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Catch-Age Analysis Of Prince William Sound, Alaska, Herring, 1973-1988

By

Fritz C. Funk and Gene J. Sandone

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Alaska Department of Fish and Game

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ABSTRACT

A modified form of catch-age analysis, which used limited observations of absolute abundance as auxiliary information, was applied to Prince William Sound herring (*Clupea harengus pallasi*). Catch-at-age data were from the 1973-88 purse seine and gill net sac roe fisheries in Prince William Sound. Estimates of spawning biomass from spawn deposition surveys conducted in 1984 and 1988 were used as auxiliary information. The catch-age analysis model estimated exploitation rates for each gear by year, gear selectivity coefficients by age and gear, partial recruitment coefficients for age-3 and age-4 herring, initial age-3 cohort sizes in each year, and the size of cohorts of all ages in 1973. From these estimates and the results of age-weight sampling, estimates of population size and spawning biomass were constructed. Spawning biomass estimates averaged almost double the peak biomass estimates from aerial surveys. Exploitation rates ranged from 25%-35% from 1972 to 1977 and averaged 12% from 1979 to 1988. Maximum gear selectivity for purse seine gear was reached about age 6, whereas gill net gear had a much more restricted dome shaped selectivity with a maximum at age 8. Over the 1973-88 period, 78% of the age-3 herring were estimated to be recruited and present on the fishing and spawning grounds. Almost all age-4 herring were estimated to be fully recruited. Based upon the range of literature estimates of natural mortality, a survival rate of 64% was used for the catch-age analysis estimates. Lower survival rates changed the biomass estimates very little but dramatically increased initial cohort sizes. Higher survival rates had the opposite effect. Based upon recruit year class strengths observed from 1973 through 1988, a strong year class of at least 300 million age-3 recruits would be expected about every 4 years on the average. No overall relationship between spawners and recruits was evident, although a positive density dependent trend was evident for recent data (1979-85 year classes). We suggest that the catch-age analysis should be updated each year and that the analysis should incorporate the latest year's stock assessment information. In addition to generating biomass estimates for the current year, this process would update the estimates of biomass for prior years. The model's estimates of partial recruitment coefficients would then be used to project the age 4 to age 9+ biomass that should return the following year. The model's estimates of average age-3 recruitment over time could be used to set a range of possible age-3 recruitment scenarios for the upcoming year.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

INTRODUCTION

Spawning biomass estimates of Pacific herring *(Clupea harengus pallasi)* stocks in Prince William Sound have provided the basis for managing the Prince William Sound sac roe fishery since its inception in 1973. Through 1987, aerial surveys were the primary means of estimating biomass. Beginning in 1988 spawn deposition surveys (Biggs and Funk 1988) became the primary means of estimating the spawning biomass on which commercial fishery harvests were based. Because a long time series of herring catch-at-age observations is available for Prince William Sound herring, we believed that catch-age analysis methods could also be used to reliably estimate spawning biomass. We compared biomass estimates from our catch-age analysis model to the historical time series of aerial survey biomass estimates. The catch-age analysis model that we used is a modified form of Doubleday's (1976) separable fishing mortality model that we extended, using methods similar to those of Deriso et al. (1985), to incorporate biomass estimates from spawn deposition surveys as auxiliary information.

Catch-age, or cohort, analysis techniques are relied upon as a primary stock assessment tool for herring populations in British Columbia (Schwiegert and Hourston 1980; Haist et al. 1985, 1986), the Northwest Atlantic (Sinclair et al. 1985), and the Northeast Atlantic (Jakobsson 1985). Other than a preliminary cohort analysis of combined Bering Sea stocks (Wespestad 1982), this is the first application of catch-age analysis techniques to Alaska herring populations.

Early forms of cohort analysis (Gulland 1965; Pope 1972) solved survival and catch equations in a backwards sequential fashion. Starting from the oldest age of the cohort, they computed unique fishing mortality rates for each age and year. The size of the cohort at the oldest age, as well as the size of each cohort at each age in the last year of the cohort analysis, had to be specified as an initial condition.

Doubleday (1976) separated fishing mortality into a year-specific exploitation rate and an age-specific gear selectivity coefficient. Cast in this form, the survival and catch equations contained far fewer parameters, enabling parameter estimation by least squares methods. Initial conditions were specified only as arbitrary starting points for the iterative parameter estimation procedure. Providing that the least squares estimation procedure converges to a unique solution, the initial conditions do not affect the final solution. Doubleday's (1976) approach was generalized by Fournier and Archibald (1982), Deriso et al. (1985) and others to include a range of assumptions about stochastic elements of the catch-age information and to incorporate auxiliary information in addition to the time series of catch-at-age.

Deriso et al. (1985) described the need to fit catch-age analysis models to other information in addition to catch-at-age data to stabilize parameter estimates. They described a potentially serious negative correlation between estimates of exploitation rates and population sizes when only catch-age data are used. Deriso et al. (1985) and Fournier and Archibald (1982) both used catch per unit of effort (CPUE) indices to stabilize catch-age parameter estimates. Spawn deposition surveys performed in Prince William Sound in 1984 and 1988 were believed to be reliable estimates of spawning

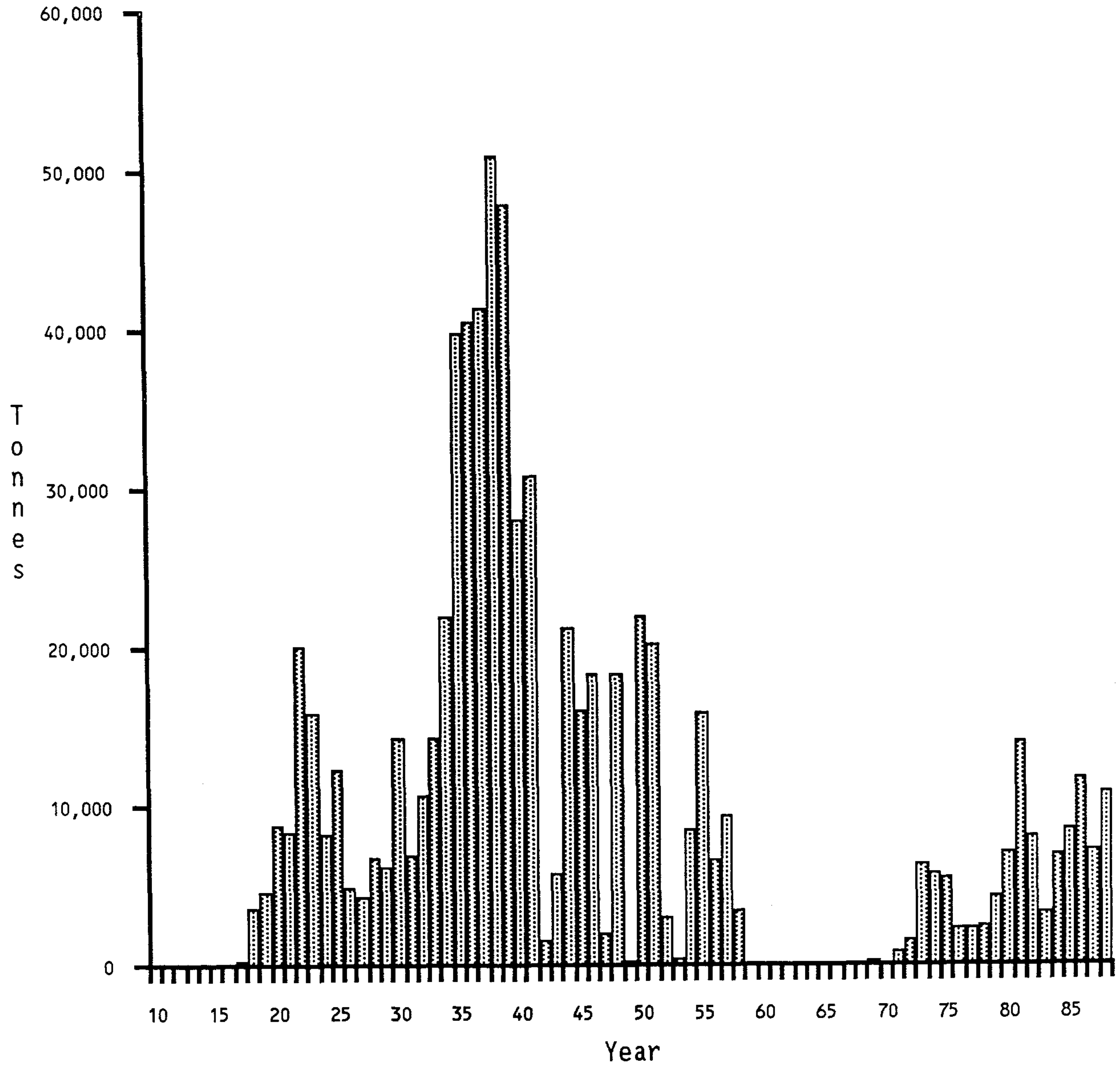

Figure 1. Prince William Sound commercial herring harvests, 1914 through 1988.

biomass. Our approach was to treat the two spawn deposition survey biomasses as estimates of absolute abundance which contained measurement error. We then used these abundance estimates as auxiliary information to stabilize catch-age analysis parameter estimates. We hoped that this method for addressing the measurement error of the annual spawn deposition surveys would result in improved annual estimates of population biomass.

Prince William Sound Commercial Herring Fisheries

Commercial exploitation of herring in Prince William Sound began in 1914, with the peak harvest of 50,948 tonnes occurring in 1938 (Figure 1). Before 1960 the catch was processed primarily by reduction plants producing oil and meal products. The reason for the large fluctuations in harvest just after 1950 and the termination of production in 1959 is not explained in historical records of the fishery. It is suspected that a combination of low production and unfavorable market conditions was the reason for the closure of the reduction plants after the 1959 season (ADF&G 1973). It is possible that catches recorded for early herring fisheries in Prince William Sound include harvests of stocks spawning in other locations because the early herring harvests did not occur on spawning populations and the location of the harvests was not always precisely known. Only small quantities of herring were harvested, primarily for bait, between 1960 and 1972.

After market conditions for herring roe improved in 1973, the herring sac roe fisheries developed rapidly, with harvests ranging between 2,000 and 12,000 tonnes. The purse seine sac roe fishery harvests the largest share of the total herring catch, followed by the food/bait fishery which employs purse seine and occasionally trawl gears and the sac roe gill net fishery (Figure 2). A substantial herring pound fishery has also developed in Prince William Sound in recent years. Herring pound fisheries use purse seines to collect ripe herring which are released to spawn in net enclosures containing harvested brown algae (primarily *Macrocystis sp.*). Although the herring are released from the pounds after spawning, mortality is thought to be high. The pound fishery harvests shown in Figure 2 are the lower range of the harvests given by Brady and CCFS (1988). Because of the uncertainty about the magnitude of the pound fishery mortality, pound harvests were not used for the catch-age analysis.

The Prince William Sound Management Area is divided into four management districts: Northern, Montague, Eastern and General (Figure 3). Purse seine harvests have come primarily from the Northern and Montague Districts, while gill net and pound harvests have primarily been from the Northern District. The food/bait fishery has harvested herring during the fall and winter months, primarily from Orca Bay, near Cordova, in the General Management District.

Prince William Sound Herring Stock Definition

Prince William Sound herring are assumed to be a closed population; i.e., losses from the population occur only from natural mortality and fishing. Under this assumption, if in a given year there was migration that resulted in a net emigration, it would upwardly bias estimates of natural mortality rates; conversely, a net immigration would appear as incomplete recruitment.

