Exxon Valdez Oil Spill
Restoration Project Final Report

Herring Natal Habitats

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Study History: This project was initiated in 1994 after an unanticipated decline in the abundance of spawning herring in Prince William Sound in 1993. The project has focused primarily on estimating the biomass of adult herring in Prince William Sound using diver spawn deposition surveys and acoustic surveys on pre-spawning adults. Spawn deposition surveys were conducted during each of the four years of the study. Field studies of egg loss between egg deposition and dive surveys were initiated in 1994. Analyses of egg loss data were conducted by Chris Rooper at the University of Alaska Fairbanks. Acoustic surveys on pre-spawning herring were conducted from 1995-1997. A study of environmental factors affecting herring recruitment was initiated in 1995 at the University of Alaska Fairbanks and is expected to be completed by December 1998. Annual reports describing project results in 1994, 1995, and 1996 were completed under the title 'Herring Spawn Deposition and Reproductive Impairment'.

Abstract: Underwater dive surveys of deposited eggs and acoustic techniques were used to estimate the biomass of adult Pacific herring *Clupea pallasi* in Prince William Sound. Diver estimates of egg numbers were corrected for systematic bias using an inverse prediction procedure that compared diver egg counts and gravimetrically determined laboratory egg counts. Rooper (1996) concluded that cumulative time of air exposure between peak day of spawn and dive surveys was the principal factor affecting egg loss. However, egg loss was also highly variable and site specific due primarily to the extent of wave exposure, kelp type, and predation. Methods used to adjust visual diver egg counts for diver-specific bias strongly affected herring biomass estimates obtained from spawn deposition surveys. Application of diver calibration models including all available data and models of egg loss as a function of cumulative time of air exposure generally resulted in higher adult herring biomass estimates than previously reported. Acoustic surveys on pre-spawning herring may provide relatively accurate and precise estimates of biomass if large overwintering aggregations of fish are present and surveys are completed before fish begin to spawn. Biomass estimates obtained from spawn deposition and acoustic surveys were not significantly different in 1997.

Key Words: *Clupea pallasi*, egg loss, *Exxon Valdez* oil spill, herring, herring recruitment, Prince William Sound, spawn deposition surveys, spawning biomass, stock assessment.

Project Data: *Description of data* - Locations of diver transects, counts of herring eggs in each quadrate, diver calibration sample counts from laboratory analysis. *Format* - R:BASE. *Custodian* - Mark Willette, Alaska Department of Fish and Game, Division of Commercial Fisheries, Cordova, AK 99574, (907) 424-3214, mark_willette@fishgame.state.ak.us. *Availability* - will provide on CD upon request.

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Introduction

This project estimated the biomass of spawning adult Pacific herring *Clupea pallasi* in Prince William Sound (PWS) using underwater diver surveys of deposited eggs and hydroacoustic techniques. This measure of abundance is necessary for monitoring recovery of the injured herring population, including recovery to population levels sufficient for sustainable commercial harvest. In addition, this project collected information about natural losses of deposited eggs which will be used to improve spawner biomass estimates and to provide early life history abundance and survival information to improve understanding of the ecological importance of herring in the PWS ecosystem. Herring provide important forage for many species including some species severely injured by the *Exxon Valdez* oil spill. Predator species include humpbacked whales, seals, sea lions, gulls, sea ducks, shorebirds, halibut, salmon, rockfish, and other fish. In addition to their ecological value, herring are a major commercial resource in PWS. From 1969 to 1993, the average annual combined ex-vessel value of five commercial PWS herring fisheries was $8.3 million. In addition, several thousand pounds of herring and herring spawn on kelp are harvested annually for subsistence purposes forming an important part of the local native culture of Chenega and Tatitlek.

The *Exxon Valdez* oil spill coincided with the spring migration of herring to spawning grounds and adult herring swam through oiled waters on their way to nearshore staging areas. Studies of oil spill injuries to herring were initiated in 1989 and research continued through 1992 with contributions from both state general funds and the Trustee Council (Biggs and Baker 1997). Significant histopathological damage was measured in adults collected in oiled areas in both 1989 and 1990 confirming exposure of the fish to toxins. Oiling of spawning areas caused elevated levels of physical and genetic abnormalities in newly hatched larvae and reduced hatching success of the embryos. Additionally, most of the PWS herring summer rearing and feeding areas were oiled in 1989, based on the oil trajectory and historic fisheries records since 1914 (Reid 1971).

Mortality of young herring was significantly greater in oiled areas in 1989 and 1990, and sublethal effects were measurable in larvae and adults in 1989 and 1990 (Biggs and Baker 1997). Persistent sheening and suspended oil-sediment droplets leaching from beaches and cleaning operations in 1989 and 1990 continued to expose adult and juvenile herring to oil. Laboratory exposures of pre-spawning adult herring to oil showed high concentrations of oil in ovarian tissue (Biggs and Baker 1997). Laboratory studies measuring the effect of known doses of oil on newly hatched larvae linked estimated doses of oil measured in PWS and injuries observed in the field. In addition, measurements of oil in mussel tissues collected at PWS beaches were significantly correlated to indices of injury in herring larvae from spawning beds adjacent to mussel collection sites, and were most correlated with genetic injury endpoints (Biggs and Baker 1997).

Although herring survival varies tremendously under normal conditions, abundance for the 1989 year class is extremely low and results to date strongly implicate the spill as a major cause. One hypothesis is that injury to germ tissue caused by exposure to oil would result in non-viable embryos and larvae. A pilot experiment to measure the ability of herring from this age class to produce viable offspring was conducted in 1992 and hatching success of eggs collected from fish spawning in previously oiled areas was less than half that of eggs collected from fish spawning in pristine areas. Additionally, there were approximately twice as many abnormal larvae from fish spawning in previously oiled areas. Information from this pilot study was used to formulate a study design for the reproductive impairment component of project 94166, which was reported under a separate cover by NOAA Auke Bay Lab.

In 1993, the total observed spawning population was less than one third of preseason predictions and the average sizes of herring in each age class were some of the smallest on record. The total commercial harvest for that year was one of the lowest on record. Pathology studies from the spring of 1993 implicated viral hemorrhagic septicemia (VHS) as a potential source of mortality and stress (Meyers et al. 1994). Investigations of the incidence and effects of diseases occurring in PWS herring have continued. Spawn deposition surveys were not conducted in 1993, but an acoustic survey was conducted near Green and Montague Islands to obtain an updated estimate of the population size following the apparent high mortality of the previous winter.

Objectives

1. Estimate the biomass of spawning herring in PWS using SCUBA diving spawn deposition survey techniques such that the estimate is within ± 25% of the true value 95% of the time using an air-exposure egg loss model.
2. Determine the feasibility of pre-spawning acoustic surveys for estimating herring biomass.
3. Compare spawn deposition, acoustic and aerial surveys biomass estimates.
4. Model herring recruitment in relation to biological and environmental variables.

Methods

Objective 1:

Three sources of information are needed to estimate herring biomass from spawn deposition surveys: (1) diver estimates of minimum number of deposited eggs, (2) age-weight-length (AWL), sex ratio, and fecundity of the spawning herring population, and (3) estimates of egg loss from egg deposition to dive surveys. Spawn deposition surveys were stratified by summary area to account for the potential for discrete herring stocks (Morstad et al. 1997). The biomass of herring spawning in each summary area (B) was estimated from

$$B = TB' \tag{1}$$

where T is the estimated total number of eggs (billions) deposited in each area obtained from dive surveys, and B' is the estimated biomass (tonnes) of herring required to produce one billion eggs. Mean fecundity, sex ratio and body weights of adult herring in each summary area were used to estimate B'. The variance of B was estimated from

$$Var(B) = T^2 Var(B') + (B')^2 Var(T) - Var(T) Var(B') \tag{2}$$

where Var(B') is an unbiased estimate of the variance of B', and Var(T) is an unbiased estimate of the variance of T (Goodman 1960)

General locations of spawning activity were determined from visible milt observed during aerial surveys. Spawning activity was summarized on maps indicating spawning locations and dates. Direct observations of egg distributions were made during dive surveys to correct aerial estimates of egg distribution. Linear distances of shoreline over which herring spawned were estimated from computerized maps of the corrected aerial survey data.

The total number of eggs deposited in each summary area was estimated from a two-stage sampling design (Schwiegert et al. 1985; Blankenbeckler and Larson 1982, 1987) with random sampling at the primary stage (transects) and systematic sampling at the secondary stage (quadrates). Spawn deposition surveys were designed to estimate the biomass of spawning herring to within ± 25% of the true biomass 95% of the time. Confidence intervals were calculated assuming a normal distribution of total egg estimates. A minimum sampling goal of 0.035 % of all potential transects was established to achieve our goals for accuracy and precision. This sampling density was derived from variances obtained from dive surveys conducted in 1984 and 1988 to 1992.

Dive surveys were generally initiated several days after spawning to allow for an improvement in water clarity and the dispersal of sea lions usually present near spawning herring. Each dive team consisted of a lead diver counting eggs (typically the most experienced at this task), a second diver recording data, and a third diver on the surface serving as a dive tender. Each transect extended seaward along a compass course perpendicular to shore from a fixed reference point. Sampling quadrates consisted of a 0.1 m^2 frame constructed of PVC pipe with a depth gauge and compass attached. The location for the first quadrate along each transect was haphazardly selected. Succeeding quadrates were systematically placed every 5-m along the transect until the apparent end of the spawn. The number of herring eggs in each sampling quadrate was visually estimated by the lead diver. Vegetation type, percent vegetation cover, substrate, and depth were also recorded.

The total number of eggs (T) in each summary area was estimated from

$$T = N \cdot \hat{y} \qquad 3$$

where N is the total number of possible transects and $\hat{y}$ is the mean of the total number of eggs for all transects. The total number of possible transects was calculated from the length of the shoreline containing spawn and transect width (0.3162 m). The mean of the total number of eggs for all transects was estimated from

$$\hat{y} = \frac{\sum_{i=1}^{n} \hat{y}_i}{n} \qquad 4$$

where $\hat{y}_i$ is the total number of eggs for transect i and n is the total number of transects. The total number of eggs for transect i was estimated from

$$\hat{y}_i = M_i \bar{y}_i \qquad 5$$

where M_i is the number of possible quadrates in transect i and $\bar{y}_i$ is the mean quadrate egg count in transect i .

The mean quadrate egg count in transect i was estimated from

$$\bar{y}_i = \frac{\sum_{j=1}^{m_i} y_{ij}}{m_i} \qquad 6$$

where m_i is the number of quadrates sampled in transect i, and y_{ij} is the number of eggs in transect i and quadrate j adjusted for diver bias and egg loss.

The variance of T was estimated from

$$Var(T) = [N^2 (10^{-6})^2 [\frac{(1-f_1)}{n} s_1^2 + \frac{f_1(1-f_2)}{\sum_{i=1}^{n} m_i} s_2^2 + \frac{f_1 f_2}{\sum_{i=1}^{n} m_i} s_3^2]] \qquad 7$$

where

$$s_1^2 = \frac{\sum_{i=1}^{n} (\hat{y}_i - \hat{y})^2}{n-1} = \qquad 8$$

variance among transects,

$$s_2^2 = \sum_{i=1}^{n} M_i^2 \sum_{j=1}^{m_i} \frac{(y_{ij} - \bar{y}_i)^2}{n(m_i - 1)} = \qquad 9$$

variance among quadrates,

$$s_3^2 = \sum_{i=1}^{n} \sum_{j=1}^{m_i} Var(y_{ij}) = \qquad 10$$

sum of the variances of the individual predicted quadrate egg counts from the diver calibration model,

$$f_1 = \frac{n}{N} = \qquad 11$$

proportion of possible transects sampled, and

$$f_2 = \frac{m_i}{M_i} = \qquad 12$$

proportion of quadrates sampled within transects (Cochran (1963).

Diver estimates of the number of eggs in each quadrate were adjusted for diver-specific biases. Diver calibration sampling was stratified by diver, vegetation type, and egg density. Two divers independently estimated the number of eggs on removable vegetation in each calibration quadrate. All egg-containing vegetation within the quadrate was then removed and placed in numbered mesh bags. A goal of 98 calibration samples was set for each diver who had less than three years survey participation, and 58 for each calibrated diver who had participated in the project for three or more years. Calibration samples for each diver were taken from each of four vegetation categories (eelgrass, fucus, large brown kelp, and hair kelp) and five egg density categories (0-10,000; 10,000-20,000; 20,000-80,000; 80,000-160,000; and >160,000). Calibration samples were preserved in Gilson's solution and the number of eggs in each sample estimated gravimetrically in the laboratory (Becker and Biggs 1992).

