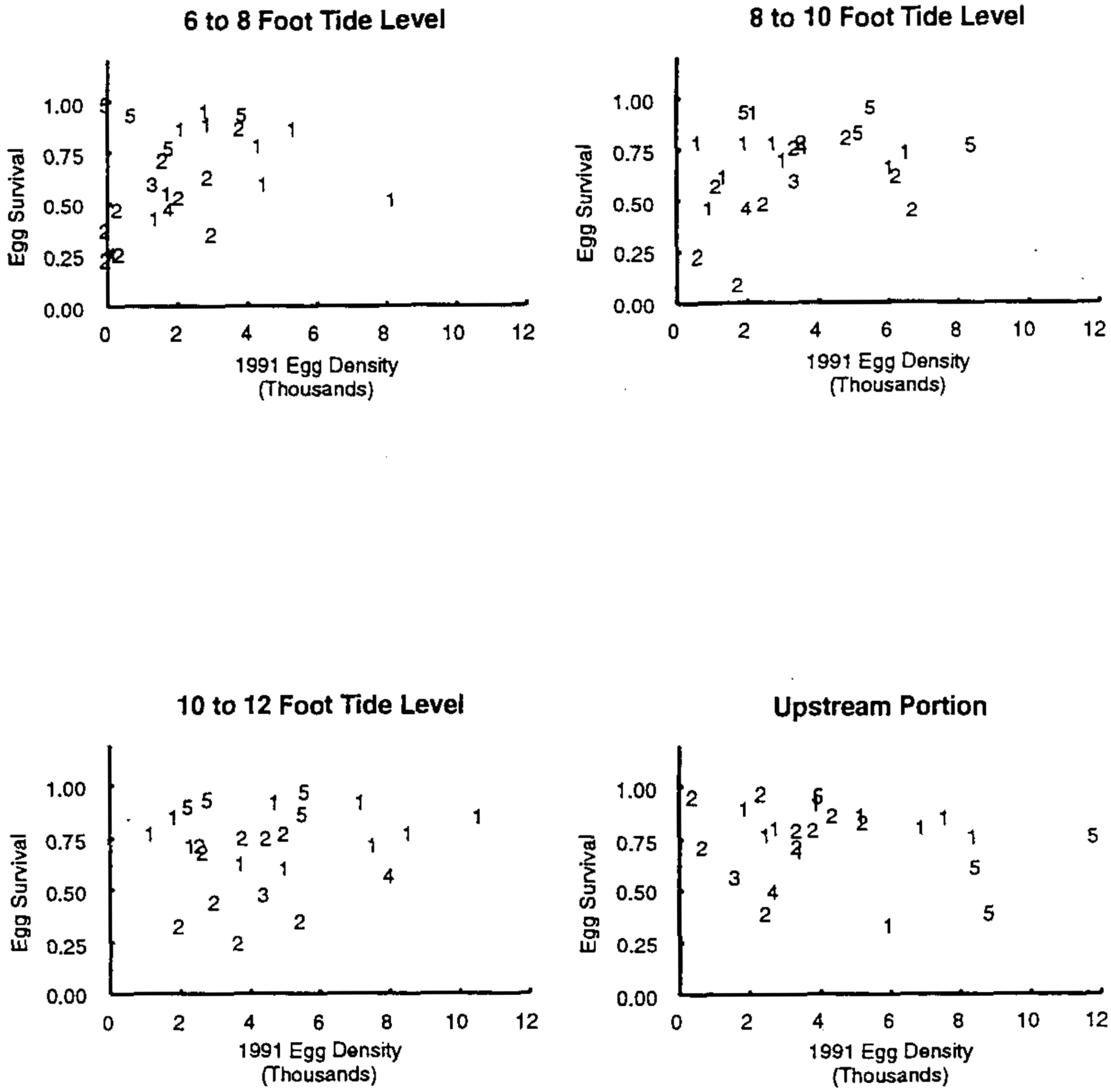

Figure 5c. Observed egg-stage survival as a function of egg density in 1991, by tide stage. The points are shown by the number 1 through 5. These numbers denote the oiling category of this egg dig. The codes are 1 for unoiled, 2 for oiled, 3 through 5 denote streams with some question about their oiling level.