Geographical barriers isolate Prince William Sound herring from other spawning

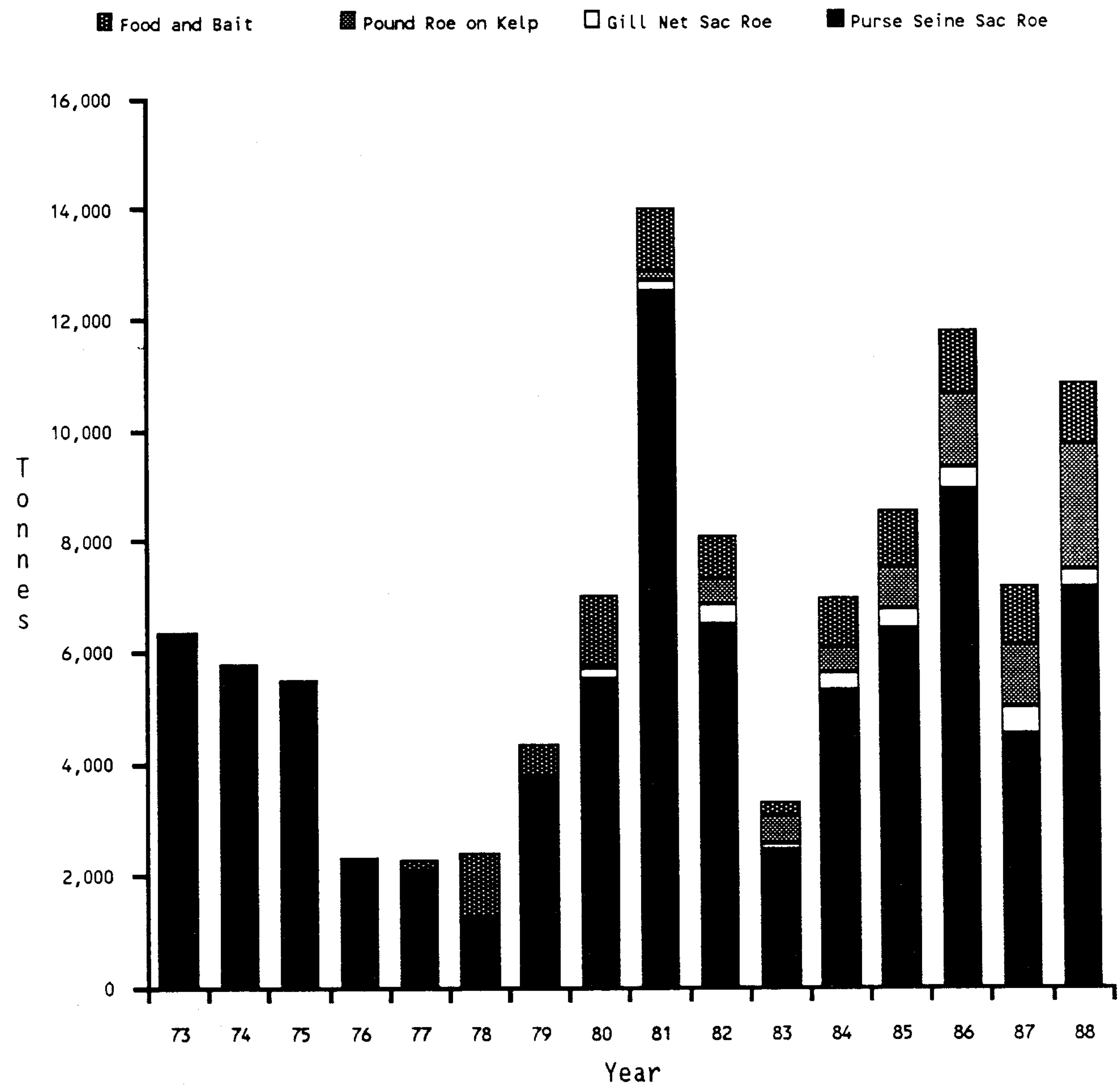

Figure 2. Recent Prince William Sound commercial herring harvests by gear, 1973 through 1988.

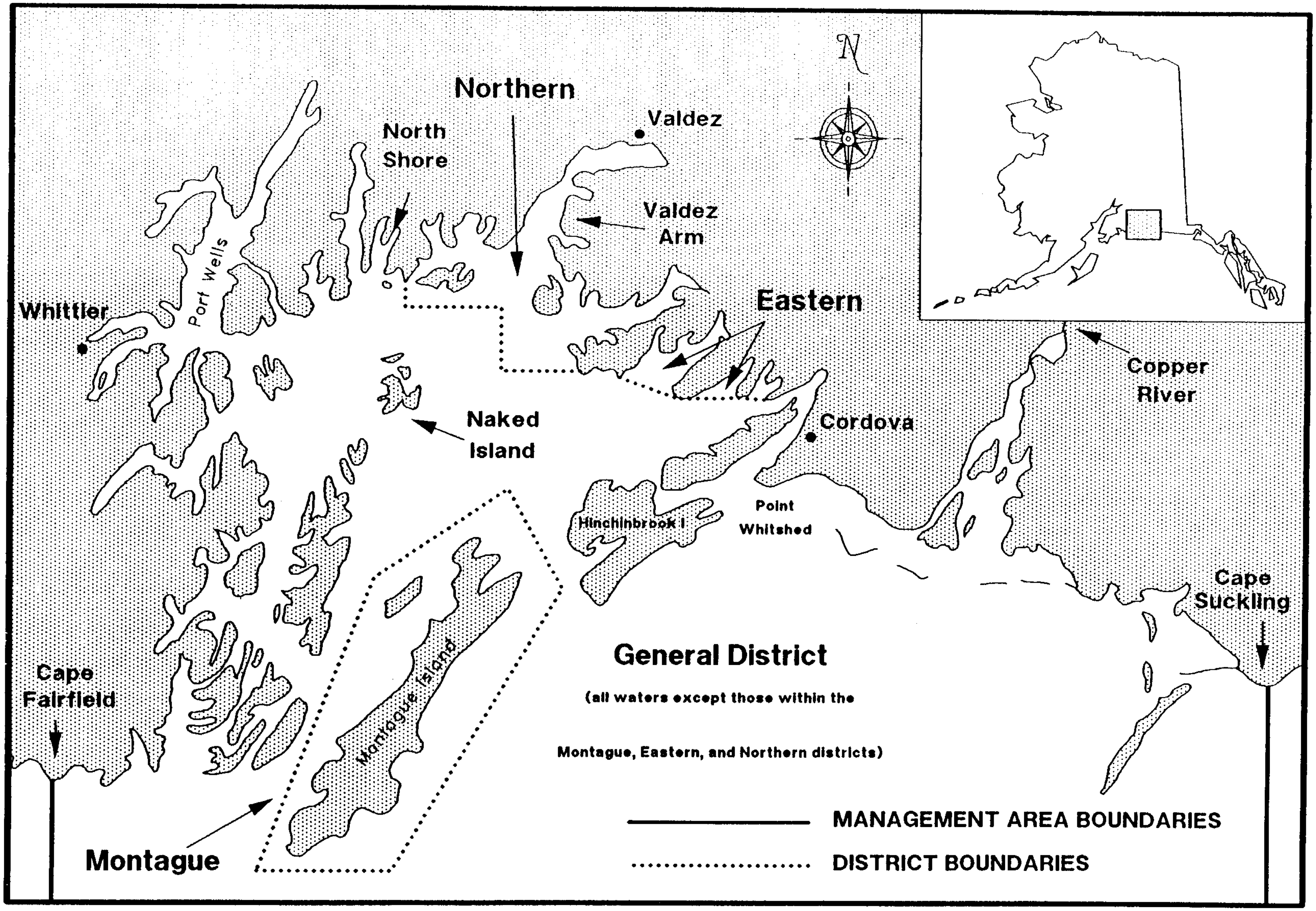

Figure 3. Herring management districts within the Prince William Sound management area.

populations (Figure 3). To the east the large expanse of exposed beaches extending for 300 km to Yakutat Bay contain little or no vegetation suitable as a herring spawning substrate. However, a small herring population is reported to spawn near Kayak Island, 100 km east of Prince William Sound and is assumed to be distinct from the Prince William Sound stock. To the west very little herring spawning is reported from the semi-exposed bays and passages of Blying Sound. Relatively small numbers of herring spawn in Resurrection Bay, about 80 km west of Prince William Sound, and in other bays along the outer Kenai Peninsula. The nearest large herring population spawns in Kamishak Bay in Cook Inlet, over 300 km west of Prince William Sound. Burkey (1986) compared Prince William Sound herring age composition, growth, and electrophoretic results with similar information from other locations in the Gulf of Alaska and concluded that detectable differences existed between Prince William Sound herring stocks and those outside Prince William Sound. Based on his findings and the geographic considerations, the straying rates of herring returning to the Prince William Sound spawning grounds are believed low enough to permit the assumption that herring spawning within Prince William Sound represent a closed population.

The geographical population structure of herring spawning within Prince William Sound is less clear. Herring spawning has usually occurred in four primary areas over the 1973-88 period: Valdez Arm, North Shore, Naked Island, and Montague Island (Figure 3). During the 1970s Montague Island was the largest herring spawning area. During the early 1980s, the North Shore area became the largest herring spawning grounds, coincident with the maturation of the large 1977-78 year classes. Whether this represented a large scale straying of these year classes from their natal spawning grounds or more successful recruitment of cohorts which had spawned in the North Shore area is not known.

Using only electrophoresis, Grant and Utter (1984) found it difficult to detect genetic differences among adjacent herring populations in the Gulf of Alaska; Prince William Sound was not included in their study. Using both electrophoresis and scale pattern analysis, Burkey (1986) found no differences among herring spawning at different locations within Prince William Sound. Even very low straying rates would preclude the separation of adjacent herring populations using genetic methods (Grant and Utter 1984; Smith and Jamieson 1986). Straying rates ranging from 6% to 33% have been found in British Columbia on a spatial scale comparable to Prince William Sound (Hourston 1982).

Recent (1984-87) samples of herring from the food/bait fishery, which occurs in the fall in southeastern Prince William Sound, show a significantly different length-at-age compared to herring collected during the spring sac roe fisheries (Sandone et al. 1988). However, Burkey's (1986) earlier study did not detect differences in length-at-age among herring sampled from food/bait and sac roe fisheries from 1979 through 1981. Because of the uncertainty over the stock composition of the food/bait fishery harvests, the food/bait harvests are not included in the catch data used for catch-age analysis. This should be a conservative approach and would pool food/bait fishery harvests with natural mortality if food/bait fishery harvests do indeed come from the same population. Bait fishery harvests have averaged only 12% of the sac roe harvest over the 1973-88 period. Other than this exception, herring spawning within the geographic boundaries of Prince William Sound from 1973 to 1988 were assumed to be a single closed population for the catch-age analysis.

METHODS

Data Sources

Data sources involved a variety of fisheries and covered different time frames. Collection methods varied accordingly.

Age Distribution of the Commercial Harvest

Samples of Pacific herring were collected for age-composition analysis from each sac roe purse seine and gill net fishery opening in each management district from 1973 through 1988. Approximately 300 fish per opening were collected for each gear type from 1973 through 1984, and approximately 600 fish per opening were collected for each gear type from 1985 through 1988 (Appendix A). Data collected from these samples included the sex, standard length (mm), round weight (g), and age of individual specimens. Ages were determined from scales read under magnification on micro-fiche readers. Descriptions of sample collection methods, and data summaries of age, sex, and size are given by Sandone (1988). Based on these commercial catch samples, the number of herring harvested in each Prince William Sound Management District by each gear type was reported by Sandone (1988) for 1973 through 1987, and by Brannian (1989) for 1988. The numbers of herring harvested in each area were summed to estimate the number of herring harvested by purse seines (Appendix B), and gill nets (Appendix C) from 1973 through 1988. All fish aged 9 and older were pooled into a single "9+" age category. Fournier and Archibald (1982) recommend pooling older age classes for catch-age analysis when confronted with ageing uncertainty.

Weight-at-Age

Weight-at-age data were needed to convert numbers at age to biomass units during catch-age analysis. Funk and Sandone (1989) compiled weight-at-age summary tables for Prince William Sound herring utilizing commercial catch and test fishing samples (Appendix D). Samples from the commercial pound fishery were excluded because specimens obtained in pound fishery samples often had partially spawned. Specimens obtained from purse seine and gill net gear were usually in a reproductive "ripe" condition but had not yet spawned. Biomass estimates from this study, therefore, refer to the weight of the population just before spawning.

The weight-at-age for the "9+" category was estimated by using the individual weights at ages 9 to 13 weighted by the age distribution of the purse seine harvest in each year. No weight-at-age data was available for several of the older age categories in some years. Average weight-at-age over the 1973-88 period was used for those years and ages.

Aerial Surveys

Brady (1987) describes Prince William Sound herring aerial survey methodology and gives the aerial survey biomass estimates for the 1974-87 period. Aerial surveys were flown throughout the spawning season in all fishing districts to determine distribution, movement patterns, relative abundance and extent of spawning. During aerial surveys observers estimated the surface area and number of herring schools. Herring school surface areas were then converted to biomass units based on a limited set of observations where individual fish schools were captured by purse seine vessels after school surface areas were estimated. Because herring arrive on the spawning grounds over a period of several weeks and often remain on the spawning grounds for several days, the biomass observed on successive days of aerial surveys is not strictly additive. Herring present during the initial phase of a spawning episode were assumed to remain on the spawning grounds until the time that the maximum or "peak" biomass estimate was made. In addition, it was assumed that no new herring arrived on the spawning grounds from the time that the peak spawning biomass estimate was made until the end of the spawning episode. In some cases, if more than one temporally distinct spawning episode occurred in an area, the peak counts of each spawning episode were summed to give the season's peak biomass for that area. These are clearly conservative assumptions so that the peak biomass estimate would be expected to underestimate the actual biomass.