Weighted-regression analyses were conducted to estimate the relationship between visual egg counts made in the field (dependent variable) and laboratory estimates of the number of eggs in each calibration sample (independent variable) assumed to be without errors. The data set used in the analysis consisted of calibration samples from 1994-1997. Calibrations models were calculated for all calibrated divers: Bill Bechtol (1994-1995), Karl Becker (1994-1997), Evelyn Brown (1994-1995), Beth Haley (1994-1997), and Matt Miller (1994-1997). All calibration data from all years was pooled to ensure that all egg counts were within the range of the calibration model. Separate regression analyses were conducted for each year, diver and vegetation type. Regression weights were calculated giving the most weight to the current year and the least weight to the most distant years. For example, a model for 1995 was calculated by giving the calibration data for 1995 a weight of one, the data for 1994 and 1996 a weight of ¼ and 1997 a weight of $^{1}/_{8}$. This method assumes that data from recent years is more relevant to the current year's calibration. The analyses were run with the intercept forced through zero. The diver calibration model was

$$\log(dc) = \beta_{jk} \log(lc) + \varepsilon_{jk} \qquad \textbf{13}$$

where dc was the diver count, lc was the lab count, and β_{jk} was the parameter estimate for diver j and vegetation type k. The inverse-prediction method used to adjust the diver egg counts from the spawn deposition survey was

$$adc_{ij} = e^{\frac{\log(dc_{ij})}{\hat{\beta}_{jk}}} \qquad \textbf{14}$$

where adc$_{ij}$ was the adjusted diver count for quadrate j in transect i and adc$_{ij}$ was the original diver count for quadrate j in transect i. The variance for the adjusted diver counts was

$$VAR(adc_{ij}) = \left(\frac{\log(dc_{ij})^2 VAR(\hat{\beta}_{jk})}{\hat{\beta}^4_{jk}}\right) e^{\frac{2\log(dc_{ij})}{\hat{\beta}_{jk}}} \qquad \mathbf{15}$$

The biomass of herring required to produce one billion eggs (B') was estimated as

$$B' = \frac{\overline{W}S}{F(\overline{W}_f)} 10^3 \qquad \mathbf{16}$$

where $\overline{W}$ is the estimated average weight (g) of male and female adult herring in each summary area, S is the estimated ratio of total adult herring biomass to adult female biomass, F($\overline{W}_f$) is the estimated fecundity at the average weight of adult female herring in each summary area, and 10^3 is a conversion factor.

Therefore, the variance of B' was approximately

$$\begin{aligned} Var(B') = (10^3)^2 (& [\frac{S}{F(\overline{W}_f)}]^2 Var(\overline{W}) \\ & +[\frac{\overline{W}}{F(\overline{W}_f)}]^2 Var(S) \\ & +[\frac{\overline{W}S}{F(\overline{W}_f)^2}]^2 Var(F(\overline{W}_f)) \\ & +2Cov(\overline{W},S)[\frac{S}{F(\overline{W}_f)}][\frac{\overline{W}}{F(\overline{W}_f)}] \\ & -2Cov[\overline{W},F(\overline{W}_f)][\frac{S}{F(\overline{W}_f)}][\frac{\overline{W}S}{F(F(\overline{W}_f))^2}] \\ & -2Cov[S,F(\overline{W}_f)][\frac{\overline{W}}{F(\overline{W}_f)}][\frac{\overline{W}S}{F(\overline{W}_f)^2}]). \end{aligned} \qquad \mathbf{17}$$

None of the covariance terms in equation 17 were included in the estimate of the variance of B', because average weight, sex ratio and fecundity were all estimated from the same samples and were not independent.

Age composition, sex ratio, and mean weight, length and fecundity were estimated from samples collected using commercial herring seines deployed from commercial seine vessels. Sampling was initiated soon after concentrations of herring appeared in nearshore areas and continued periodically throughout the spawning migration. Sampling was stratified by date and locality in each summary area. Sample sizes for each stratum (n=450) were established to estimate the age composition of the population to within ± 25% of the true proportion 95% of the time (Thompson 1987) assuming that less than 5% of the collected scales were unreadable. Herring AWL sampling procedures are described in greater detail by Baker et al. (1991) and followed standard protocols outlined in project operational manuals (Wilcock et al. 1997).

Fecundity was estimated from subsamples of female herring taken from AWL samples stratified by fish length. Egg and gonad weights were used to estimate the fecundity of average-size female herring ($F(\overline{W}_f)$). Sample sizes (n=200) were established to insure that fecundity estimates would contribute less than 1% to the confidence intervals on the biomass estimate. Fecundity was measured for 20 to 30 females within each 10-mm length category from 181 to 250-mm standard length and for 20 to 30 females 180-mm or smaller.

The weighted mean body weight and sex ratio was estimated for the Montague Island summary area. The observed aerial survey biomass at each locality was used to weight the mean. Only samples from Montague Island were used because spawning in other areas was limited.
Sex ratio (S) was calculated as the ratio of the number of herring of both sexes in AWL samples to the number of female herring. The variance of S was

$$Var(S) = \frac{S^2(S-1)}{n} \qquad \textbf{18}$$

where n is the number of fish in the AWL sample.

Mean fecundity was estimated from mean female body weight and a linear regression equation relating fecundity to body weight for PWS herring (Hourston et al. 1981). The variance of estimated mean fecundity was approximated by the variance of predicted means from the fecundity-weight regression

$$Var[F(\overline{W}_f)] = s^2 [\frac{1}{n} + \frac{1}{q} + \frac{(\overline{W}_f - \overline{WF})^2}{\Sigma(W_i - \overline{WF})^2}] \qquad \textbf{19}$$

where s^2 is the residual mean square from the fecundity-weight linear regression, $\overline{W}_f$ is the mean female body weight in the spawning population, $\overline{WF}$ is the mean body weight in the fecundity sample, W_i is the weight of individual females in the fecundity sample from each summary area, n is the total number of females in the fecundity sample, and q is the total number of females in the AWL samples from each summary area (Draper and Smith 1981)

Egg loss studies were conducted in 1994-1995 to improve diver survey biomass estimates and our understanding of the mechanisms affecting early life history survival. We will use the term 'egg loss' to refer to the proportion of eggs lost through physical removal and mortality between spawn deposition and dive surveys. In earlier PWS spawn deposition surveys, egg loss was assumed to be 10% between spawn deposition and dive surveys conducted 5-6 days later (Haegele et al. 1981; Blankenbeckler and Larson 1982). In the present study, the effects of depth, air exposure, vegetation type, wave action, and bird and fish predation on egg loss were investigated. Analyses of egg loss data were conducted by C.N. Rooper, L.J. Haldorson and T.J. Quinn at the University of Alaska Fairbanks. Their methods are summarized in appendix I. Rooper (1996) provides a detailed description of the methods used in this analysis.

Cumulative time of air exposure between peak day of spawn and dive surveys was found to be the principal factor affecting egg loss (Rooper 1996). The square root of cumulative time of air exposure was a linear function of depth (Rooper 1996). Regression analyses were conducted to determine the relationship between cumulative air exposure and depth for each day and location dive surveys were conducted. Regression equations were used to estimate the cumulative air exposure for each quadrate in the intertidal zone. Egg loss rate was then calculated for each intertidal quadrate using equations 20 and 21 calculated from the 1994 and 1995 egg loss data

$$z = 0.0809(0.0130) + 0.0004(0.0002) * AE \qquad \textbf{20}$$

$$z = 0.0524(0.0115) + 0.0006(0.0001) * AE \qquad \textbf{21}$$

where z is the daily egg loss rate and AE is the cumulative air exposure between peak day of spawn and dive surveys (standard errors for the parameter estimates are indicated in parentheses). Equation 20 was applied to 1994, 1996 and 1997 spawn deposition data, because it included all substrates. Equation 21 was applied only to the 1995 data, because it was derived using egg loss study data collected in 1995 but only rocky substrates were included. For quadrates in the subtidal zone, a regression analysis was conducted to estimate the relationship between egg loss and number of days from peak spawn using all data from the egg loss study. This analysis indicated that the daily egg loss rate for subtidal quadrates was 0.05.

All egg counts were first adjusted for diver bias, then assuming a constant instantaneous rate of egg loss, the number of eggs at peak spawn was calculated from the following equation

$$y_{ij} = adc_{ij}\, e^{zt} \qquad \textbf{22}$$

where y_{ij} is the number of eggs in quadrate j and transect i adjusted for diver bias and egg loss (Eqn. 6), adc_{ij} is the number of eggs in quadrate j in transect i adjusted for diver bias, and t is the number of days between peak spawn and the dive survey.

Objective 2:

Standard acoustic techniques (Thorne 1983b; Ehrenberg and Lytle 1972) for echointegration and dual beam processing of target strength were used to independently estimate the biomass of herring present near spawning grounds during the spring migration. Energy reflected from fish concentrations was measured and converted to fish density using measurements of energy reflected from single fish (target strength) and knowledge of the sample volume (transducer directivity). Net sampling was conducted to subsample the acoustic targets to verify species, size and obtain other biological information on the insonified fish.

The acoustic survey employed one commercial purse seiner under short-term vessel charter to assist in searching for herring schools and to conduct net sampling. The acoustics vessel was outfitted with either a BioSonics 120 or 200 Khz echo sounder with a dual beam pre-amplified transducer mounted on a 1.2 m BioSonics Biofin in a down-looking configuration (Table 1). The Biofin was towed at a depth of about 2-m at approximately 5-m off to one side of the vessel. Acoustic signals were processed in real-time using the BioSonics ESP 221 Echo square integration software, a digital audio tape recorder for signal backup, and a chart recorder for high-resolution paper echograms. The catcher vessel was equipped with a seine approximately 30-m deep typical of the gear-type used in the commercial sac roe herring fishery. Twenty-meter and 35-m deep anchovy seines (stretch mesh 1.5 cm) were used in 1997.

A stratified-systematic design was used for acoustic surveys. Several large geographic strata were established based on herring densities observed in previous years and spring aerial surveys. Each stratum was sampled using a series of evenly spaced parallel transects orthogonal to the coastline. Zigzag transects were sometimes used in areas of low herring abundance. Sampling efforts were allocated to the entire stratum including areas of lower fish density. A starting point was selected at random from the first half kilometer of each stratum. The location and length of each transect was determined using coordinates recorded from a Global Positioning System (GPS) located on each vessel. Based on variances obtained from the 1995 spring survey a minimum of 0.79% of all possible transects in each stratum was sampled. This level of sampling was set to achieve an acoustic biomass that was within plus or minus 25% of the true biomass within each stratum 95% of the time.

To determine if future acoustic sampling could be confined to large schools an effort was made in 1997 to evaluate the importance of small schools in the total biomass estimate. Studentized t-tests were conducted to test for differences between biomass estimates obtained from sampling the entire stratum and biomass estimates obtained from sampling just the largest herring schools found in the stratum. Two areas were used for this comparison. First, the biomass estimate for the Montague summary area was compared to the biomass estimate calculated from a large school occurring in Zaikof Bay. Second, the biomass estimate for the Southeast summary area was compared to the biomass estimate for several large herring schools occurring in Saint Matthews Bay.

Herring target strength was estimated from a relationship between mean length and target strength (decibels) per kg of fish (Thorne 1983a). Thorne's (1983a) empirical relationship assumes the following logistical equation:

$$\gamma = \frac{\bar{\sigma}}{\overline{W}} = a(\bar{l})^{-b} \qquad \textbf{23}$$

where σ is the mean acoustic backscattering coefficient, $\overline{W}$ is the mean weight (kg), , $\bar{l}$ is the mean length (cm), and a and b are constants. Values for the constants (a and b) were obtained from data for a variety of fisheries presented by Thorne using a linear regression of $\log_{10} l$ versus 10 log (σ/w), where 10 log (σ/w) was referred to in Thorne (1983a) as "target strength per kg." Average herring length and weight data was compiled from samples obtained by the purse seine catcher vessel. These measured data were applied to Thorne's (1983a) empirical relationship to obtain the ratio $\gamma = \sigma/w$ and the mean backscatter coefficient (σ). As a cross check, *in situ* measurements of target strength from dual beam acoustic data were generated and compared with Thorne's (1983a) empirical formula.

Echo integration was used to determine the density of acoustic targets within each depth interval. The echo integral (E_k) for depth interval *k* is given by

$$E_k = \int_{t_1}^{t_2} |v(t)|^2 \, dt \qquad \textbf{24}$$

where v(t) is the voltage produced by the echosounder at time t. The time gate t_1 to t_2 was chosen to correspond to a specific depth interval to be sampled (Ehrenberg and Lytle 1972).

Each sample transect was divided into *j* elementary distance sampling units (EDSU). The length of the EDSU's was chosen to minimize serial correlation without unnecessarily eliminating information on fish distribution. The mean echo integral (E_{jk}) was then calculated for each depth interval-EDSU cell (MacLennan and Simmonds 1992). The biomass of fish per unit area in each cell (β_{jk}) is given by

$$\beta_{jk} = [(C\,\bar{g}/\Psi < \sigma >)]\ E_{jk} \qquad \mathbf{25}$$

where C is a calibration factor, g is the mean TVG correction factor, Ψ is the equivalent beam angle (a measure of beam width), $\langle\sigma\rangle$ is the mean acoustic cross section per unit weight of the target, and E_{jk} is the mean echo integral (MacLennan and Simmonds 1992). A relationship provided by Thorne (1983b) was used to estimate target strength per kg using mean lengths of herring in each stratum estimated from net samples.