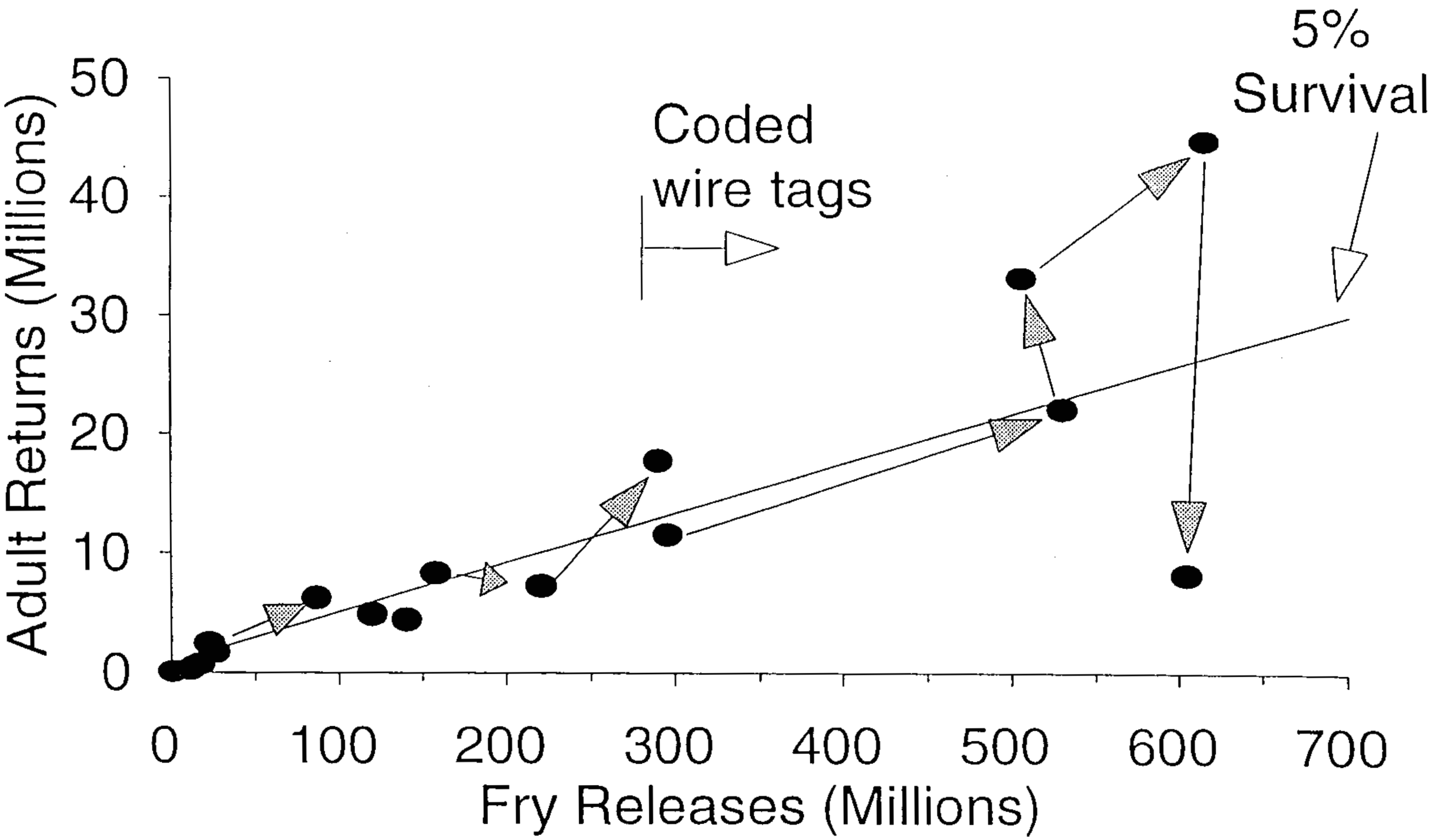

Figure 6. Production of pink salmon from Prince William Sound hatcheries as a function of fry released. Arrows show the time sequence . Coded wire tags were used to estimate survival from 1987 to the present for most hatchery releases.