Brady (1987) also proposed a relative abundance index based on the sum of the shoreline miles of milt observed on daily aerial surveys. This new "mile-day" index may compensate for the unknown residence time problem inherent in aerial survey biomass estimates based on school surface area observations. Peak annual aerial survey biomass and the miles of milt index from Brady (1987) and Brannian (1989) are given for 1974 through 1988 in Appendix E.

Spawn Deposition Surveys

Herring spawn deposition surveys provide another estimate of herring spawning biomass. Spawn deposition surveys rely on intertidal and subtidal quadrat sampling to estimate the number of herring eggs deposited on vegetation and other substrates. Using estimates of average fecundity, the biomass of spawning females required to deposit the eggs is calculated. The estimated sex ratio is then used to estimate the spawning biomass of males and females. Preliminary herring spawn deposition surveys were carried out in limited areas of Prince William Sound in 1983 (Jackson and Randall 1983) and were expanded to a large area of Prince William Sound in 1984 (Jackson and Randall 1984). Spawn deposition surveys were again used to estimate biomass in 1988 (Biggs and Funk, 1988). Spawn deposition survey estimates of the spawning biomass of Prince William Sound herring for 1984 and 1988 are given in Appendix E.

Fecundity

The relationship between fecundity and age was needed to explore the relationship between spawners and recruits for Prince William Sound. Because fecundity is size-related, the relationship between spawning biomass and the number of recruits produced is best expressed as the relationship between the number of eggs produced and the number of age-3 fish recruited three years later. Fecundity data collected during the 1984 and 1988 spawn deposition surveys reported by Jackson and Randall (1984) and Biggs and Funk (1988) were used to estimate the relationship between fecundity and age. Biggs and Funk (1988) found that the relationship between fecundity and weight was approximately linear. Because the von Bertalanffy model is usually used to describe the relationship between weight and age, we used

$$F_a = c1 \cdot [1 - e^{-K(a-a_0)}]^3 + c2 \qquad (1)$$

to describe the relationship between fecundity (F) and age (a), where $c1$ and $c2$ are constants to be estimated, and K and a_0 are von Bertalanffy coefficients to be estimated.

Nonlinear least squares methods were used to estimate $c1$, $c2$, K, and a_0.

Natural Mortality

Independent estimates of the rate of natural mortality are required for the catch-age analysis model. Direct estimates of natural mortality rates were not available for Prince William Sound herring. A range of likely natural mortality rates for Prince William Sound herring was established based on life history features and literature estimates of natural mortality rates for herring populations in other areas.

A number of methods for estimating the rate of natural mortality depend on estimating the oldest age fish in unfished populations. Herring older than age 13 are rare in Alaska populations, even in populations that have only recently received fishing pressure, such as those around Nelson and Nunivak Islands in the Bering Sea. Age 14 was assumed to be the maximum age of herring in Alaska.

Alverson and Carney (1975) noted for a wide range of fish populations that cohorts maximize their biomass at an age approximately one-fourth of the maximum observed age. Since the time at which cohort biomass is maximized is a function of growth and mortality, they suggested that natural mortality could be estimated by

$$M = \frac{3K}{e^{0.25(K)(T_{max})} - 1}, \qquad (2)$$

where M is the instantaneous rate of natural mortality, K is a coefficient from the von Bertalanffy growth model, and T_{max} is the maximum observed age. We used equation (2) with $K = 0.293$ from an analysis of the growth of Prince William Sound herring (Funk and Sandone 1989) and assumed 14 to be the maximum age.

Hoenig (1983) developed empirical relationships between maximum age and total mortality for various fish, cetacean and mollusk stocks. His regression model for 84 fish stocks was

$$\log_e(Z) = 1.945 - 1.225\,[\log_e(T_{max})], \qquad (3)$$

where Z is the instantaneous total mortality rate and T_{max} is the maximum observed age. We estimated a natural mortality rate for Prince William Sound herring using this equation and assumed age 14 was the appropriate maximum age for an unfished population.

Based on r-K selection theory, Gunderson (1980) investigated models relating natural mortality rates for a wide variety of fish species to body size, age at maturation, longevity, and energy devoted to gonadal development. He found that the ratio of gonadal weight to body weight of females explained a large amount of variation in natural mortality rates over a wide taxonomic range of fish species from northern temperate latitudes. Gunderson's (1980) regression for the prediction of natural mortality was

$$M = 4.64(GI) - 0.370, \qquad (4)$$

where GI is the ratio of gonadal weight to body weight of females. Surprisingly Gunderson (1980) noted that adding longevity to regression equation in addition to the gonadal index explained little more of the residual variability. The average gonadal index (roe content) for Prince William Sound herring females was 22% for the 1987 commercial purse seine harvest (J. Brady, Alaska Department of Fish and Game, Cordova, personal communication). We used this value for GI to derive another estimate of the instantaneous rate of natural mortality for Prince William Sound herring.

Pauly (1980) also attempted to develop an empirical relationship to predict natural mortality rates for a large number of species. His model regressed natural mortality rates against growth parameters and mean environmental temperatures as follows:

$$\log(M) = -0.0066 - 0.2797[\log(L_\infty)] + 0.6543[\log(K)] + 0.4634[\log(\tau)] \ , \quad (5)$$

where L_∞ is the asymptotic length in cm from the von Bertalanffy growth equation, K is the von Bertalanffy growth coefficient, and τ is the mean annual water temperature in °C. Pauly (1980) obtained an r^2 of 0.718 applying the model to 175 fish stocks from widely varying habitats. However, Pauly (1980) noted that natural mortality estimates for clupeids estimated by his model tended to be high. He suggested that the lower than expected mortality rates resulted from the schooling behavior of clupeids, which reduced predation. We used model (5) with $L_\infty = 0.293$ cm, K = 0.293 from an analysis of the growth of Prince William Sound herring (Funk and Sandone 1989) and a mean temperature of 8°C to estimate a natural mortality rate for Prince William Sound herring.

We also reviewed literature estimates of natural mortality of herring populations in other areas. Beverton (1963) reviewed early literature values for Pacific herring and concluded that M was between 0.4 and 0.6 for the commercially important age groups in British Columbia. Ricker (1975) analyzed a catch curve from a lightly fished stock from the Queen Charlotte Islands and estimated that natural mortality was approximately 0.45, although mortality increased with age. Schwiegert and Hourston (1980) used M = 0.36 in their cohort analysis of Barkley Sound, British Columbia, herring stocks, and Haist et al. (1985, 1986) used M = 0.45 in their age-structured model for all British Columbia herring stocks. In the Bering Sea, Wespestad (1982) estimated that M was 0.39 based on the Alverson-Carney method and growth data obtained from Shaboneev (1965) from near-virgin stock conditions. Tester (1955) analyzed Vancouver Island herring catch, age-composition, and effort data and concluded that natural mortality was strongly age-dependent, with instantaneous natural mortality rates ranging from 0.40 to 0.85. We used the literature estimates of natural mortality to help establish a likely range of natural mortality estimates for Prince William Sound herring.

Instantaneous rates of natural mortality (M) were converted to annual percent survival (S) using

$$S = 100(e^{-M}) \ . \quad (6)$$

Because sac roe fisheries occur over very short time intervals, this expression is an appropriate method of describing survival between annual fishing seasons. The annual survival rate (S) encompasses all sources of mortality other than the spring sac roe fishery.

Catch-Age Analysis

Catch-age analysis models estimate initial cohort sizes and annual exploitation rates by fitting catches predicted by equations describing natural and fishing mortality to a time series of observed catches at age. Because only sac roe fisheries were modeled for Prince William Sound herring, and these occur over a very short period of time, discrete forms of catch and survival equations were used rather than the conventional continuous forms used by Deriso et al. (1985), Doubleday (1976), and other catch-age analysis applications. This allowed the survival of a cohort from one year to the next to be modeled very simply as

$$N_{a+1,y+1} = S(N_{a,y} - \sum_g \hat{C}_{a,y,g}) \ , \quad (7)$$

where $N_{a+1,y+1}$ is the number of fish in the cohort which were aged a+1 just before the fishery in year y+1, S is the proportion of the cohort surviving from the end of the fishery in year y to the beginning of the fishery in year y+1, $N_{a,y}$ is the number of fish in the cohort just before the fishery in year y, and $\hat{C}_{a,y,g}$ is the catch of fish of age a in year y by gear g estimated from a catch model. Years were arbitrarily indexed to start in the spring, shortly before the fishery and spawning events.

The model tracks cohorts beginning with age-3, the first year that a significant proportion of a cohort appears in the catch or on the spawning grounds. Because ageing errors are frequent for old herring, all fish age 9 and older are pooled into a single age '9+' category, so that the survival model for the '9+' category is

$$N_{9+,y+1} = S[(N_{8,y} - \sum_g \hat{C}_{8,y,g}) + (N_{9+,y} - \sum_g \hat{C}_{9+,y,g})] \quad (8)$$

Young herring are not fully mature and do not all migrate to the spawning grounds where they are vulnerable to the fishery. In expression (7), $N_{a,y}$ refers to all fish in the cohort, regardless of whether they are mature, present on the spawning grounds, and vulnerable to the fishery. We used a partial recruitment or maturity proportion, ρ_a, for each age to describe the proportion of a cohort that migrates to the spawning grounds and is potentially vulnerable to the fishery. The number of fish in the cohort that are potentially vulnerable to fishing gear is then $\rho \cdot N_{a,y}$. The catch model used for catch-age analysis assumes that fishing mortality on the recruited proportion of the cohort can be partitioned into an age-specific gear selectivity coefficient for each gear, $v_{a,g}$, multiplied by a year-specific exploitation fraction for each gear, $v_{a,g}$, such that

$$\hat{C}_{a,y,g} = v_{a,g} \cdot \mu_{y,g} \cdot \rho_a \cdot N_{a,y} . \quad (9)$$

The separability of fishing mortality into multiplicative components v and μ was first proposed by Doubleday (1976) and is an important assumption of catch age analysis. The separability assumption reduces the number of fishing mortality parameters to be estimated so that least squares methods can be used.

To further reduce the number of parameters to be estimated and to smooth the relationship between gear selectivity and age, the two-parameter gamma-type function used by Deriso et al. (1985) was used to describe gear selectivity, $v_{a,g}$, as a continuous function of age $v'_g(a)$, such that

$$v'(a) = \frac{a^{\alpha} e^{-\beta \cdot a}}{\max_j (j^{\alpha} e^{-\beta \cdot j})} , \quad (10)$$

where α and β are parameters specific to each gear to be estimated by the catch-age analysis model and subscript j ranges over all age classes. The denominator scales the function $v'(a)$ to unity for the age(s) of full selectivity. This function allows a wide range of functional forms encompassing selectivities that increase gradually with age and dome-shaped forms. The subscript g is omitted from equation (10) for notational simplicity, but gear-specfic selectivity functions, $v'_g(a)$, were estimated by the model with parameters α_g and β_g specific to each gear.

To reduce the number of partial recruitment parameters to be estimated, we used a two-parameter logistic model to describe the partial recruitment or maturity proportion, ρ_a, as a continuous function of age, $\rho'(a)$, such that

$$\rho'(a) = \frac{1}{1 + \varphi \cdot e^{-\theta a}} , \quad (11)$$

where φ and θ are parameters to be estimated by the catch-age analysis model. For positive values of φ and θ this function can assume a range of asymptotic forms similar to those expected for partial recruitment. We also assumed that herring cohorts age 5 and older were fully recruited and mature.

In addition to estimating parameters α_g, β_g, φ, θ, and $\mu_{y,g}$, the catch-age analysis model estimates the number of age-3 fish recruiting in each year, $N_{3,y}$, and the number of fish at each age in the first year, $N_{a,73}$. From initial cohort sizes $N_{3,y}$ and $N_{a,73}$, equations (7), (8), and (9) were used to construct estimates of population numbers for each age and year, $N_{a,y}$, from 1973 through 1988. Catch-age analysis estimates of total population biomass ($\hat{B}_y$) were constructed from the estimated population numbers and year-specific mean weights at age, $W_{a,y}$, from Appendix D as follows:

$$\hat{B}_y = \sum_a (W_{a,y} \cdot N_{a,y}) \ . \tag{12}$$

Where weights were needed for years and ages for which data were not available, the average weight-at-age over all years from Appendix D was used. Because of the method of indexing ages and years, all biomass estimates resulting from the catch-age analysis refer to the weight of the population just prior to spring sac roe fisheries and spawning events.