The mean biomass per meter squared of herring along the *i*th transect in the *h*th stratum (β_{ih}, kg m^{-2}) is given by

$$\bar{\beta}_{ih} = \frac{\sum_j \sum_k \beta_{jk}}{n_{jk}} \qquad \mathbf{26}$$

where n_{jk} is the number of depth interval-EDSU cells in the *i*th transect (MacLennan and Simmonds 1992). The mean biomass sampled in the *h*th stratum (β_h, kg m^{-2}) is estimated from

$$\bar{\beta}_h = \frac{\sum_i (\bar{\beta}_{ih}\, w_{ih})}{n_h} \qquad \mathbf{27}$$

where n_h is the number of transects in the *h*th stratum, and $w_{ih} = L_{ih} / \bar{L}_{ih}$, where L_{ih} is the length of the *i*th transect within the *h*th stratum (Jolly and Hampton 1990; MacLennan and Simmonds 1992).

The variance of β_h is given by

$$Var(\bar{\beta}_h) = \sum_i W^2_{ih} \frac{S_h^2}{n_h} + 2 \sum_i \sum_j w_{ih} w_{jh} Cov(B_{hi}, B_{hj}) \qquad \mathbf{28}$$

where

$$S_h^{\,2} = \Sigma \frac{(\beta_{ih} - \bar{\beta}_h)^2}{(n_h - 1)} \qquad \mathbf{29}$$

where n_h is the number of transects in stratum h (Thompson and Seber 1996). A covariance term was included in the biomass variance estimate to account for autocorrelation among transects.

The total biomass of herring in each survey area (β, kg) is then given by

$$\beta=\sum_{h}\overline{\beta_h}\cdot A_h \qquad \mathbf{30}$$

where A_h is the area (m^2) of the *h*th stratum in the survey area. The variance of β is given by

$$Var(\beta) = \sum_{h} A_h^2 \; Var(\overline{\beta_h}) \qquad \mathbf{31}$$

Objective 3:

Studentized t-tests were conducted to test for differences between spawn deposition biomass estimates obtained using an air-exposure egg loss model and those obtained using a constant 10% egg loss. Studentized t-tests were also conducted to test for differences between spawn deposition biomass estimates obtained using an air-exposure egg loss model and acoustic and aerial survey biomass estimates. A regression analysis was conducted to estimate herring biomass from aerial survey estimates of linear shoreline kilometers of milt. The dependent variable in the analysis was the age-structured analysis (ASA) model estimate of herring biomass for PWS as a whole, and the independent variable was the total shoreline kilometers of observed milt. All tests were conducted between estimates obtained within the same year. We did not test for differences between the spawn deposition biomass estimates obtained using an air-exposure egg loss model and the acoustic biomass estimates in 1995 and 1996. We were unable to conduct these tests, because the variance of the acoustic biomass estimate was not calculated in 1995 (Thorne et al. 1996), and the acoustic survey in 1996 did not include all of the fish known to be present in the survey area (Thomas et al. 1996). We conducted separate tests among estimates for the Montague and Southeast summary areas in 1997, because we were able to thoroughly survey both areas that year.

Objective 4:

E. H. Williams evaluated environmental factors affecting the recruitment of herring in PWS, British Columbia, Sitka Sound, the eastern Bering Sea, and Norton Sound. The methods used in this work are described in a Ph.D. dissertation completed by E.H. Williams (Appendix II).

Results

Objective 1:

The total shoreline kilometers of herring spawn in PWS increased from 23.3 to 68.5 from 1994 to 1997 (Figure 1). During this period, the shoreline kilometers of spawn increased every year in the Northeast summary area. The locations of spawn deposition survey dive transects in 1994 through 1997 are indicated in Figures 2 and 3. Analyses of diver calibration data indicated that divers consistently underestimated the number of deposited eggs at low egg densities during all years (Figure 4) and on all kelp types (Tables 2-5). The relationship between female body weight and fecundity varied little during the 4 years of this project (Figure 5).

The biomass of the 1988 year class dominated total biomass from 1994 to 1996 (Tables 6-9). In 1994, herring less than age 6 composed only 11% of total biomass, whereas by 1997 these younger fish composed nearly 50% of total biomass. This increased contribution to total biomass by younger fish was largely due to the additional biomass contributed by the 1992 and 1994 year classes.

Cumulative time of air exposure as a function of the depth of deposited eggs was found to be the predominant variable affecting herring egg loss (Appendix I). Results from analyses of egg loss data conducted by C.N. Rooper, L.J. Haldorson and T.J. Quinn are summarized in appendix I. Rooper (1996) provides a detailed description of the results from this analysis.

The total biomass of adult herring in PWS during 1994 was estimated to be 25,852 tonnes from spawn deposition diver surveys (Table 10). The 95% confidence limits ranged from 10,236 tonnes to 41,467 tonnes (Table 11). The Montague Island summary area accounted for a large majority of the estimated biomass (25,813 tonnes), but small amounts of spawning herring were present in the Southeastern (28.9 tonnes) and Northeastern (9.5 tonnes) summary areas.

The total biomass of adult herring in PWS during 1995 was estimated to be 31,245 tonnes from spawn deposition diver surveys (Table 12). The 95% confidence limits ranged from 9,966 tonnes to 52,524 tonnes (Table 13). Most of the estimated biomass spawned in the Montague Island summary area (28,742 tonnes), but small amounts of spawning herring were present in the Southeastern (1944 tonnes) and Northeastern (558 tonnes) summary areas. The total biomass estimate in 1995 was approximately 5,393 tonnes more than the 1994 biomass estimate which was primarily due to more spawn in the northeast and southeast areas of PWS.

The total biomass of adult herring in PWS during 1996 was estimated to be 35,021 tonnes from spawn deposition diver surveys (Table 14). The 95% confidence limits ranged from 12,228 tonnes to 57,813 tonnes (Table 15). Most of the estimated biomass spawned in the Montague Island summary area (31,301 tonnes), but small amounts of spawning herring were present in the Southeastern (760 tonnes) and Northeastern (2,960 tonnes) summary areas. The total biomass estimate in 1996 was approximately 3,776 tonnes more than the 1995 biomass estimate, which was primarily due to more spawn in the northeast area of PWS.

The total biomass of adult herring in PWS during 1997 was estimated to be 21,839 tonnes from spawn deposition diver surveys (Table 16). The 95% confidence limits ranged from 8,842 tonnes to 34,835 tonnes (Table 17). Most of the estimated biomass spawned in the Montague Island summary area (15,099 tonnes). Additional herring biomass was present in the Southeastern (4,178 tonnes), Northeastern (2,354 tonnes), and Northern (207 tonnes) summary areas. The total biomass estimate in 1997 was approximately 13,182 tonnes less than the 1996 estimate. Although the total herring biomass decreased, the total miles of spawn in 1997 increased by approximately 57% from 1996 mainly due to increased spawning in the Southeast and Northern areas of PWS.

It should be noted that our biomass variances were slightly underestimated, because 3 covariance terms were omitted from the calculations due to a lack of independence.

Objective 2:

The biomass of herring in the spring of 1995 was estimated from five acoustic surveys in the Montague Island summary area (Thorne et al. 1995). Two daytime surveys were conducted in both Rocky Bay and Zaikof Bay, and two nighttime surveys in Rocky Bay. The average length of herring from samples collected in Rocky Bay was 218 mm resulting in a scaling factor of -32.3 dB/kg. Average length of herring from samples collected in Zaikof Bay was 184 mm resulting in a scaling factor of -31.9 dB/kb. The resulting biomass estimates for Rocky Bay and Zaikof Bay were 10,480 and 2,804 tonnes (Table 18).

The biomass of herring in the spring of 1996 was estimated from seven acoustic surveys in the Montague Island summary area (Thomas et al. 1996). Two evening surveys were conducted in Rocky Bay and five evening surveys in Stockdale Harbor. The average length of herring from samples collected in Rocky Bay was 215 mm resulting in a scaling factor of -32.3 dB/kg. Average length of herring samples in Stockdale Harbor was 210 mm resulting in a scaling factor of -32.3 dB/kb. The resulting biomass estimates for Rocky Bay and Stockdale Harbor were 1,319 and 3,227 tonnes (Table 18). A substantial portion of the biomass known to be present in these two bays was not included in the survey, because the fish moved into water too shallow for the survey vessel.

The biomass of herring in the spring of 1997 was estimated from several acoustic surveys conducted during two trips between March 26 and April 6, 1997 (Kirsh and Thomas 1997). The Montague Island, Northeast and Southeast summary areas were surveyed. Large aggregations of herring were found primarily in Zaikof and Rocky Bays on Montague Island and in Olsen Bay in the Southeast summary area. The largest aggregation was observed in Zaikof Bay in late March. Net sampling indicated that juveniles composed 48% of the biomass in this aggregation. Average length of herring from samples collected from all the areas ranged between 175 to 233 mm. The appropriate target strength scaling factor was applied for each area. The total adult herring biomass for the Montague, Southeast, and Northeast summary areas was 22,985 tonnes (Table 18). The 95% confidence intervals on this estimate ranged from 18,603 tonnes to 27,367 tonnes.

The total herring biomass (adults and juveniles) estimated from all transects in the Southeast summary area in 1997 (3,882 tonnes) was significantly greater than the biomass estimated only at the highest density site at St. Matthews Bay (2,766 tonnes) within the Southeast summary area (p=0.0001). The total herring biomass estimated from all transects in the Montague summary area in 1997 (28,008 tonnes) was not significantly greater than the biomass estimated only at the highest density site at Zaikof Bay (25,823 tonnes) within the Montague summary area (p=0.3102).

Objective 3:

In 1994-1996, spawn deposition biomass estimates obtained using an air-exposure egg loss model were significantly different from estimates obtained from aerial surveys and spawn deposition surveys using a constant 10% egg loss (Tables 18-19). In 1997, spawn deposition biomass estimates obtained using an air-exposure egg loss model were not significantly different from all biomass estimates obtained using other methods except an estimate obtained using a constant 10% egg loss for the Montague summary area (Tables 18-19). Several variables related to comparison of biomass estimates obtained from aerial and spawn deposition surveys are indicated in Table 20. Regression analysis indicated that the ASA model estimate of herring biomass for PWS as a whole and the total shoreline kilometers of observed milt were significantly correlated (R^2=0.892, df=18, p<0.001). The regression slope estimate indicated that each kilometer of observed milt corresponded to 521.2 tonnes of herring biomass on average.

Objective 4:

E. H. Williams evaluated environmental factors affecting the recruitment of herring in PWS, British Columbia, Sitka Sound, the eastern Bering Sea, and Norton Sound. The results of this work are described in a Ph.D. dissertation completed by E.H. Williams (Appendix II).

Discussion

Accurately estimating the biomass of herring populations is difficult, because herring are a highly mobile species, exhibiting large changes in distribution and aggregation throughout the year. However, during the 2-3 week period from egg deposition to hatch, embryos are immobile and the locations of spawn deposition can be readily determined from aerial surveys. Application of the egg production method to herring eggs deposited on kelp (Humphreys and Haegele 1976) may be a relatively accurate method of estimating adult herring biomass, but the method is relatively costly. Spawn deposition survey estimates of adult herring biomass are based on the assumption that all fully recruited age classes spawn annually after recruitment and that all spawning is observed. The extent of incomplete participation in spawning is not known, but large deviations between spawn deposition biomass estimates in PWS during the late1980's and those obtained from other methods suggest that this may be a problem (Morstad et al. 1997).

Although our surveys were designed to estimate the biomass of adult herring in PWS as a whole, our biomass estimates and associated variances apply only to those schools or spawn patches that were located during acoustic or aerial surveys. Every effort was made to locate herring throughout PWS by conducting frequent surveys and utilizing information obtained by the private pilots and fishermen. But, some adult herring present in PWS may not have been observed during periods of poor weather when aerial and acoustic surveys were not practical. The likelihood that some schools of herring were not located during acoustic surveys was greater than during aerial surveys, due to the relatively small volumes of water scanned for fish during acoustic surveys. As a result, acoustic biomass estimates were less than those obtained by other methods in 2 of 3 years (Table 18).

Loss of eggs between spawn deposition and dive surveys and adjustments for diver-specific bias in visual egg counts appeared to be important factors affecting the accuracy of spawn deposition biomass estimates. In the present study, divers generally underestimated the number of deposited eggs, but this bias was greater at low egg densities (Figure 4). Our diver calibration method utilized all available data yet gave the current year the greatest weight in the regression. This approach increased the precision of our diver calibrations due to the greater degrees of freedom in the regressions. Rooper (1996) concluded that cumulative time of air exposure between peak day of spawn and dive surveys was the principal factor affecting egg loss. However, egg loss was also highly variable and site specific due primarily to the extent of wave exposure, kelp type, and predation. Rooper's (1996) air-exposure model accounted for 28% of the variability of egg loss when data from all years was pooled. Egg loss rates based upon air exposure were greatest at the shallowest depths and decreased exponentially with depth. Interannual variation in the magnitude of other factors affecting egg loss may cause actual egg loss rates to vary substantially from those estimated from an air-exposure model, but the annual cost of estimating actual egg loss rates is prohibitive. Nevertheless, an air-exposure model probably provided a more accurate estimate of actual egg loss rates than the constant 10% loss from peak day of spawn to dive surveys that was used in previous years (Wilcock et al. 1995; Willette et al. 1996, 1997). Rooper (1996) found that mean daily egg loss rates ranged from about 5% in the subtidal zone to 20% at the shallowest depths. The mean number of days from peak day of spawning to dive surveys ranged from 6 to 11 days (Table 20).