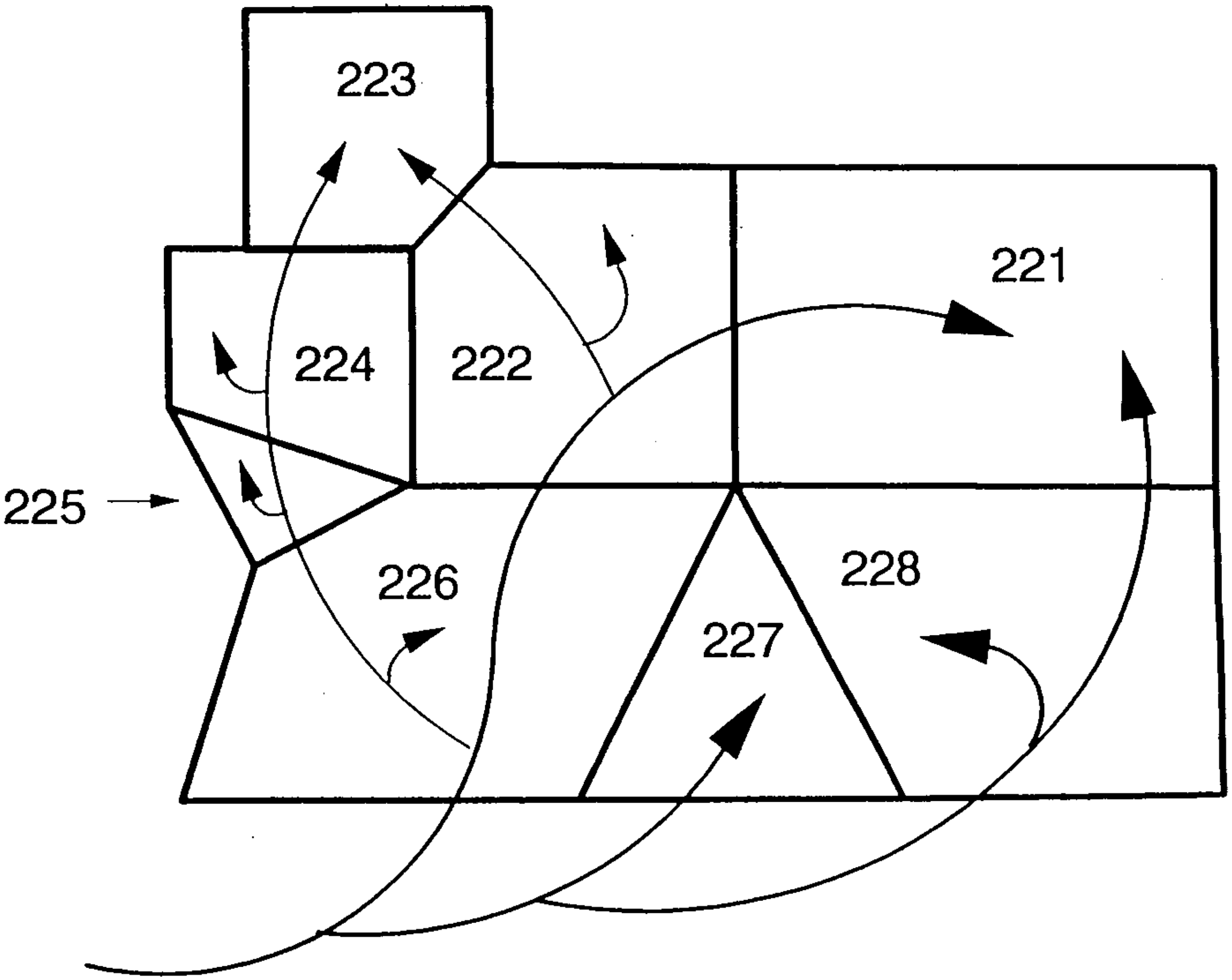

Figure 7. Assumed migration pathways between districts.