Catch-age analysis estimates of the total numbers in each cohort, $N_{a,y}$, included all members of the cohort, regardless of whether all fish in the cohort were fully mature and present on the fishing and spawning grounds. However, spawn deposition and aerial surveys only estimated the proportion of the population that was fully mature and present on the spawning grounds. To make estimates of spawning biomass ($\hat{B}'_y$) comparable to aerial survey and spawn deposition biomass estimates, catch-age population numbers were multiplied by the partial recruitment coefficient at each age, ρ_a, as follows:

$$\hat{B}'_y = \sum_a (W_{a,y} \cdot \rho_a \cdot N_{a,y}) \ . \tag{13}$$

Using estimates of fecundity at age (F_a) from equation (1) and assuming a 1:1 sex ratio, the number of eggs produced in a given year, E_y, was estimated using

$$E_y = \sum_a [F_a \cdot 0.5(\rho_a \cdot N_{a,y})] \ . \tag{14}$$

A biomass-based exploitation rate, $\mu'_{y,g}$, for gear g in year y, comparable to those which have been used for managing the commercial fishery was estimated as

$$\mu'_{y,g} = \sum_a (C_{a,y,g} \cdot W_{a,y}) / \hat{B}'_y . \tag{15}$$

Errors in predicted catches were assumed to be lognormally distributed, so that

$$\log_e (C_{a,y,g} + 1) = \log_e (\hat{C}_{a,y,g} + 1) + \varepsilon_{a,y,g} \ , \tag{16}$$

where $C_{a,y,g}$ are the actual catches, the $\hat{C}_{a,y,g}$ are the estimated catches from equation (9), and the $\varepsilon_{a,y,g}$ are normally distributed with mean 0 and variance σ^2. Because some observed catches at age were zero, it was necessary to add one to each catch before taking logarithms in equation (16). Logarithms of errors in the catch residuals have been assumed to be normal in other catch-age analyses (Doubleday 1976, Deriso et al. 1985). For fitting the model to the catch data, nonlinear least squares procedures were used to minimize SSQ_{catch} over all ages (a), years (y), and gears (g), where

$$SSQ_{catch} = \sum [\log_e(C_{a,y,g} + 1) - \log_e(\hat{C}_{a,y,g} + 1)]^2 \ . \tag{17}$$

Spawn deposition survey biomass estimates were incorporated into the catch-age analysis model by minimizing SSQ_{spawn}, the difference between catch-age estimates of spawning biomass ($\hat{B}_y$) from equation (13), and the spawn deposition survey biomass estimates (B_y) over years (y), where

$$SSQ_{spawn} = \sum_{y}[\log_e(B_y) - \log_e(\hat{B}_y)]^2. \quad (18)$$

The summation was performed only over y for which spawn survey estimates of biomass were available (1984 and 1988). The total sum of squares for the model was then given by

$$SSQ_{total} = SSQ_{catch} + \lambda SSQ_{spawn}, \quad (19)$$

where λ is a term used to assign relative weights between the catch and spawn sums of squares.

Because there were no gill net harvests in 1973, 1975, 1976, and 1979, exploitation rates for gill net gear were not estimated for these years. With seven age groups (3-9+), 16 years of purse seine observations (1973-1988), and 12 years of gill net observations, there was a total of 196 catch-age observations and 2 spawn deposition survey biomass observations. The catch-age analysis model equations contain 4 gear selectivity parameters (2 for each gear), 2 partial recruitment parameters, 28 exploitation rates (16 for purse seine gear and 12 for gill net gear), and 22 initial population sizes for a total of 56 unknown parameters, resulting in a ratio of data to parameters of 3.54.

The catch-age analysis program was coded in FORTRAN and uses IMSL[1] Math Library subroutine DBCLSF (IMSL 1988) to perform bounded nonlinear least squares parameter estimation on the resulting system of equations, using a modified Levenberg-Marquardt algorithm. Bounds on parameter estimates were specified such that all parameters were non-negative and exploitation rates were ≤1. A procedure internal to subroutine DBCLSF was used to scale all parameters to be estimated to a similar order of magnitude. Parameter estimation methods were verified using simulated populations, similar in structure to the Prince William Sound herring population, into which lognormal errors in the observed catches were introduced to assure that the model correctly recovered the known parameters. Because of the uncertainty in natural mortality rate estimates, a range of survival rates (*S*) was used to investigate the sensitivity of the catch-age model to survival rate.

Initial values for parameter estimates for the iterative nonlinear least squares routines were derived from cohort analysis using Pope's (1972) method where terminal fishing mortalities were derived from aerial survey biomass estimates. A relatively wide range of initial values were used to ensure that the algorithm converged to a unique solution.

RESULTS

Natural Mortality

Applying the Alverson-Carney method (equation 2) with a maximum age of 14 resulted in an estimated instantaneous natural mortality rate of 0.49. Using equation (3) with a maximum age of 14, Hoenig's method predicted a natural mortality rate of

1 Company names are listed only for archival purposes and do not represent an endorsement of any kind.

Table 1. Summary of methods used to estimate natural mortality rates for Alaska and British Columbia herring, natural mortality rates estimated by each method, and data required by each method.

Source or Method	Data Required	Source of Data	Natural Mortality
Alverson and Carney (1975)	Growth, maximum age	Prince William Sound	0.49
Hoenig (1983)	Maximum age	Prince William Sound	0.28
Gunderson (1980)	Gonadal index	Prince William Sound	0.65
Pauly (1980)	Growth, temperature	Prince William Sound	0.48
Beverton (1963)		British Columbia	0.4-0.6
Ricker (1975)	Age distributions	Queen Charlotte Is., B.C.	0.45
Schwiegert and Hourston (1980)		Barkley Sound, B.C.	0.36
Haist et al. (1985, 1986)		British Columbia	0.45
Wespestad (1982)	Growth, maximum age	Bering Sea	0.39
Tester (1955)	Age distributions, effort	Vancouver Island, B.C.	0.40-0.85

0.28. Using an average gonadal index (roe content) for Prince William Sound female herring of 22%, Gunderson's regression (equation 4) predicted that the natural mortality rate would be 0.65. Using Pauly's method (equation 5) and a mean environmental temperature of 8°C, the estimated natural mortality rate was 0.48.

The estimates of natural mortality that we derived using equations (2)-(5) ranged from 0.28 to 0.85 and averaged 0.47. This range is comparable to other herring studies (Table 1). The average of all the natural mortality rates in Table 1, including literature estimates, was 0.46. We assumed a value of $M = 0.45$ to be a reasonable rounded estimate to use for an average instantaneous rate of natural mortality for Prince William Sound herring. We represented the effects of the uncertainty in natural mortality rates on the catch-age analysis by investigating the sensitivity of the catch-age analysis results to a range of natural mortality from $M = 0.35$ to $M = 0.55$. An instantaneous rate of natural mortality of 0.45 corresponds to an annual survival rate (S) of 64% using equation (6), while the range of instantaneous natural mortality rates of $M = 0.35$ to 0.55 corresponds to a range of annual survival rates from S = 70% to 58%.

Catch-Age Analysis

Spawning Biomass Estimates

Spawning biomass estimates from the catch-age analysis model ($\hat{B}_y$), fit only to catch-at-age from the two gear types (no auxiliary information) and using S = 64%, were higher than peak aerial survey biomass estimates in all years and higher than spawn deposition survey biomass estimates in 1984 and 1988 (Figure 4). From 1978 to 1988 aerial survey biomass estimates and catch-age biomass estimates show similar relative trends. When auxiliary information from the 1984 and 1988 spawn deposition surveys was incorporated into the model, spawning biomass estimates were reduced; values were very similar to the spawn depositionsurvey biomass estimates in 1984 and 1988. Fluctuations in abundance roughly parallelled the aerial survey estimates, but aerial survey biomass estimates averaged only 54% of the catch-age analysis biomass estimates from 1979 through 1988. The aerial survey milt index (Appendix E) shows a trend quite different from aerial survey peak biomass, catch-age analysis biomass estimates, and spawn deposition survey biomass estimates.

Parameter estimates readily converged to unique values within 25-50 iterations in most cases. While we initially derived parameter initial values from cohort analysis using Pope's (1972) method, variation in parameter initial values of up to 50% resulted in identical parameter estimates from the model in almost all cases. However, when λ was <0.1, displacing parameter initial values by more than ± 25% caused the estimation algorithm to converge to a local minimum where biomass estimates were about 20% higher than at the global minimum. The residual sum of squares when the model converged to this local minimum was about 2% higher than when the model converged to the global minimum. Biomass estimates at the global minimum from the model when auxiliary information was weighted lightly ($\lambda < 0.01$) were almost identical to those when auxiliary information was weighted heavily ($\lambda \approx 200$). Estimates of all parameters estimated by the model for S = 64% and $\lambda = 100$ are given in Table 2.

Effect of Survival Rates on Spawning Biomass

Varying annual survival rates (*S*) from 58% to 70% had only a small effect on the biomass estimates (Figure 5). The use of heavily weighted auxiliary information essentially forced the biomass to be very similar to that of the 1984 and 1988 spawn deposition surveys, regardless of the survival rate. However, initial cohort sizes varied by a considerable amount. With high survival rates (S=70%) initial cohort sizes were 10%-25% lower than with S=64%. When survival rates were low (S=58%), initial cohort sizes where 20%-50% higher than when S=64%. Catch-age analysis biomass estimates were much more sensitive to survival rates when auxiliary information was not used.

Residual Analysis

The assumption that fishing mortality is separable into multiplicative age-specific and year-specific components is critical to catch-age analysis. This assumption reduces the number of parameters to be estimated so that least squares parameter estimation techniques are feasible. Following Doubleday (1976), residuals ($\varepsilon_{a,y,g}$) from equation (16) were examined for patterns

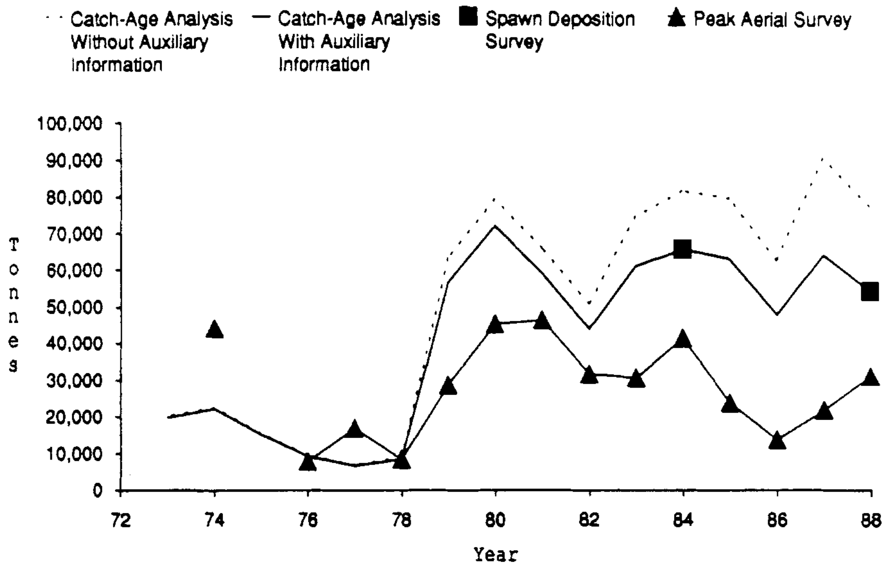

Figure 4. Spawning biomass estimates for Prince William Sound herring from catch-age analysis with and without auxiliary information, spawn deposition survey biomass estimates from 1984 and 1988, and peak aerial survey biomass estimates from 1974 through 1988.