We underestimated spawn deposition biomass variances, because 3 covariance terms were omitted from the calculations. However, the magnitude of the underestimate was probably small, because there was no logical reason for the covariances among average weight of male and female herring, the ratio of total adult biomass to female biomass, and fecundity at average female weight to be substantially greater than zero.

Application of diver calibration models including all available data and models of egg loss as a function of cumulative time of air exposure generally resulted in higher adult herring biomass estimates than previously reported (Table 18). Our previously reported spawn deposition biomass estimates for 1994-1996 were obtained using a constant 10% egg loss rate and various methods for diver calibrations (Wilcock et al. 1995; Willette et al. 1996, 1997). In the present study, we have applied the same methods for estimating diver calibration parameters and egg loss rates for all the years included in the analysis. Cumulative time of air exposure between peak day of spawn and dive surveys was used to estimate egg loss rates (Rooper 1996).

The differences between our original and revised spawn deposition biomass estimates for 1994 (67%) and 1995 (72%) were due to application of different diver calibration and egg loss methods. In an analysis of the 1994 data, Wilcock et al. (1995) tested for differences in the diver calibration model parameters among years, divers and kelp types and pooled those that were not different. Data was pooled for the three most consistent divers using data from 1990-1994. Data from 1992-1994 was pooled for two less consistent divers. Data for the various kelp types was pooled into three groups. The effect of this method on the biomass estimate relative to the method used in the present study is not clear. In an analysis of the 1995 data, Willette et al. (1996) estimated the calibration model parameters separately for each diver and kelp type using a weighted-regression procedure with more recent years given a greater weight. In addition, the range of the quadrate counts exceeded the range of the available calibration data. The slope of the calibration line was determined from multiple linear regression within the range of the calibration data, and it was assumed to be equal to one above the range of the data. This method probably resulted in a lower biomass estimate than was obtained in the present study, because the higher egg counts were adjusted less. The relatively large difference between our original and revised biomass estimates in 1995 was probably also due to the variables affecting the air-exposure model. Egg loss rates obtained from our air-exposure model were a function of the depth of deposited eggs and the time between peak spawn and the dive survey. The depth of deposited eggs was relatively shallow and the time between peak spawn and the dive survey was greater in 1995 than in 1994 (Table 20). Both of these factors probably increased the revised estimate above that previously reported.

The differences between our original and revised spawn deposition biomass estimates for 1996 and 1997 were probably also due to differences in the variables affecting the air-exposure model. Our biomass estimates obtained using a constant 10% egg loss versus an air-exposure model differed by 39% in 1996 and 14% in 1997 (Table 18). The greater difference for 1996 was probably due to the shallower mean depth of deposited eggs and the later mean number of days between peak spawn and dive surveys compared to 1997 (Table 20). Both of these factors probably increased the egg loss estimates in 1996 compared to 1997.

Biomass estimates obtained from total shoreline kilometers of observed milt were generally more closely related to spawn deposition biomass estimates obtained using a 10% egg loss rate than to estimates obtained using an air-exposure egg loss model (Table 18). This is probably because spawn deposition biomass estimates obtained using a 10% egg loss rate were used in the ASA model, and ASA model biomass estimates were used to convert total shoreline kilometers of milt to biomass. Our regression analysis indicated that each shoreline kilometer of milt (spawn) corresponded to 521.2 tonnes of biomass on average. This value is substantially less than the 1,633 tonnes per kilometer estimated by Stevenson and Outram (1953) for herring spawning at Vancouver Island.

Variation in mean egg density probably accounted for much of the difference between biomass estimates obtained from total shoreline kilometers of milt versus spawn deposition surveys. During the four years of this study, mean egg density varied by a factor of three, whereas mean patch width varied less than 50% (Table 20). The highest mean egg density was observed in 1994 when the biomass was composed primarily of older fish (89% age 6 and older). The lowest egg density occurred in 1997 when the biomass was composed of younger fish (50% age 6 and older). The total kilometers of milt observed in 1997 was also substantially greater than in the other three years (Figure 1), but the spawn deposition biomass estimate obtained using an air-exposure egg loss model was relatively low. This difference was probably due to the low mean egg density observed in 1997. Early efforts to estimate herring biomass from spawn deposition surveys relied primarily on measurements of patch area and mean egg density (Hourston et al. 1972).

Acoustic surveys on pre-spawning herring may provide relatively accurate and precise estimates of biomass if large overwintering aggregations of fish are present and surveys are completed before fish begin to spawn. Our acoustic biomass estimate in 1997 was not significantly different from our spawn deposition estimate using an air-exposure egg loss model. This may have occurred, because our acoustic survey in 1997 provided a more accurate estimate than in the other years. Acoustic methods are limited in the amount of area that can be surveyed, and the biomass of herring beyond areas surveyed is uncertain. In late March or early April, herring in PWS begin to disperse from overwintering habitats to spawning areas. Acoustic surveys on overwintering aggregations may provide the most accurate estimate of adult herring biomass, but a sufficient number of net samples must be taken to accurately estimate the proportions of adult and juvenile fish present in overwintering aggregations. Relatively deep small-mesh purse seines rather than commercial herring seines are needed for this purpose to insure that juveniles and adults are adequately represented in the samples. After adults begin to disperse to spawning grounds, relatively accurate acoustic surveys are still possible on large aggregations of fish in deep water. However, the fish are highly mobile at this time, so there is always some uncertainty about whether all fish have been included in the survey or some fish have been included more than once. Use of more than one acoustic vessel provides a more synoptic survey reducing these problems. During this period, less intensive net sampling is needed to estimate mean length and age composition, because the sizes and ages of fish in pre-spawning aggregations is less variable than in overwintering aggregations. The timing of acoustic surveys during the pre-spawning period is critical, because if the fish move into shallow water to spawn acoustic surveys are not practical. This occurred during our survey in 1996 resulting in an acoustic biomass estimate that was much less than what was known to be present in the area.

Conclusions

1. Methods used to adjust visual diver egg counts for diver-specific bias strongly affect herring biomass estimates obtained from spawn deposition surveys.
2. Cumulative time of air exposure as a function of the depth of deposited eggs was found to be the predominant variable affecting herring egg loss between egg deposition and dive surveys.
3. Application of diver calibration models including all available data and models of egg loss as a function of cumulative time of air exposure generally resulted in higher adult herring biomass estimates than previously reported.
4. Acoustic surveys on pre-spawning herring may provide relatively accurate and precise estimates of biomass if large overwintering aggregations of fish are present and surveys are completed before fish begin to spawn.

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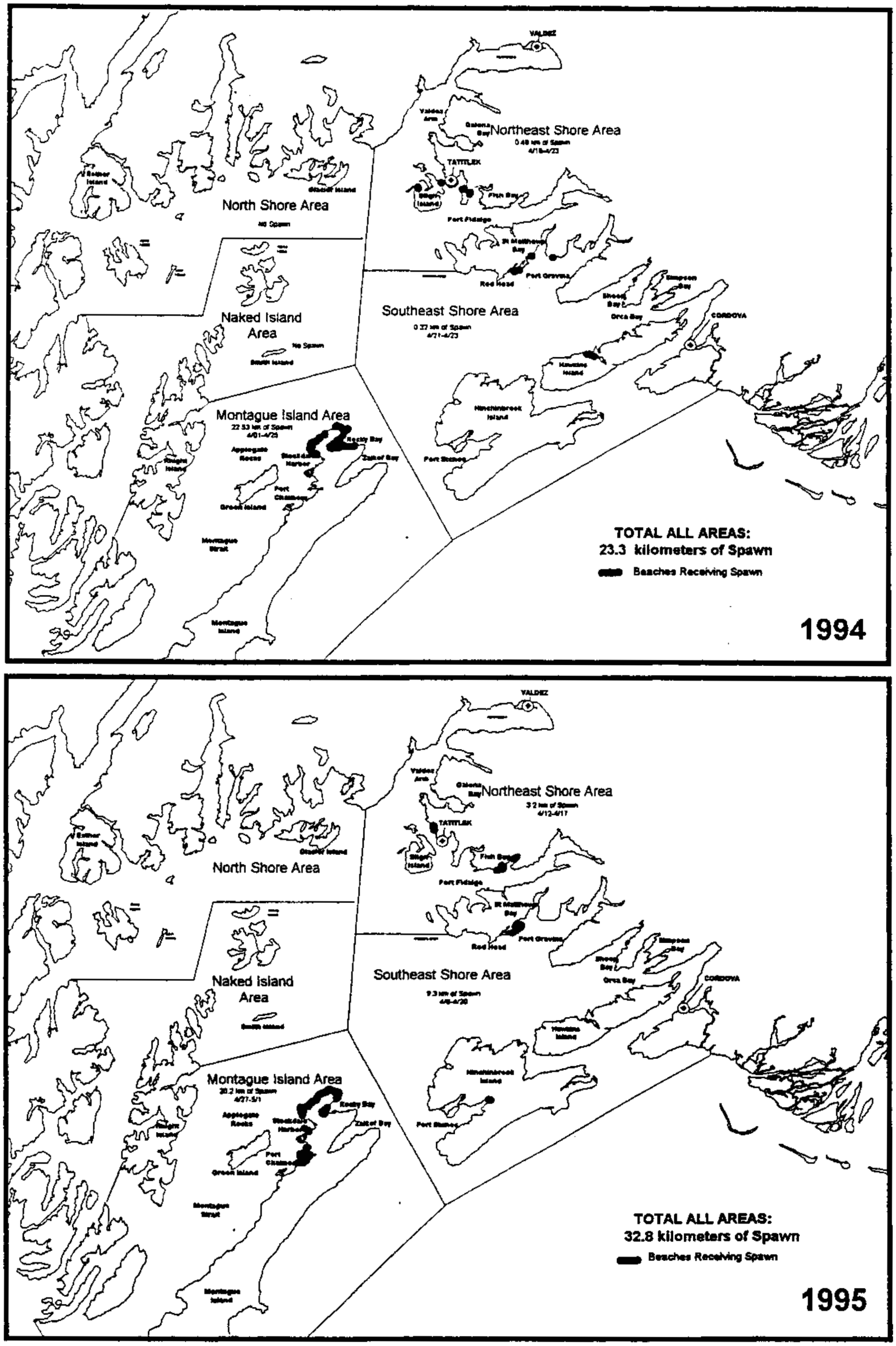
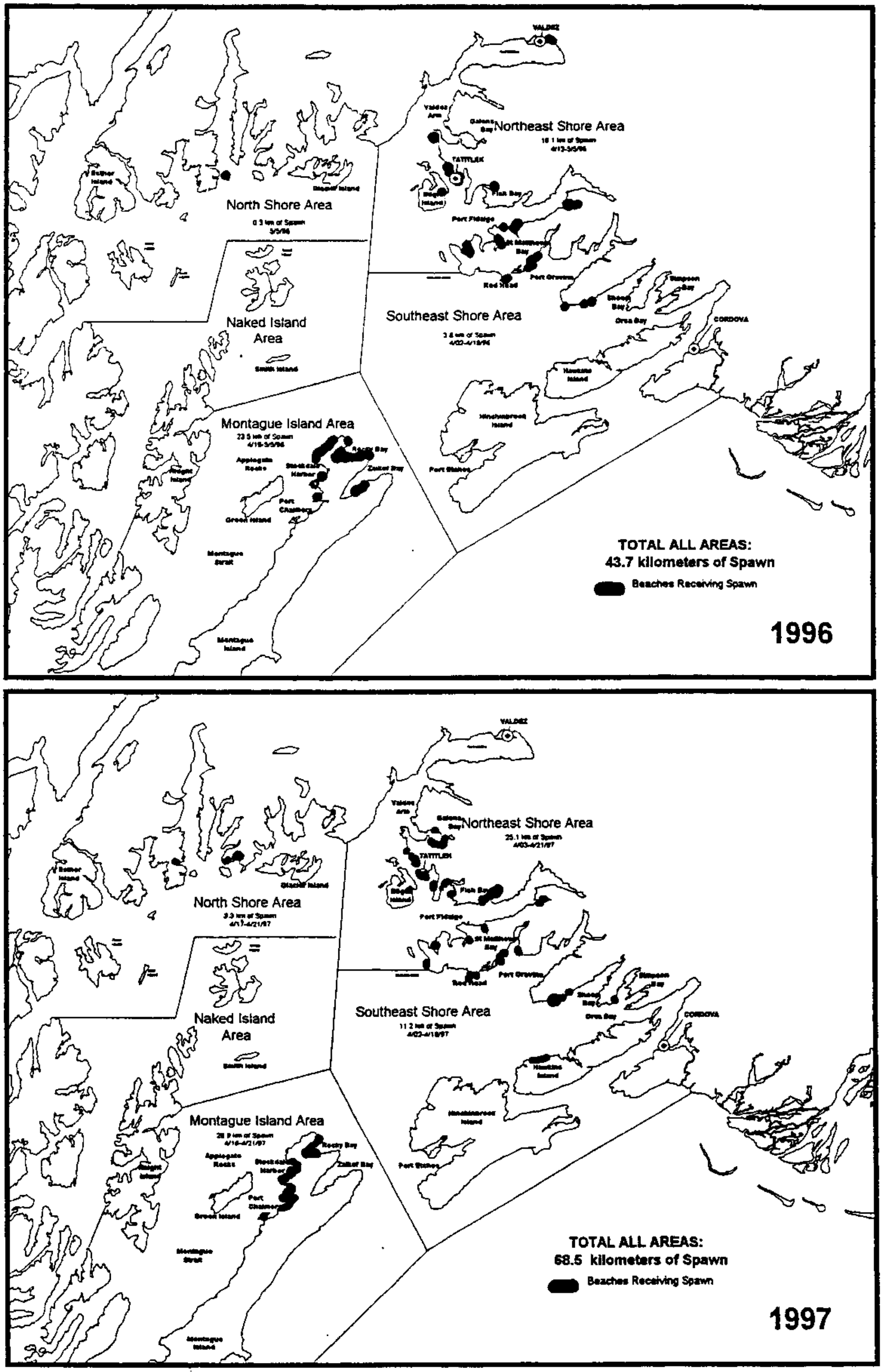