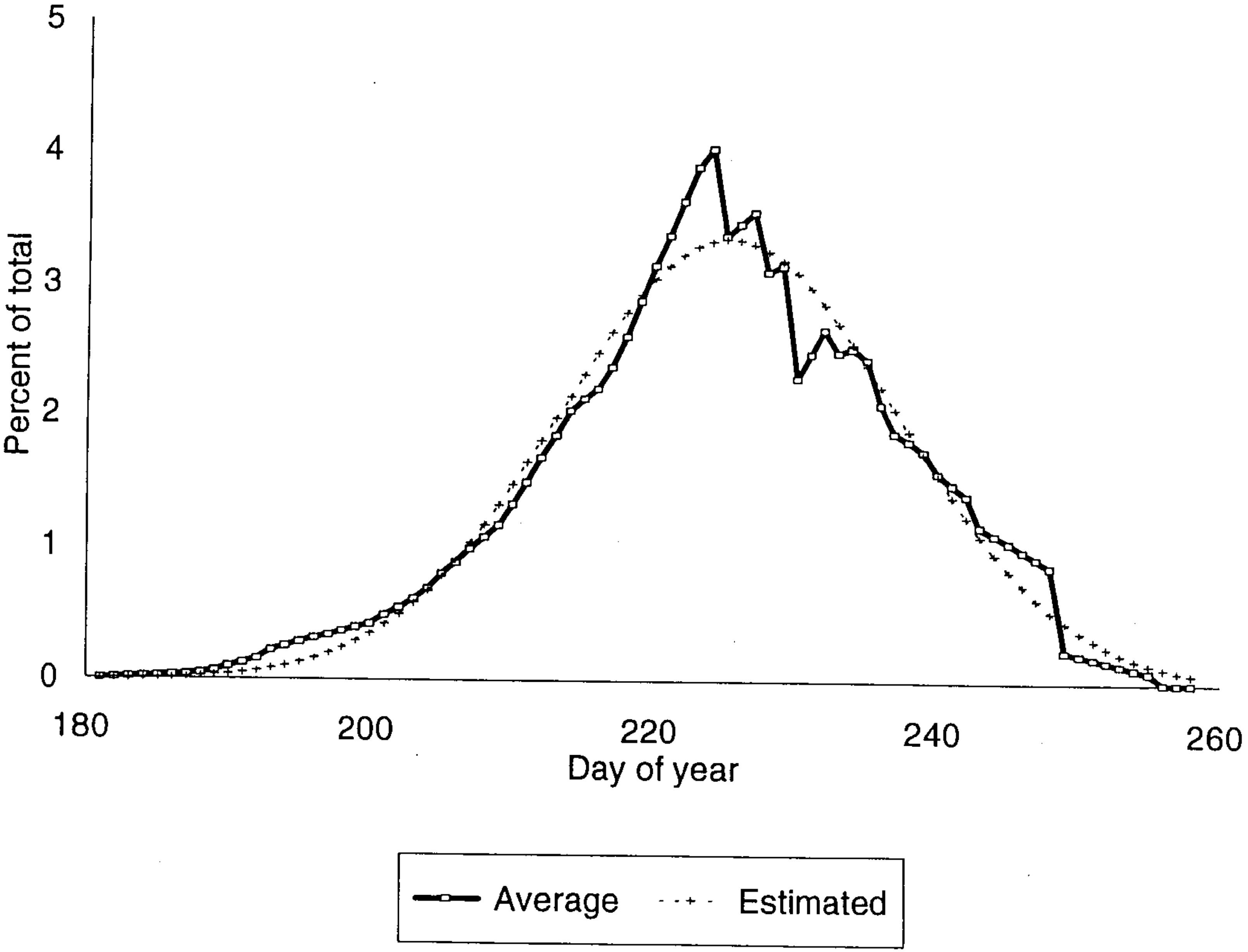

Figure 8. The estimated distribution of the daily percent of total fish-days in the stream, and the observed daily percent of total fish-days in the stream, for the Northwestern district (224) in 1989.