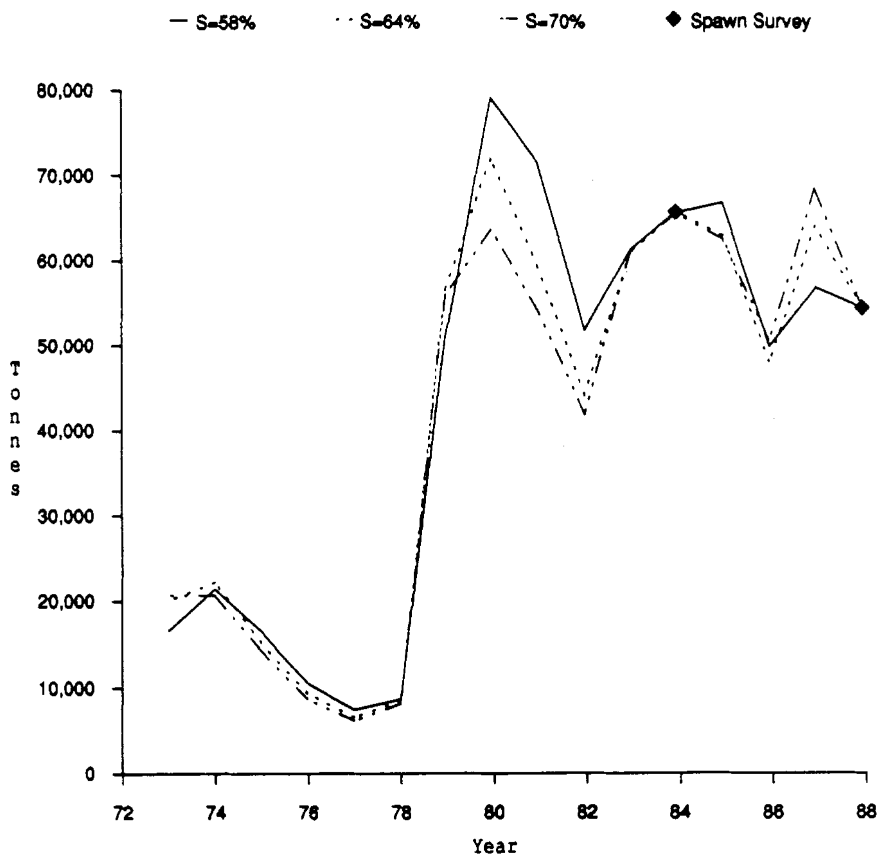

Figure 5. Spawning biomass of Prince William Sound herring from 1973 through 1988 estimated by the catch-age analysis model with auxiliary information for survival rates ranging from 58% to 70%.

Table 2. Parameter estimates from the catch-age analysis model, using 1984 and 1988 spawn deposition survey biomass estimates as auxiliary information with λ = 100, and a survival rate of 64%.

	Purse Seine	Gill Net
Gear Selectivity[a]		
α_g	1.95	13.67
β_g	0.30	2.26
Partial Recruitment[a]		
ϕ	176.49	
θ	6.43	
Exploitation Rates		
$\mu_{73,g}$	1.000	[b]
$\mu_{74,g}$	0.664	0.057
$\mu_{75,g}$	0.684	[b]
$\mu_{76,g}$	0.568	[b]
$\mu_{77,g}$	0.508	0.007
$\mu_{78,g}$	0.384	0.059
$\mu_{79,g}$	0.269	[b]
$\mu_{80,g}$	0.228	0.192
$\mu_{81,g}$	0.369	0.043
$\mu_{82,g}$	0.315	0.033
$\mu_{83,g}$	0.076	0.007
$\mu_{84,g}$	0.166	0.022
$\mu_{85,g}$	0.192	0.033
$\mu_{86,g}$	0.275	0.031
$\mu_{87,g}$	0.151	0.036
$\mu_{88,g}$	0.202	0.026

Initial Cohort Sizes (millions of fish)

Age:	3	4	5	6	7	8	9
$N_{3,73}$ - $N_{"9+",73}$	257.03	26.98	16.51	7.82	2.15	0.15	0.08
$N_{3,74}$	67.71						
$N_{3,75}$	46.52						
$N_{3,76}$	25.47						
$N_{3,77}$	28.61						
$N_{3,78}$	93.65						
$N_{3,79}$	851.77						
$N_{3,80}$	233.08						
$N_{3,81}$	108.59						
$N_{3,82}$	165.25						
$N_{3,83}$	431.15						
$N_{3,84}$	349.32						
$N_{3,85}$	75.63						
$N_{3,86}$	81.87						
$N_{3,87}$	577.11						
$N_{3,88}$	37.76						

[a] Ages were coded such that a=1 for age 3, a=2 for age 4 etc. when using these parameter estimates with expressions (10) and (11).
[b] No gill net fishery occurred in 1973, 1975, 1976, or 1979. Exploitation rates were not estimated for these years.

with respect to year and age. To aid in the detection of year and age patterns, the response surface of catch residuals plotted against year and age was smoothed by distance-weighted least squares. The response surfaces of residuals for purse seine (Figure 6) and gill net gear (Figure 7) did not show definite, consistent patterns with respect to year or age. In 1974, 1978, and 1987, fewer age-3 fish were present in the purse seine catch than were expected. Gill net catches of older (age-8 and age-9+) fish were higher than expected from 1986 through 1988, perhaps indicating some targeting by the gill net fleet on the strong 1978-79 year classes. The combined log residuals are approximately normal (Figure 8), although gill net residuals were smaller in magnitude than purse seine residuals.

Exploitation Rate Estimates

Spawning biomass-based exploitation rates were computed using equation (15), consistent with the exploitation rates used in the management of the fishery. These exploitation rates display the opposite trend from spawning biomass (Figure 9), ranging from 25% to 35% from 1972 to 1977 and averaging 12% from 1979 to 1988. The highest estimated exploitation rate was 36% in 1975, and the lowest was 4% in 1983.

Partial Recruitment Proportions

The model's estimates of the proportion of the population recruited to the fishing and spawning grounds at ages 3 and 4 were strongly affected by the assumed survival rate (Figure 10). For S = 58%, only 44% of

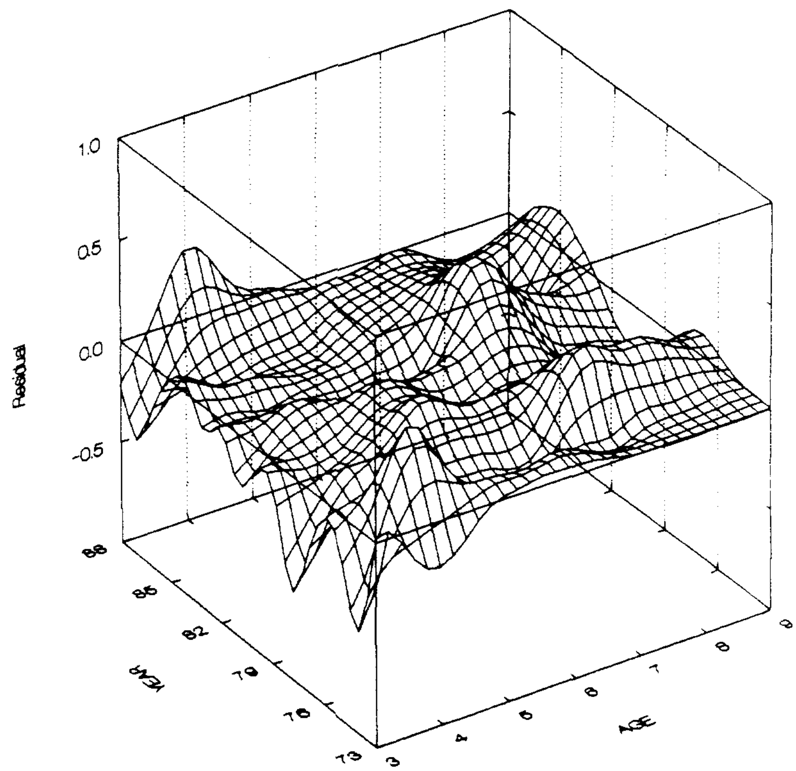

Figure 6. Response surface of residuals $\varepsilon_{a,y,g}$ from the catch model with respect to year and age for purse seine catches of Prince William Sound herring from 1973 through 1988, smoothed by distance weighted least squares.

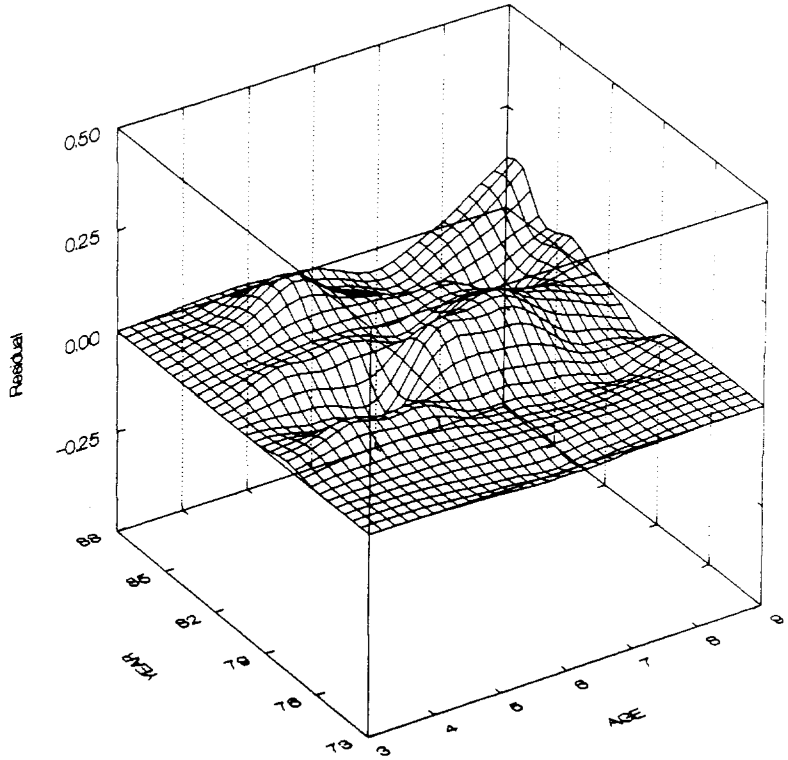

Figure 7. Response surface of residuals $\varepsilon_{a,y,g}$ from the catch model with respect to year and age for gill net catches of Prince William Sound herring for 1973 through 1988, smoothed by distance weighted least squares.

the age-3 fish were estimated to be recruited. For *S* = 64%, 78% of age-3 fish were estimated to be recruited; for *S* = 70%, age-3 fish were estimated to be 99% recruited to the fishery. Low survival rates increased initial cohort sizes so that the model tended to decrease ρ to fit the observed pattern of catches at age. Age-4 fish were estimated to be fully recruited except for low survival rates (*S* = 58%) when age-4 fish were estimated to be only 82% recruited. Age-5 and older fish were forced to be fully recruited in the formulation of the model.

Gear Selectivity

The catch-age analysis model indicated that herring became fully vulnerable to purse seine gear at about age 6 (Figure 11). Less than 20% of the recruited cohorts were vulnerable to purse seine gear at age 3. The tendency for the right limb of the purse seine gear selectivity curve to descend in some cases is probably an artifact of the limited functional form of the gamma function. Gear selectivity for gill net gear has a much more restricted dome-shaped pattern because of the active size selection by the gill net mesh. Herring reached maximum vulnerability to gill net gear at age 8. The form of the functions estimated by the model represent gear selectivities typical for the entire 1973-88 period. This means the gill net gear selectivities of Figure 10 were for the approximate average mesh size used over the period.