Figure 1. Location of spawning herring and kilometers of shoreline observed during aerial surveys, Prince William Sound, Alaska, 1994 to 1997.



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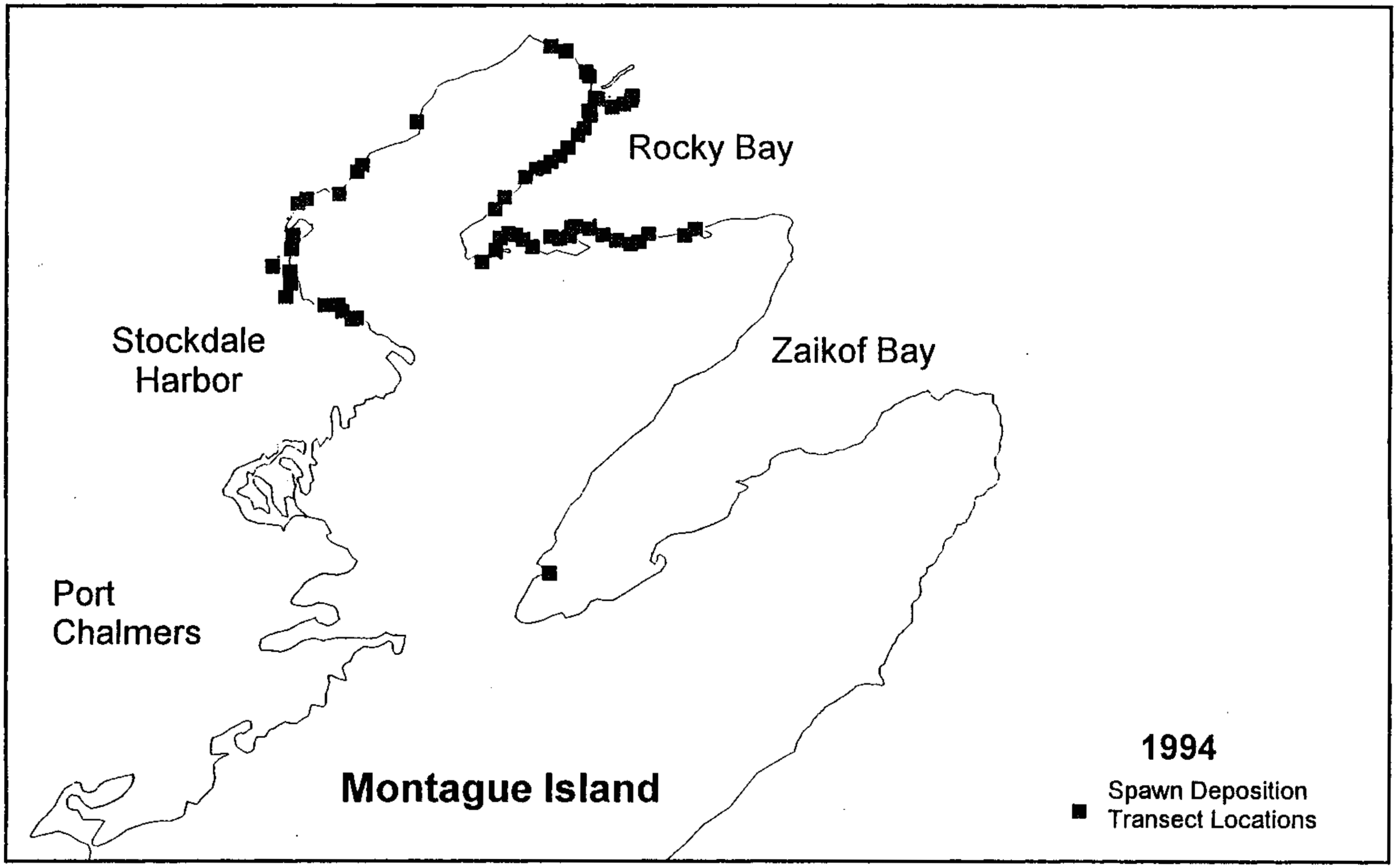
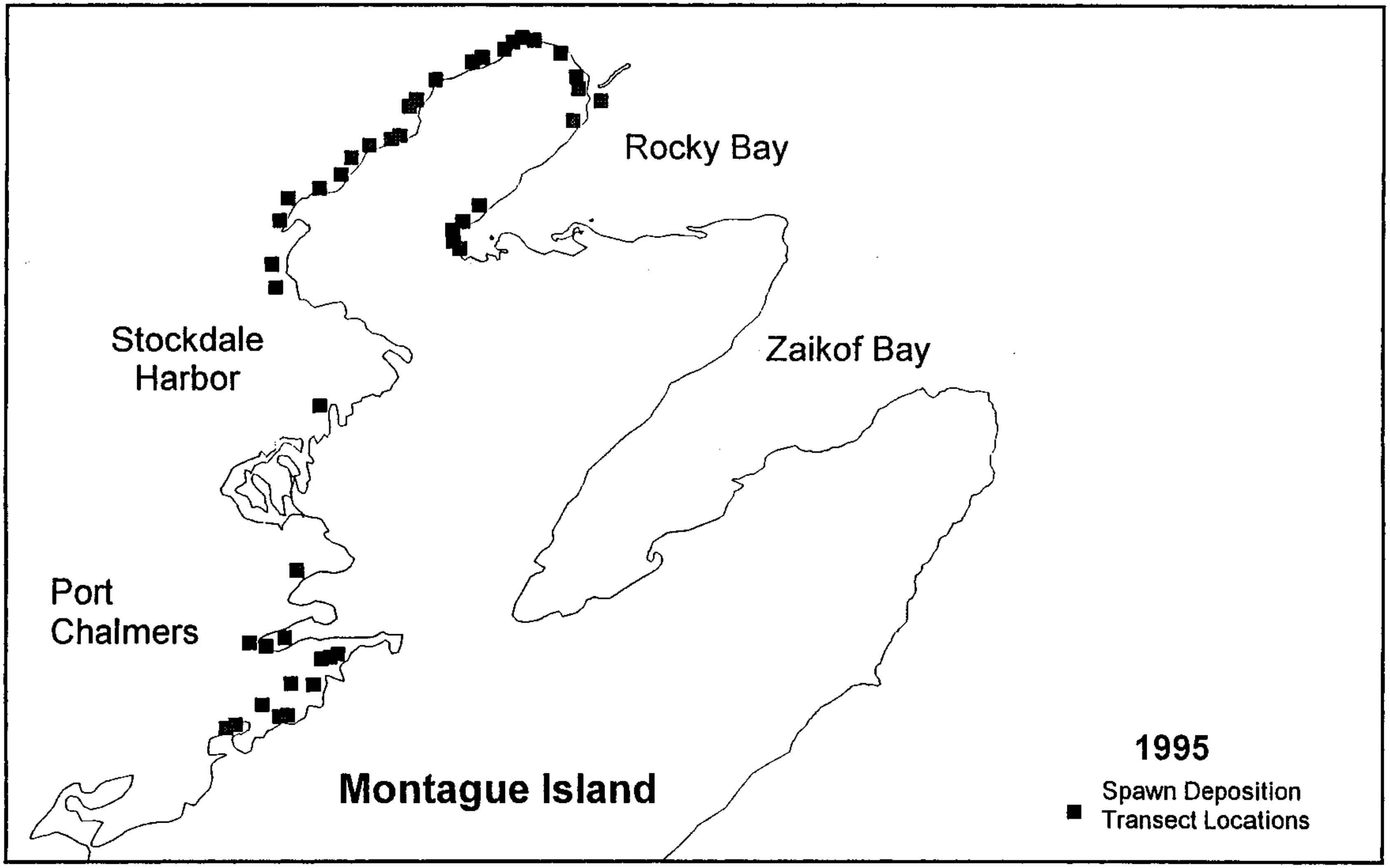


Figure 2. Spawn deposition transect locations in the Montague Island summary area, Prince William Sound, Alaska, 1994 to 1997.



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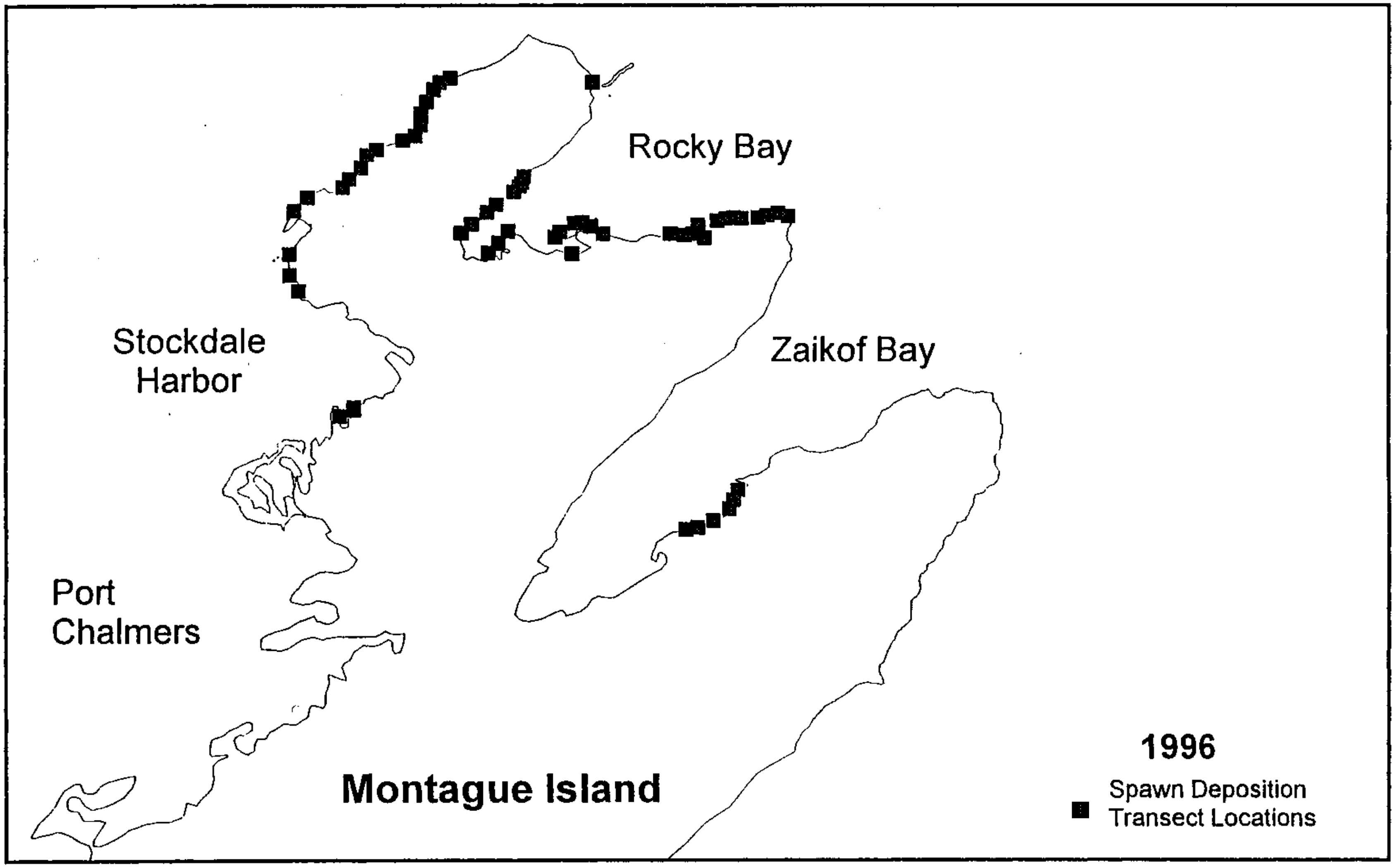