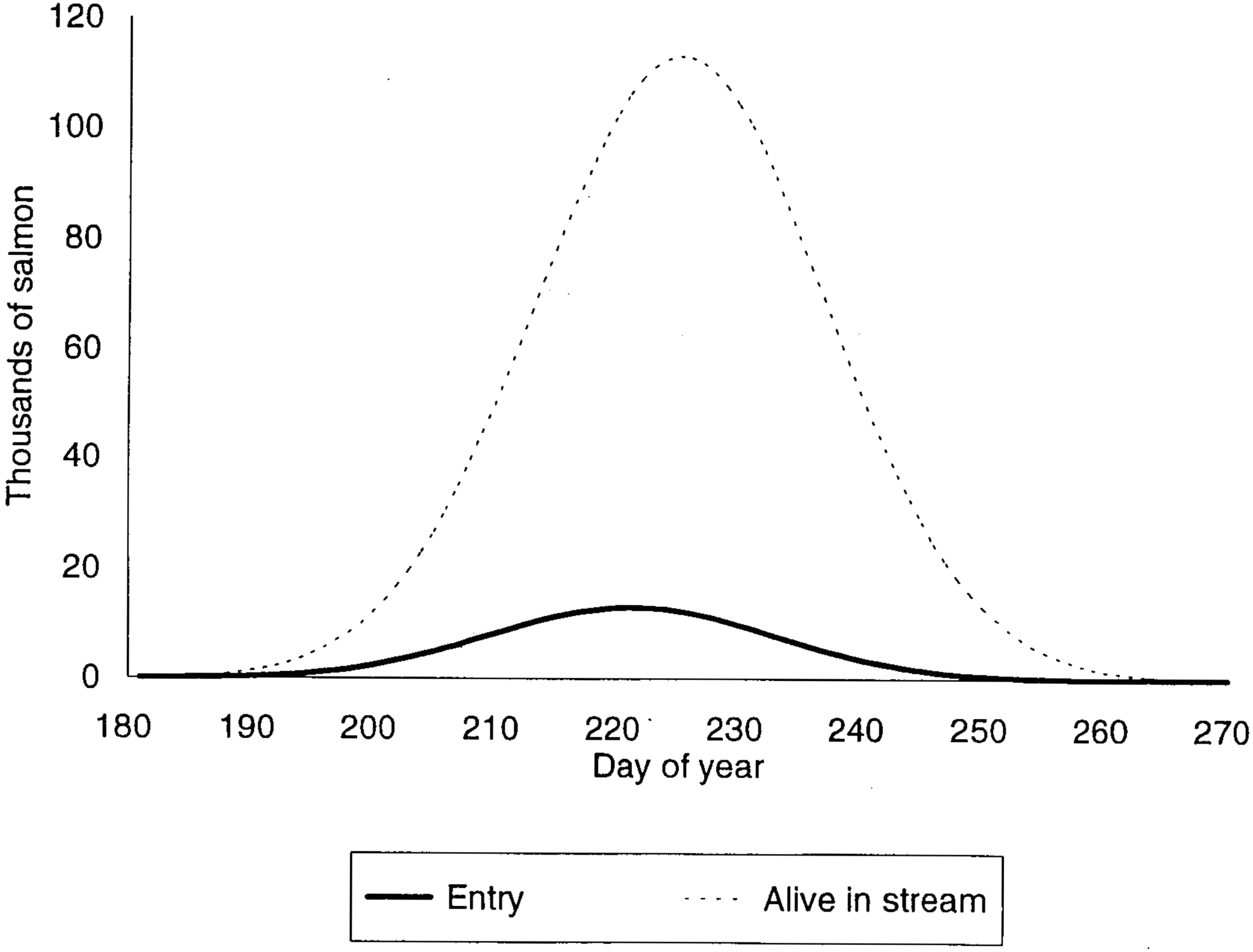

Figure 9. The daily entry of fish to the streams and the resulting number of fish that may be observed in the streams for the Northwestern district (224) in 1989.