Gear selectivities of both purse seine and gill net gear were affected in similar ways by varying the rate of survival assumed for the catch-age model. When survival rates were

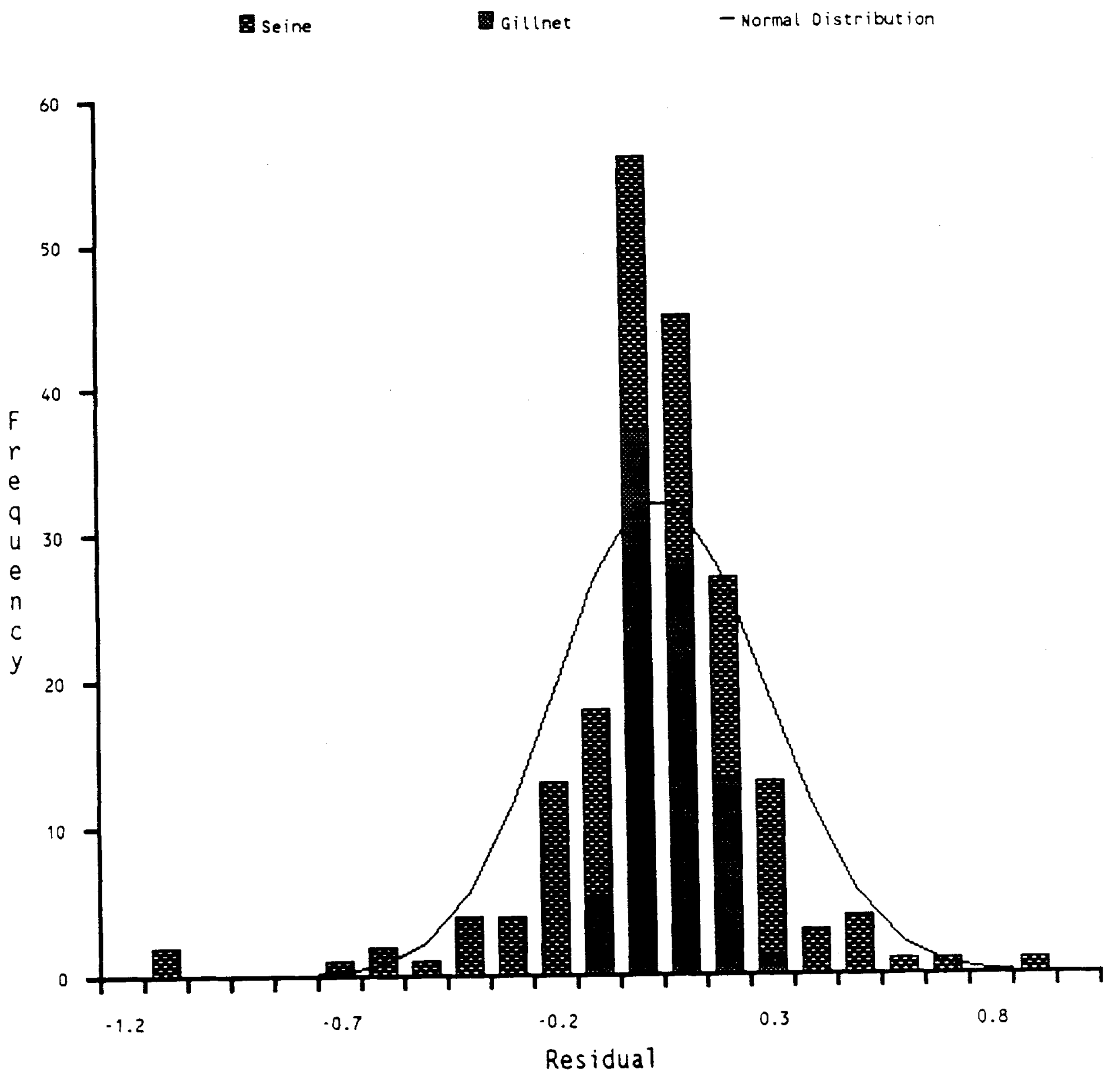

Figure 8. Frequency distribution of the log residuals, $\epsilon_{a,y,g}$, from the catch model for purse seine and gill net gears and a normal distribution fitted to the mean and variance of the observed log residuals for Prince William Sound herring.

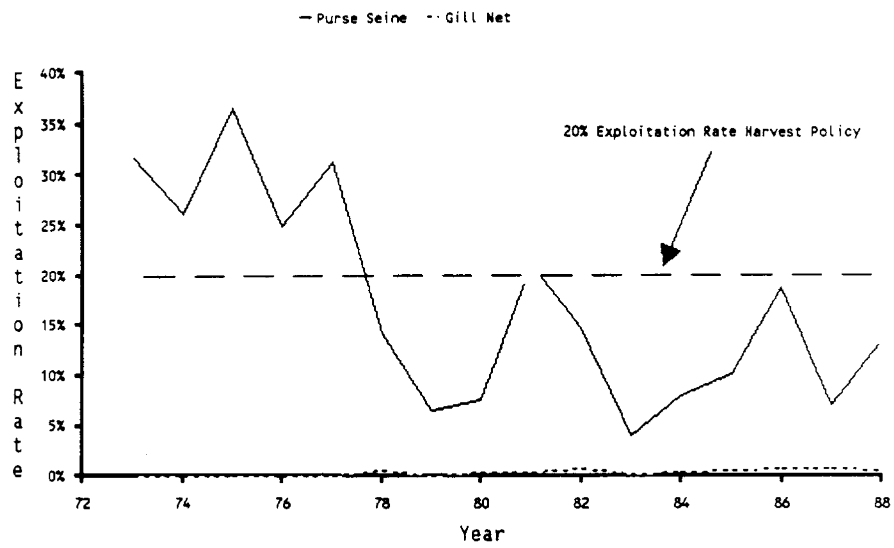

Figure 9. Spawning biomass-based exploitation rate (catch weight divided by age-3+ spawning biomass) for Prince William Sound herring estimated by catch-age analysis with auxiliary information for purse seine and gill net gears, 1973 through 1988.

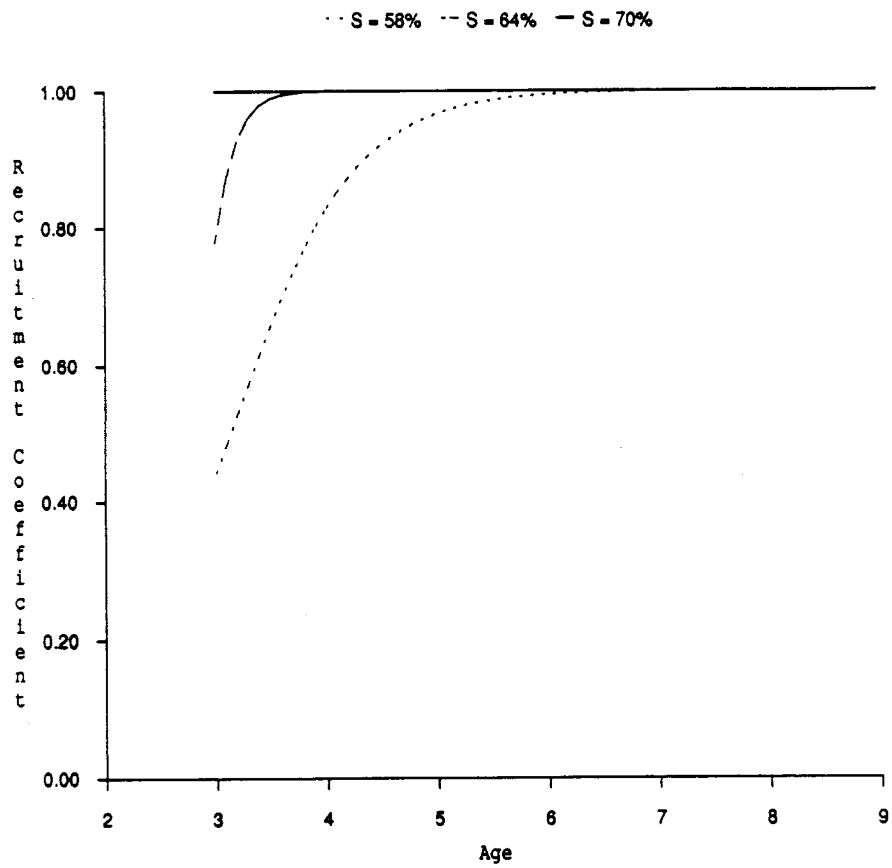

Figure 10. Partial recruitment functions, $\rho'(a)$, estimated by the catch-age analysis model for Prince William Sound herring for survival rates ranging from 58% to 70%.

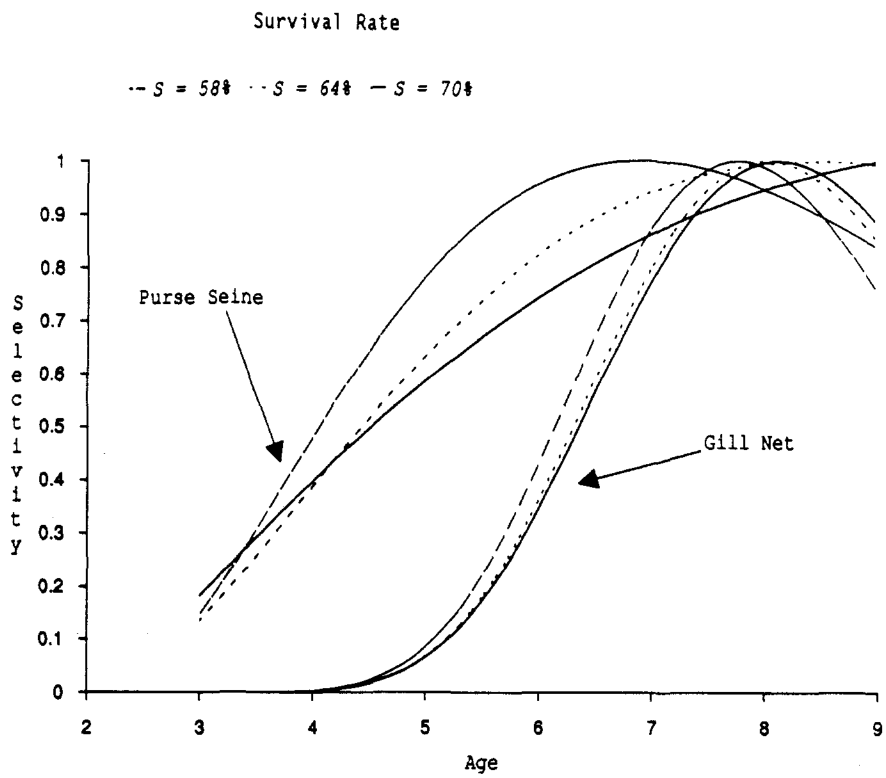

Figure 11. Gear selectivity gamma functions ν_g' (a) estimated by the catch-age analysis model for Prince William Sound herring for survival rates ranging from 58% to 70%.

low (S = 58%), initial cohort sizes were relatively high, and gear selectivities estimated by the model decreased at young ages to maintain close fits to the observed pattern of catches at age. When survival rates were high (S = 70%), initial cohort sizes were relatively low; i.e. the model estimated high selectivities for young herring in order to fit the observed pattern of catch-at-age.

Year Class Strength and Spawner-Recruit Relationship

Very strong cohorts were produced in 1976 and 1984 (Figure 12). The weakest cohort (25 million fish at age 3) was produced in 1973, and the strongest cohort (852 million fish at age 3) was produced in 1976. The size of most cohorts at age 3 was less than 200 million fish so that the frequency distribution of the 16 age-3 cohort strengths is reasonably well described by a lognormal distribution with mean 4.836 and variance 1.175 (Figure 13). If the pattern of the last 16 years is typical, a moderately strong year class of at least 300 million age-3 recruits would be expected about every 4 years on the average. The recruited proportion of the age 3 cohorts averaged 31% of the total spawning biomass over the 1973-88 period.

Fecundity increased rapidly with age from ages 3 to 6 and then reached an asymptotic value of about 28,000 eggs per female by age 8 (Figure 14). This fecundity-age relationship and the catch-age analysis estimates of population numbers at age with S=64% were used to estimate (equation 1) the numbers of eggs spawned in each year (E_y). This number was relatively low from 1973 to 1978 and

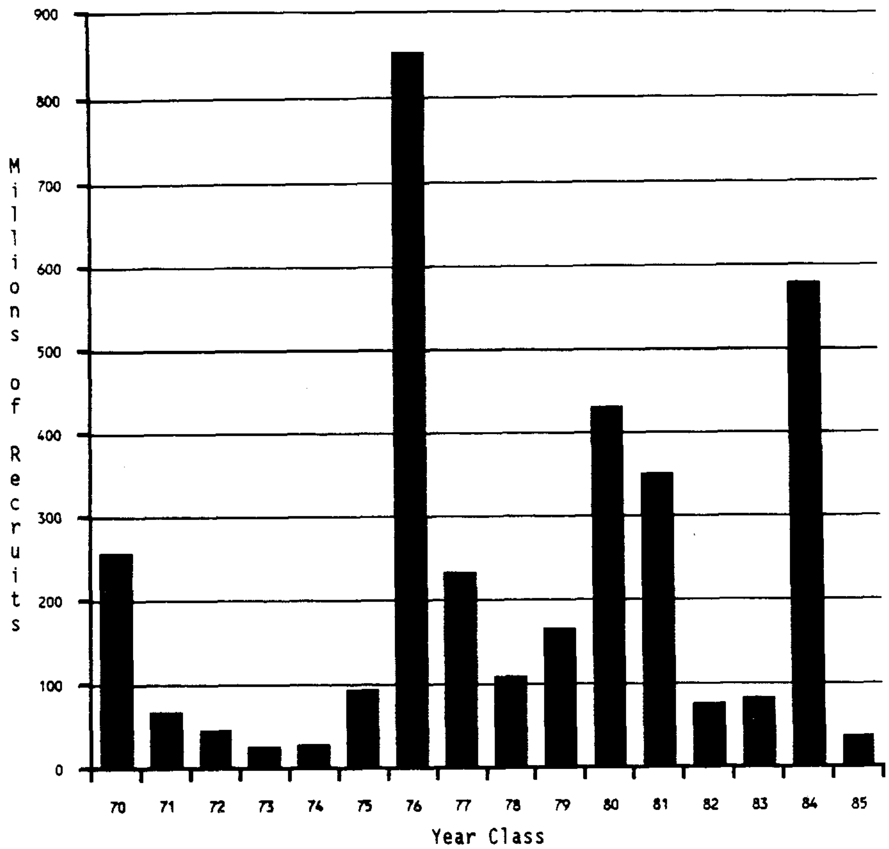

Figure 12. Size of the 1970-85 year classes at age 3 estimated by the catch-age analysis model for Prince William Sound herring.