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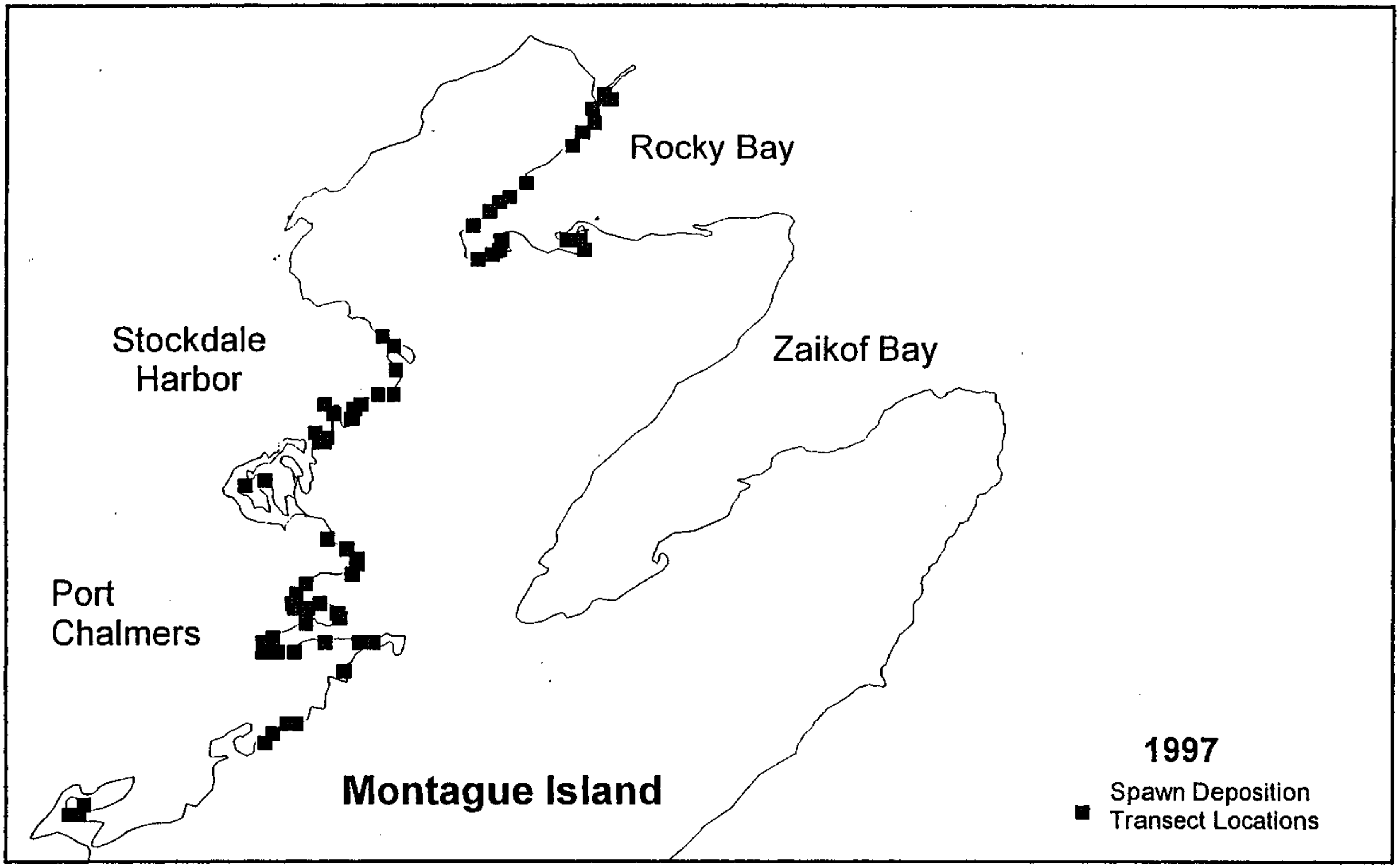

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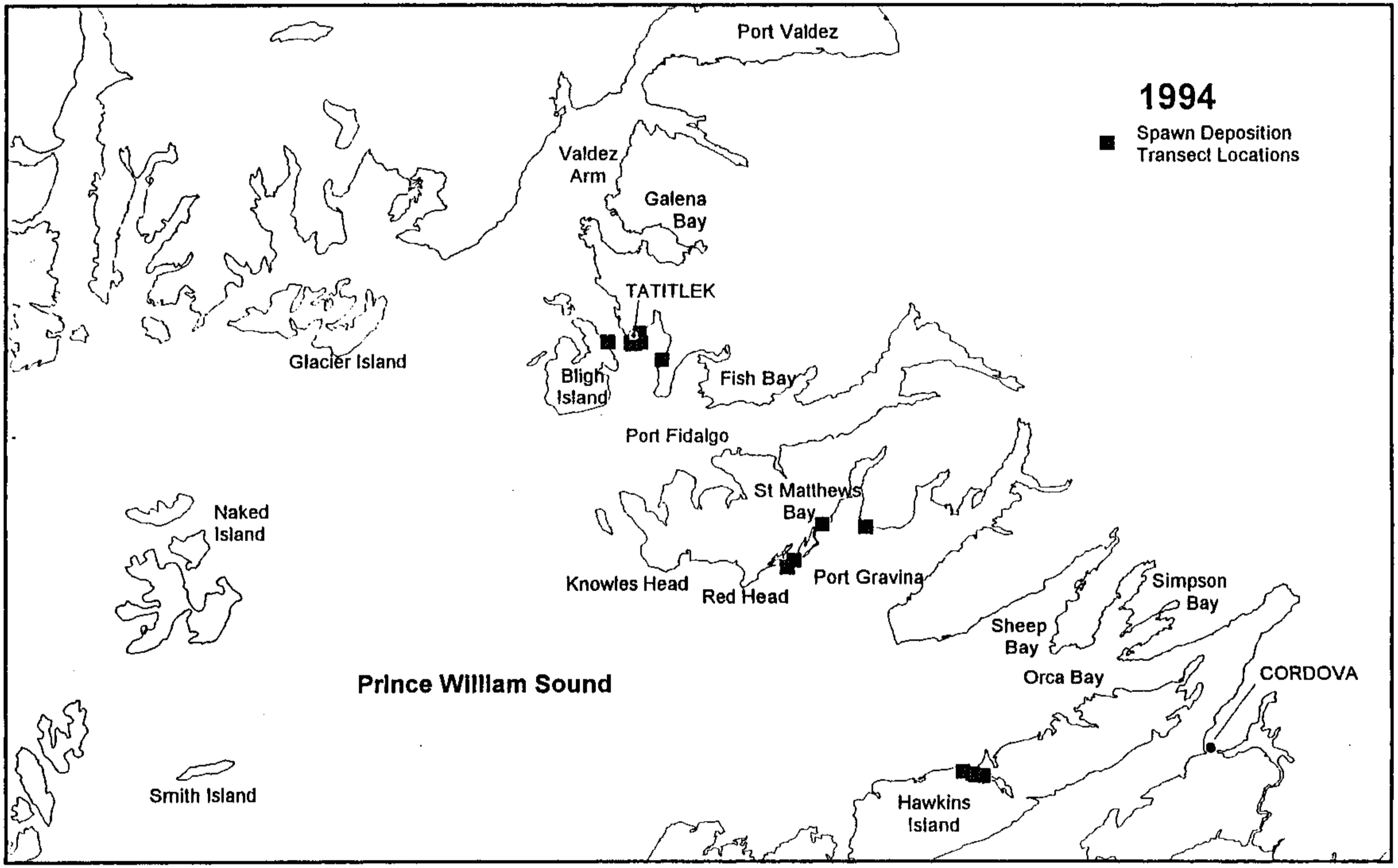
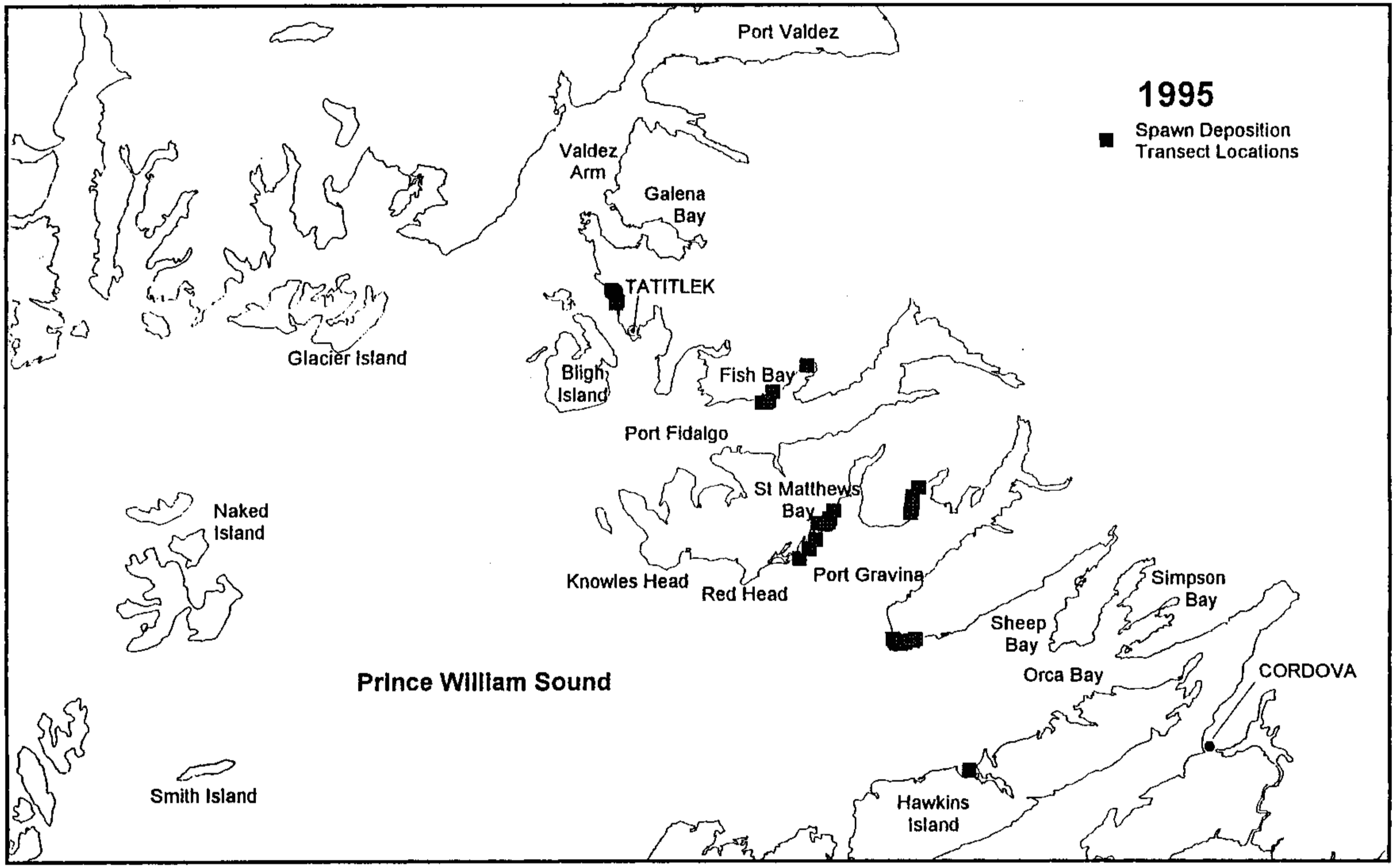


Figure 3. Spawn deposition transects in the Southeastern, Northeastern and Northern summary areas, Prince William Sound, Alaska, 1994 to 1997.