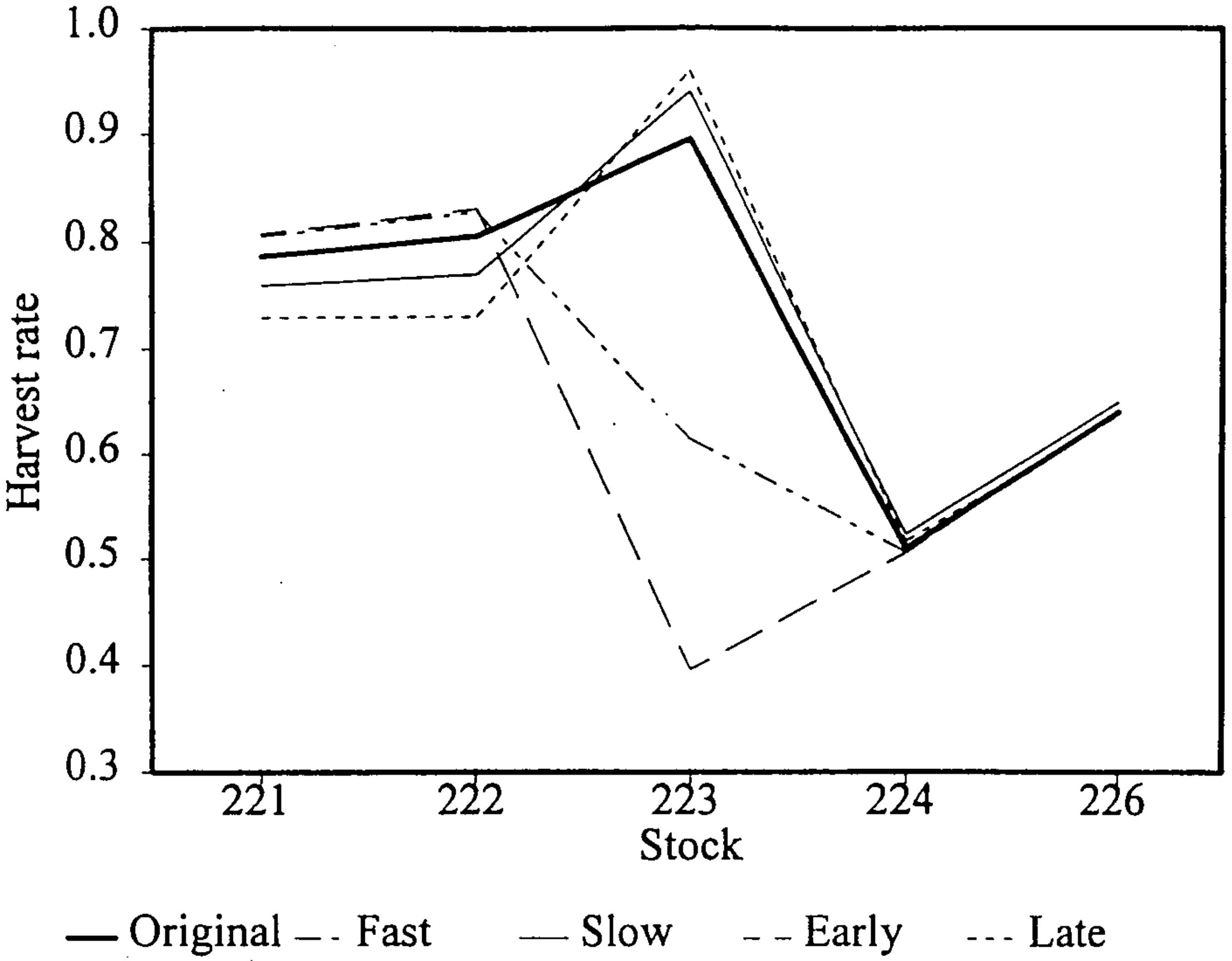

Figure 10. Calculated harvest rates from a sensitivity analysis of migration speed and run timing for stock 223. The reconstruction program was run the escapement timing of stock 223 shifted ten days earlier (denoted Early) and later (denoted Late) to shift its temporal distribution within each of the fisheries it traverses. The transition rates of stock 223 were changed to affect an individual fish's vulnerability by changing its rate of travel. The original transition rates for stock 223 were doubled (Fast), then halved (Slow).