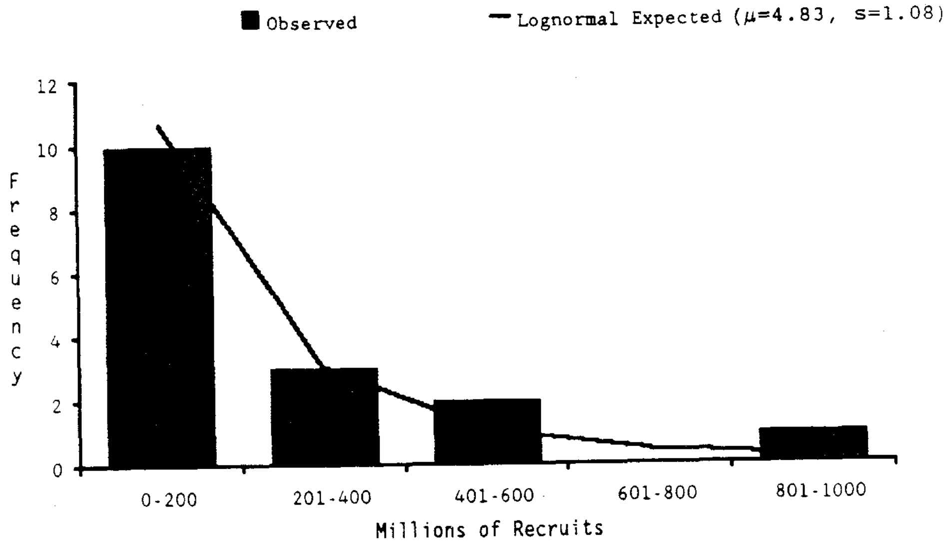

Figure 13. Frequency distribution of the size of the 1970-85 year classes at age 3 estimated by the catch-age analysis model for Prince William Sound herring, and a lognormal distribution fit to the estimated mean and variance.

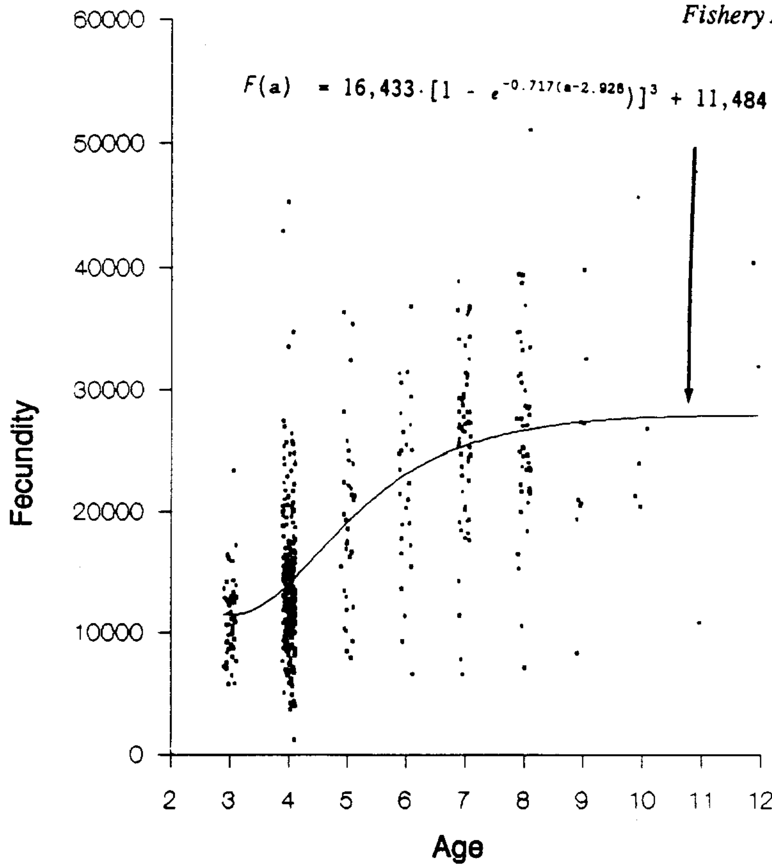

Figure 14. Estimated fecundity at age from 1984 and 1988 spawn deposition survey fecundity sampling, and a von Bertalanffy-type model fit to the fecundity at age observations for Prince William Sound herring.

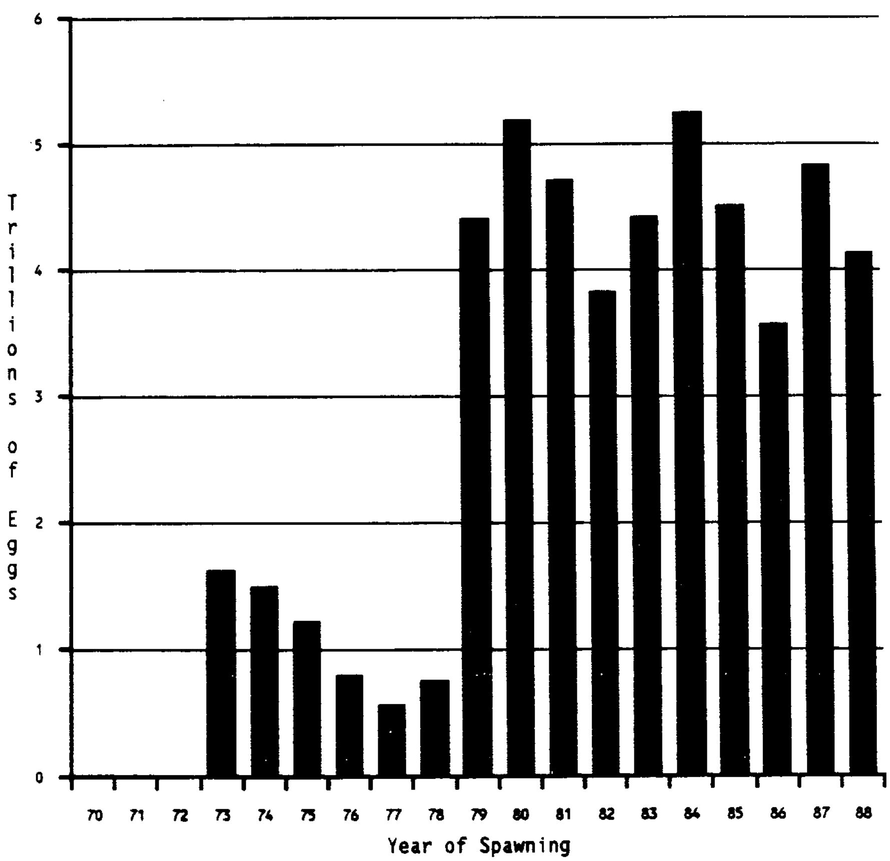

Figure 15. Numbers of eggs produced during 1973 through 1988 spawning events, as estimated from the fecundity-age relationship and catch-age analysis estimats of numbers of fish at age for Prince William Sound herring.

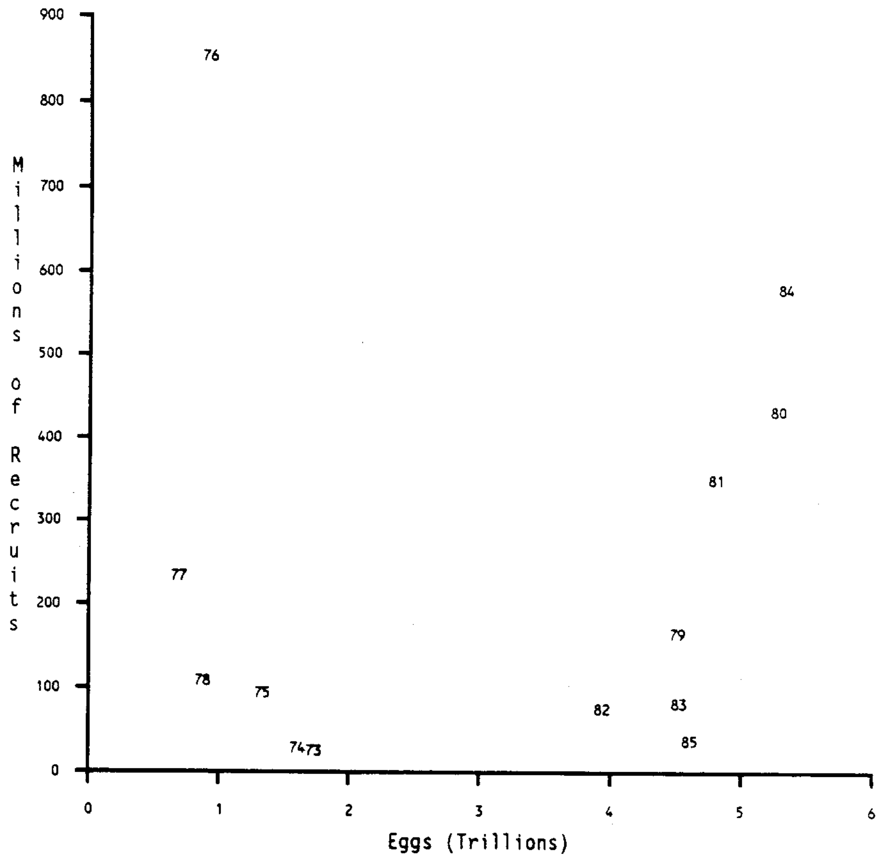

Figure 16. Spawner-recruit relationship for year classes of Prince William Sound herring, using estimates of age-3 recruits, numbers of spawning fish from the catch-age analysis model, and the estimated fecundity-age relationship.

then increased sharply and remained relatively constant at approximately 4-5 trillion eggs through 1988 (Figure 15).

Examining the number of eggs spawned each year and the number of age-3 recruits 3 years later provides little evidence of a typical density-dependent spawner-recruit relationship (Figure 16). The strongest year class (1976) was produced from one of the smallest egg depositions. However, using only the 1979-85 year classes for which better data were available, a positive density dependent relationship is evident.

DISCUSSION

Although peak aerial survey biomass estimates have often been considered conservative, the degree of underestimation of almost 50% compared to catch-age analysis (with spawn deposition survey auxiliary information) is surprising. Peak aerial survey biomass estimates do appear to follow general trends in biomass and may still be useful as a relative abundance indicator.

Nonlinear iterative estimation problems can be sensitive to initial parameter estimates. It is important to try various combinations of initial conditions to help detect the presence of local minima in the residual response surface. For the Prince William Sound model, in most cases the model would successfully converge to the global minimum, if initial conditions were within 50% of their values at the global minimum. However, the model was more likely to converge to local minima when relatively large

($\lambda > 100$) or relatively small ($\lambda < 0.0001$) weights were assigned to the auxiliary information.

Partial recruitment coefficients estimated by the model for age-4 herring were almost always very close to 1, so that the effect of partial recruitment could be described by only a single parameter, ρ_3, or the proportion recruited at age 3. This would reduce the number of parameters to be estimated and increase the precision of the model's results.

The occurrence of maximum gear selectivity by both purse seine and gill net gears for relatively old herring (age 8) indicates that the fishing fleet effectively targets on older fish. At young ages all herring are not sexually mature and do not migrate to the spawning grounds. Young herring also tend to spawn later than the older herring sought by the commercial fleet. Older herring have larger, more valuable roe and fishery managers and fishermen attempt to maximize the value of the harvest by selecting older fish, to the extent possible. Gill net fishermen can actively select for large herring by using large mesh sizes. Purse seine fishermen attempt to select schools of older, larger herring and will release purse seine sets of small fish or fish with low roe content.

Gill net catches were substantially lower in magnitude than purse seine catches over the entire 1973-88 period and had less effect on the estimation of model parameters. Although the model's use of the logarithm of the catches partially compensated for the difference in catch magnitude between the two gear types, gill net catches still had substantially less effect on the parameter estimates than purse seine catches.