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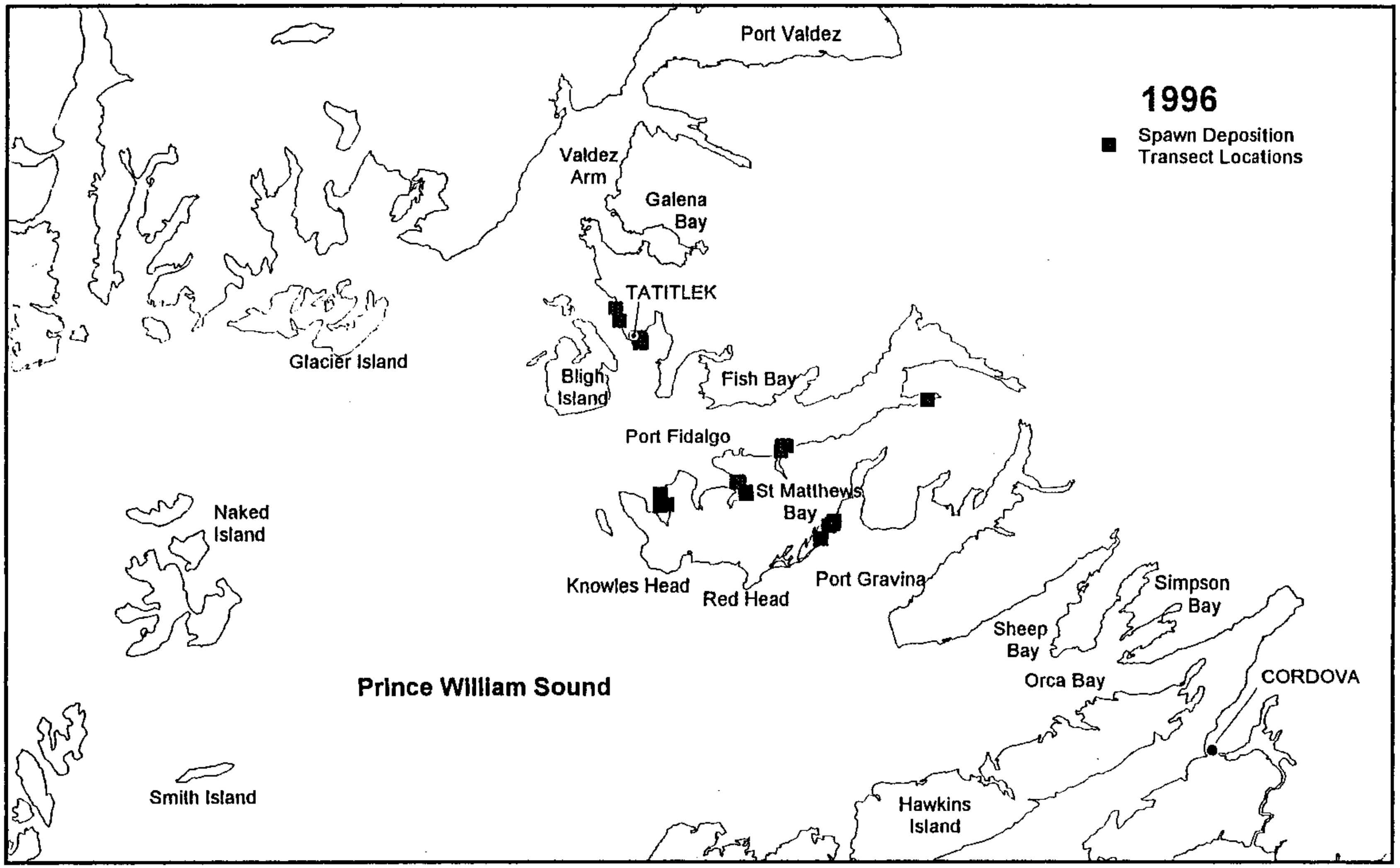

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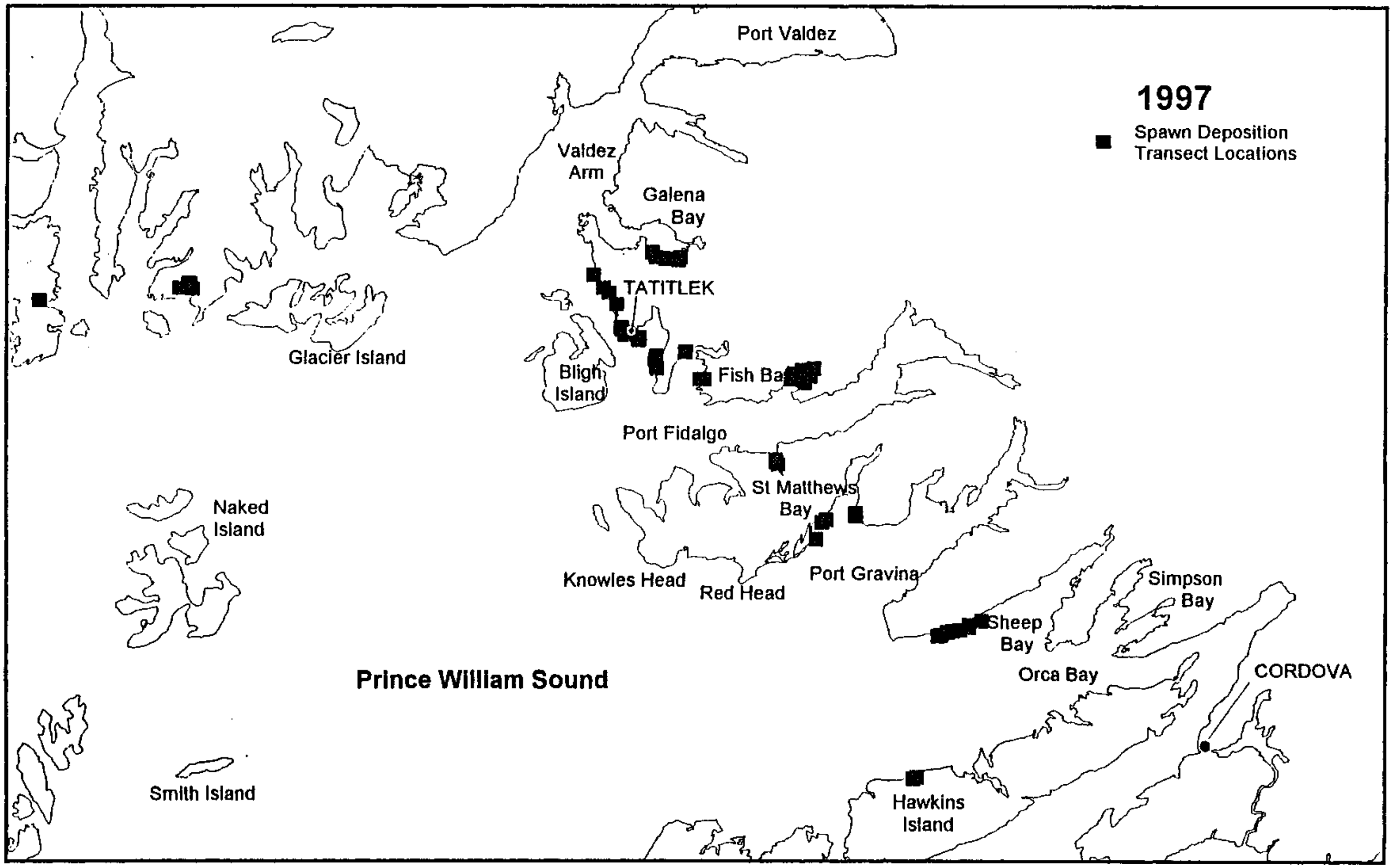

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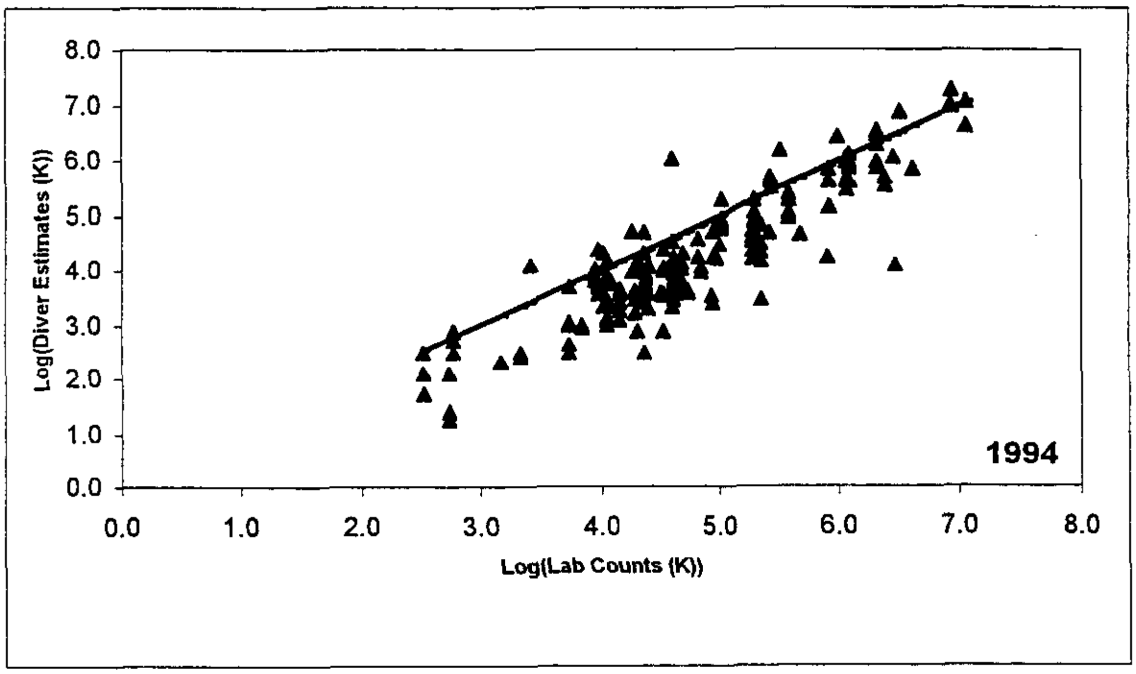


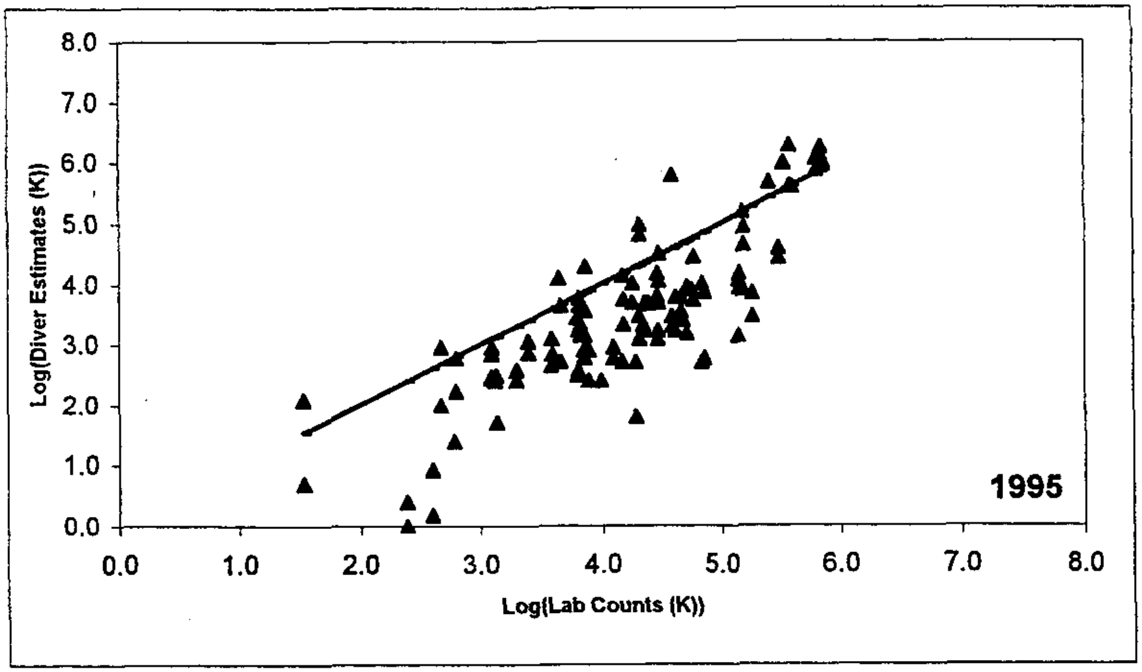
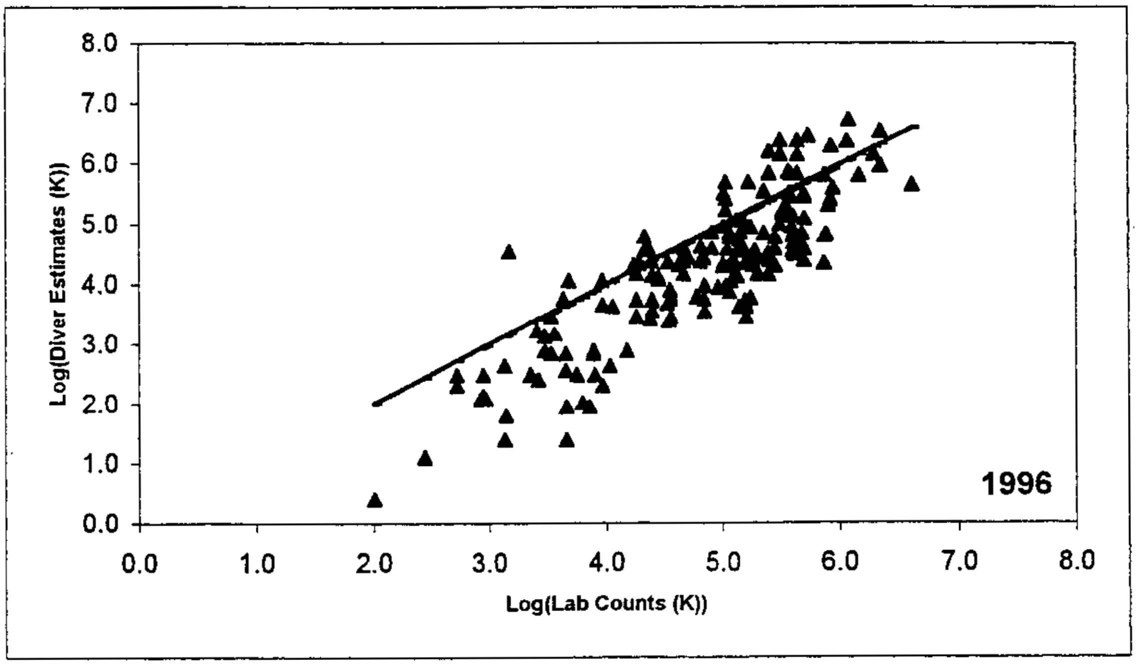
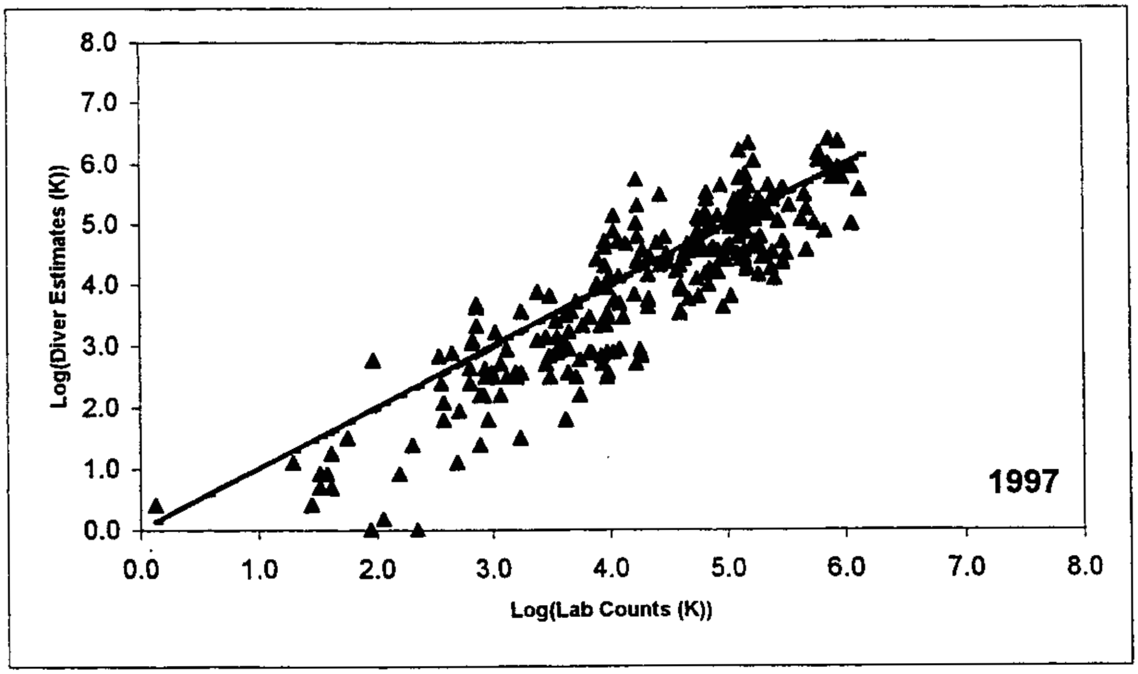