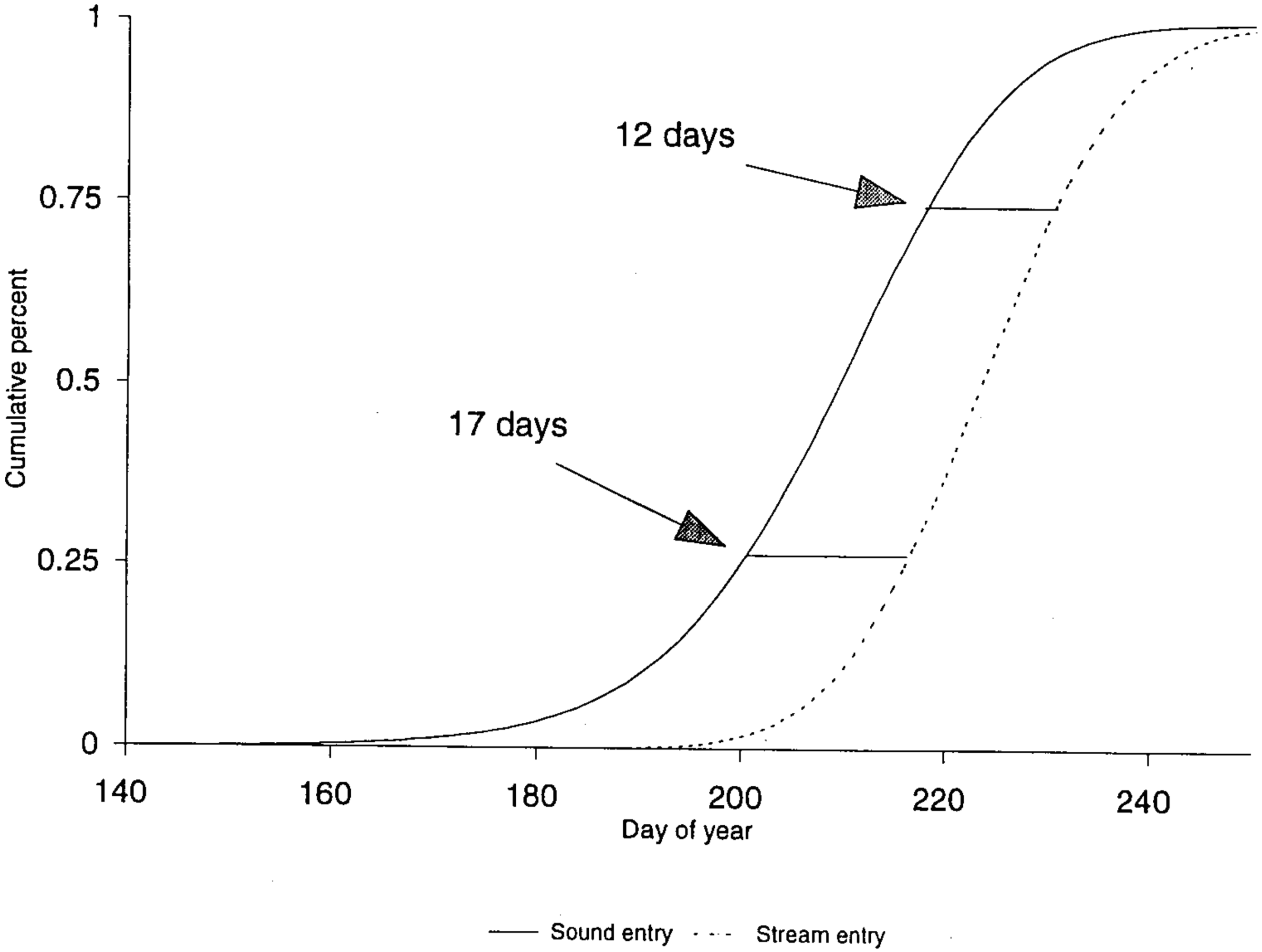

Figure 11. Cumulative entry into the fishery and cumulative entry into the escapement for district 227.