Spawn deposition surveys estimate only the number of eggs on the spawning grounds at the time of the survey. Some eggs disappear from the spawning grounds before the survey because of wave action and predation. The proportion of eggs disappearing before the surveys is believed to be about 10%, based on limited studies in other areas. Catch-age analysis could provide another means of estimating the proportion of eggs lost. Spawn deposition survey biomass estimates could be treated as a relative, rather than absolute, index of abundance and the model could estimate the egg-loss proportionality constant. Although egg loss undoubtedly varies from year to year, this method could only estimate an average egg loss over a range of years. A longer time series of spawn survey data would be needed before egg loss could be estimated by this method.

It may also be possible to obtain direct estimates of natural mortality from catch-age analysis, after a longer time series of spawn deposition surveys become available. Although Ricker (1975) and Tester (1955) indicate that herring natural mortality increases with age, it is unlikely that age-dependent natural mortality schedules could be estimated using the present catch-age analysis model because other age-dependent parameters are estimated. Because of uncertainties about the natural mortality rate, we did not investigate the impacts of age-dependent natural mortality schedules on our catch-age analysis model results.

Because auxiliary information about stock size was used for 1984 and 1988, biomass estimates for recent years are more certain than for earlier years. The auxiliary information places constraints on estimates about the size of cohorts that were present in 1984 and 1988. A cohort that was age 8 in 1984 would have recruited at age 3 in 1979. It is unlikely that the 1984 and 1988 auxiliary information had much effect on estimates of exploitation rates (μ) and initial cohort sizes before 1979.

The apparent density dependent trend in the spawner-recruit relationship for 1979 to 1985 may merely be a result of random variation about a higher biomass level caused by some unknown factor. It is also possible that biomass estimates from 1973 through 1978 may be incorrect because of the lack of auxiliary information in those years or because of inaccuracies in the catch-age data caused by the smaller age sample sizes used in earlier years. The 1979-85 spawner-recruit observations do not appear to be serially ordered. Several more years of data will be required before hypotheses about density dependence can be reasonably examined.

Estimates from catch-age analysis could be improved by using age-specific auxiliary information. The age distribution of the spawning population, as well as the total biomass, is estimated during annual spring stock assessment sampling. Using the spawning biomass at each age, rather than the total spawning biomass, would particularly help the catch-age model resolve the estimates of partial recruitment (ρ_a) and gear selectivities ($\nu_{a,g}$). Additional emphasis needs to be placed on age sampling to provide better estimates of the age distribution of the spawning population. Because spawn deposition surveys are relatively new, sampling requirements for estimating the age distribution of the spawning population are not yet fully developed and sample sizes are often quite small. Particular attention needs to be focused on sampling the spawning population throughout the spawning run and on developing a method of weighting the age distribution estimates by the biomass spawning at a particular time. Because the results of this study indicate that aerial surveys provide at least an approximate relative abundance index, aerial survey biomass estimates stratified by day and area may be appropriate weights for combining age distribution samples.

CONCLUSIONS AND RECOMMENDATIONS

We concluded that catch-age analysis with auxiliary information should provide a useful tool for increasing the precision and accuracy of prior biomass estimates and forecast abundance estimates in Prince William Sound and elsewhere in Alaska. Catch-age analysis provides a method of incorporating all information about a herring stock, both from current year stock assessment surveys and from prior years. The most recent year's stock assessment information is treated as measuring an underlying quantity with error, so that aberrant results from a single year's stock assessment survey would not cause an inappropriate radical shift in harvest strategy.

We recommend updating the catch-age analysis each year, incorporating the latest year's stock assessment information, and that the catch-age model be used to estimate the current year biomass. In addition to generating biomass estimates for the current year, this process would update the estimates of biomass in all prior years. The model's estimates of partial recruitment coefficients should then be used in the annual forecast to project the age 4-9+ biomass which should return the following year. There is no reliable method of predicting size of the cohort which will recruit at age 3 each year. Based on the model's estimates of average age-3 recruitment over time, a range of age-3 recruitment scenarios could be generated for the forecast for the upcoming year. Because the age 3 cohort typically accounts for only about 30% of the spawning biomass and fishery managers and the fishing fleet attempt to target older fish, the inability to precisely forecast age 3 cohort strength is not as important as the ability to forecast the biomass at age 4 and older. Applying catch-age analysis on an annual basis in this manner should provide a useful tool for increasing the precision and accuracy of prior and forecast abundance estimates.

The following specific recommendations should be considered in future analyses.

1. Incorporate bootstrap methods to place confidence limits on the catch-age analysis parameter estimates.

2. Describe partial recruitment with only a single parameter, ρ_3, the proportion recruited at age 3.

3. Use age-specific estimates of abundance as auxiliary information.

4. Use differential weighting to allow catch-at-age observations from the two gear types to have equal effects on parameter estimates.

5. When several additional years of spawn deposition survey data are available, treat spawn deposition surveys as estimates of relative abundance, and estimate the egg loss proportionality constant.

6. Update the catch-age analysis for Prince William Sound herring every year, incorporating the latest stock assessment information.

7. Base herring forecasts on catch-age analysis estimates of current biomass rather than directly on spawn deposition survey biomass; this will allow for measurement error effects.

8. Use partial recruitment proportions derived in the catch-age analysis for forecasting purposes.

9. Use ranges of weak, average, and strong recruit year class strengths determined from catch-age analysis of historical data to establish a range of probable age-3 recruit strengths when forecasting biomass.

SUMMARY

1. Instantaneous rates of natural mortality for Prince William Sound probably range from 0.35 to 0.55. The midpoint of this range, 0.45, was assumed to be representative of natural mortality.

2. Recent peak aerial survey biomass estimates averaged only 54% of the catch age analysis biomass estimates when 1984 and 1988 spawn deposition survey biomass estimates were used as auxiliary information.

3. Aerial survey and catch-age analysis biomass estimates follow similar relative trends so that aerial surveys may provide a useful relative abundance index.

4. Catch-age analysis biomass estimates were not affected by varying rates of natural mortality when auxiliary information was used. However, estimates of the initial numbers of fish in each cohort were strongly affected by varying natural mortality rates. Catch-age biomass estimates were strongly affected by varying natural mortality rates when the auxiliary information was not used.

5. Catch-age analysis estimates of exploitation rates averaged only 12% from 1979 through 1988.

6. The proportion of the population recruited to the fishing and spawning grounds at age 3 was estimated to be 78%. This proportion was very sensitive to the assumed rate of natural mortality. Essentially all age-4 fish were estimated to be fully recruited, regardless of the assumed rate of natural mortality.

7. Gill net gear selectivities were dome shaped, reaching maximum selectivity at age. Purse seine selectivities were nearly

asymptotic, reaching higher selectivities at lower ages than for gill net gear.

8. Over the last 16 years, strong year classes of at least 300 million age-3 recruits have been produced every 4 years on average.

9. No overall spawner-recruit relationship was evident, although a positive density-dependent trend is evident for recent years.

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APPENDIX

Appendix A. Number of fish collected in age-composition samples of the commercial catch from Prince William Sound purse seine and gill net fisheries by management district for 1973 through 1988.

	Purse Seine Sac Roe				Gill Net Sac Roe			
Year	Northern-General	Montague	Eastern	Total	Northern	Montague	General	Total
1973	345	222		567				
1974	637	[a]			637			637
1975	686	512		1,198				
1976		196	104	300				
1977	429			429	223			223
1978	412			412	244			244
1979	333		529	862				
1980		310	201	511	121			121
1981		113	124	237	145			145
1982	605			605	267			267
1983	435	379		814	197			197
1984		536		536		265	228	493
1985	561	566		1,127		509		509
1986	1,280			1,280	645	676	650	1,971
1987	1,730			1,730	586			586
1988	1,493			1,493	565			565

[a] Age-composition samples were not available for the Montague purse seine fishery in 1974, and the age composition was assumed to be similar to the Northern District.

Appendix B. Prince William Sound commercial sac roe purse seine harvest (numbers of fish in thousands), 1973-1988, from Sandone (1988) for 1973-87 and from Brannian (1989) for 1988.

	Age							
Year	3	4	5	6	7	8	9+	Total
1973	45,155	7,400	10,361	6,496	2,039	151	76	71,678
1974	1,314	43,346	5,655	3,001	581	36	0	53,934
1975	4,242	26,900	21,744	1,408	60	0	0	54,355
1976	2,407	5,751	6,001	8,544	2,171	444	74	25,392
1977	1,345	1,543	4,114	3,323	5,617	791	237	16,969
1978	801	3,060	3,511	2,726	1,530	682	201	12,512
1979	41,971	4,707	1,457	440	264	196	0	49,034
1980	6,942	42,742	6,153	527	501	0	0	56,865
1981	2,501	22,205	82,129	7,757	998	0	0	115,591
1982	10,206	9,323	11,089	23,062	4,809	294	0	58,784
1983	2,481	1,629	1,815	2,932	8,426	697	123	18,103
1984	10,841	22,813	5,750	3,299	4,148	3,017	566	50,435
1985	2,059	11,874	17,487	6,382	2,912	2,022	6,084	48,820
1986	2,700	4,168	19,276	21,454	5,115	1,989	5,873	60,575
1987	5,028	2,637	3,227	10,032	8,397	1,117	1,974	32,412
1988	796	45,991	3,921	2,128	6,337	3,931	1,561	64,665
Average Percent:	17.8%	32.4%	25.8%	13.1%	6.8%	1.9%	2.1%	100.0%

Appendix C. Prince William Sound commercial sac roe gill net harvest (numbers of fish in thousands), 1973-1988, from Sandone (1988) for 1973-87 and Brannian (1989) for 1988.

Year	Age 3	4	5	6	7	8	9+	Total
1973								
1974	0	19	6	4	1	0	0	30
1975								
1976								
1977	1	1	3	3	3	0	0	11
1978	32	160	162	83	76	39	12	566
1979								
1980	0	162	216	622	474	135	27	1,637
1981	0	11	742	502	274	103	23	1,655
1982	0	135	376	1,619	337	106	0	2,574
1983	3	9	27	92	412	49	9	601
1984	0	23	114	308	644	731	146	1,965
1985	0	88	656	456	228	251	688	2,368
1986	4	23	474	1,080	376	174	418	2,549
1987	0	0	92	799	1,086	374	651	3,003
1988	0	37	71	162	676	608	355	1,909
Average Percent:	0.2%	3.6%	15.6%	30.4%	24.3%	13.6%	12.3%	100.0%

Appendix D. Mean round weights (g) for Pacific herring from Prince William Sound age-weight-length samples from all gear types and test fishing samples for 1973 through 1988.

	Age												
Year	2	3	4	5	6	7	8	9	10	11	12	13	9+[a]
1973		69	99	124	142	151	193	196	180				180
1974		100	101	129	148	152							
1975	46	70	96	114	154	166							
1976		62	92	115	130	150	171	166					166
1977		65	86	112	133	145	165	179					179
1978		68	83	94	108	123	134	128		152			133
1979	28	75	81	108	125	137	148	136					
1980	42	79	99	113	146	150	165	179					
1981		72	101	115	126	138	136						
1982	35	60	83	116	134	136	139						
1983		85	101	125	143	155	161	155	204				155
1984	35	73	90	112	139	154	162	167	203	173			173
1985	47	82	108	127	142	160	175	183	180	173			183
1986	46	86	102	129	146	156	171	180	187	190	174	173	186
1987	63	77	103	127	146	160	169	182	189	196	191		188
1988[b]		67	94	122	148	158	173	188	196	191	210		194
Average:	43	74	95	118	138	149	162	170	191	179	192	173	174

[a] Average weights for the 9+ category were computed from average weights for ages 9 to 13, weighted by the purse seine age frequency for each age and year.

[b] Average weights for 1988 are for purse seine pound and sac roe samples only from Brannian (1989).

Appendix E. Estimates of population abundance for Prince William Sound herring from aerial surveys and spawn deposition surveys.

Year	Aerial Survey[a]		Spawn Deposition Survey
	Peak Biomass (tonnes)	Mile-Days of Spawn	Biomass (tonnes)
1974	44,110		
1975			
1976	7,990		
1977	16,910		
1978	8,372	36.3	
1979	28,695	72.2	
1980	45,217	73.9	
1981	46,348	140.1	
1982	31,625	65.1	
1983	30,665	99.7	
1984	41,418	86.8	65,590[b]
1985	23,733	149.5	
1986	13,744	152.3	
1987	21,854	155.9	
1988	31,089[c]	236.9	54,230[d]

[a] Aerial survey data for 1974-87 from Brady (1987).

[b] 1984 spawn deposition survey data from Jackson and Randall (1984).

[c] Aerial survey biomass estimate for 1988 from Brannian (1989).

[d] Spawn deposition survey data for 1988 from Biggs and Funk (1988).