Figure 4. Relationship between diver count and lab count for all divers on all kelp types for 1994 to 1997. Line has intercept = 0 and slope = 1.





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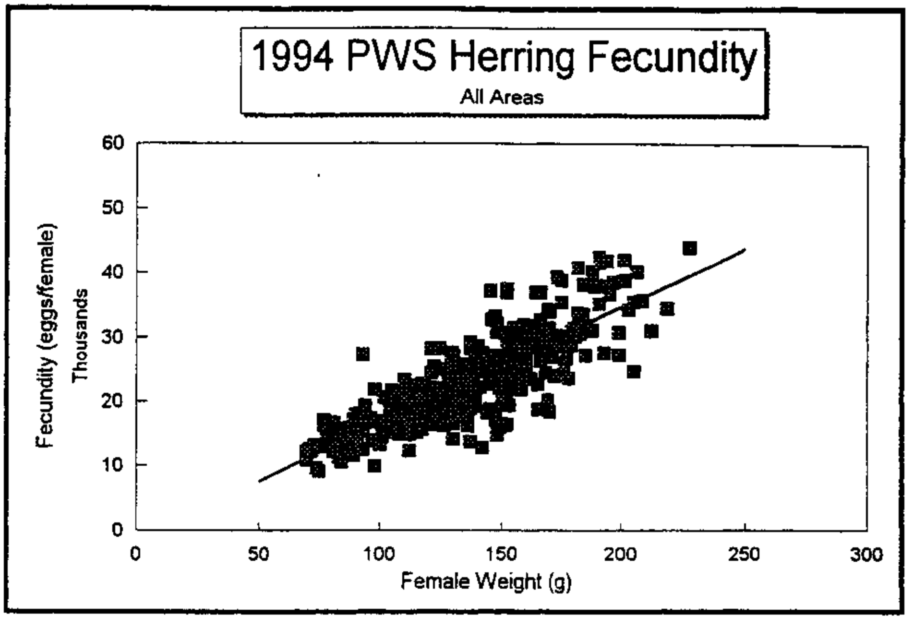
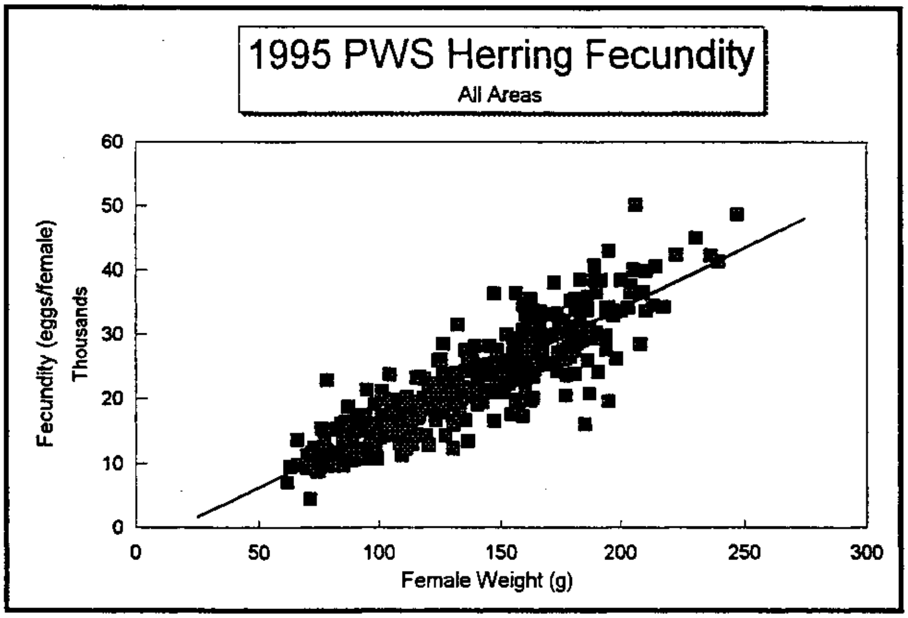
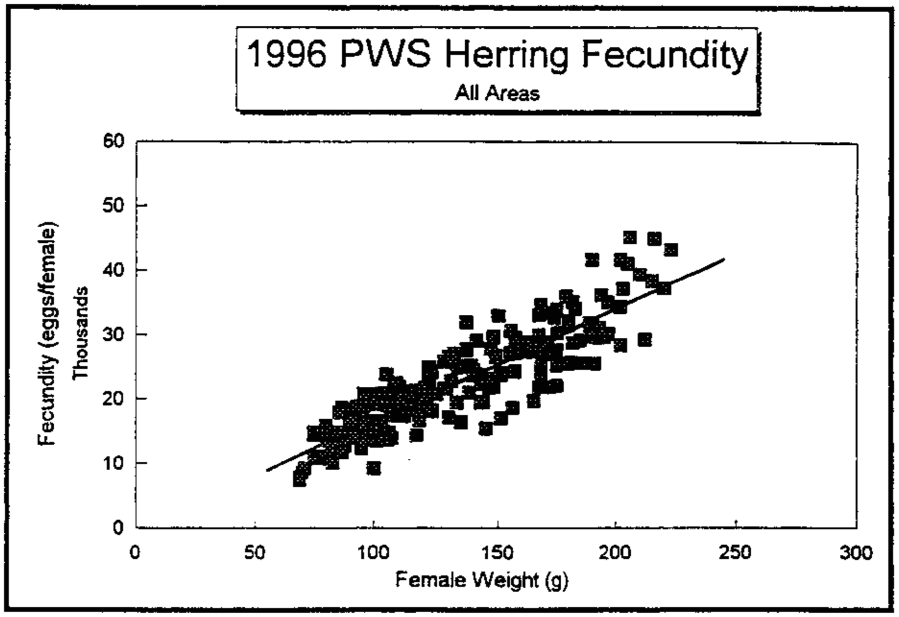


Number of Observations	342
Degrees of Freedom	340
Slope of Regression	182.462
Standard Error	6.448306
Intercept of Linear Regression	-1592.53
Standard Error of Y Estimate	3980.06
R Squared	0.701931

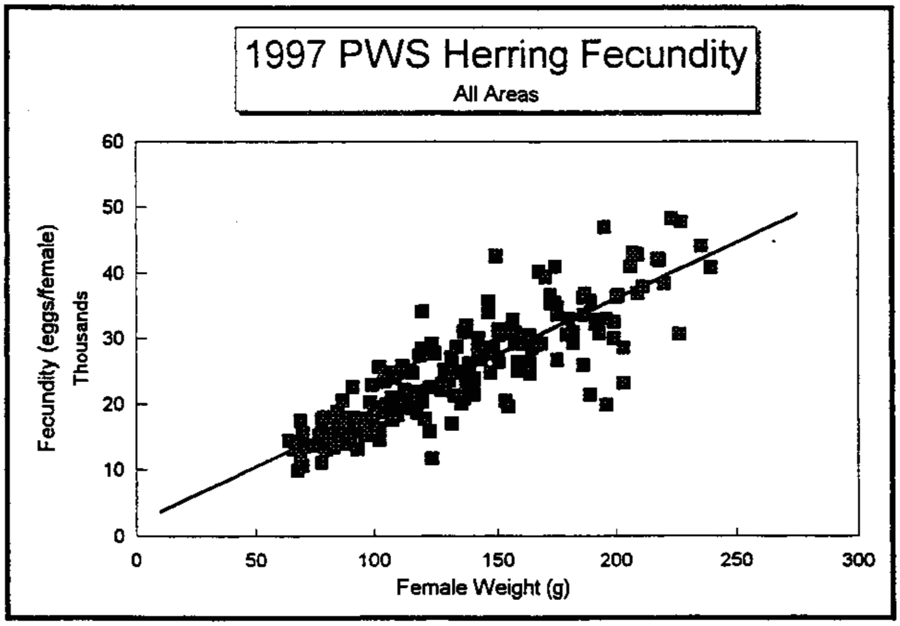


Number of Observations	310
Degrees of Freedom	308
Slope of Regression	185.413
Standard Error	5.842
Intercept of Linear Regression	-2941.69
Standard Error of Y Estimate	4095.207
R Squared	0.765822

Figure 5. Regression of female weight and number of eggs per female for Pacific herring from Prince William Sound, Alaska 1994 to 1997.



Number of Observations	205
Degrees of Freedom	203
Slope of Regression	173.178
Standard Error	6.473242
Intercept of Linear Regression	-593.306
Standard Error of Y Estimate	3602.232
R Squared	0.779040



Number of Observations	200
Degrees of Freedom	198
Slope of Regression	171.131
Standard Error	6.893745
Intercept of Linear Regression	1941.887
Standard Error of Y Estimate	4217.149
R Squared	0.756827

Figure 5. (continued).

Table 1. Summary of acoustic surveys of herring in Prince William Sound, Alaska, 1994 to 1997.

Management Year	Date of Survey	Vessel	Transducer	Areas Surveyed
1993-1994	10/20-10/26/93	Commercial Seiner	120 Khz	Green Island, Montague Strait
1994-1995	10/27-11/06/94	Commercial Seiner Commercial Seiner	200 Khz 120 Khz	Montague Strait, Green Island, Knowles Head Montague Strait, Green Island, Knowles Head
	4/17-4-18/95	R/V Montague	120 Khz	Rocky Bay, Zaikof Bay
1995-1996	4/14-4/18/96	R/V Montague	120 Khz	Rocky Bay, Stockdale Harbor
1996-1997	3/26/-4/06/97	Commercial Seiner R/V Montague	120 Khz	Rocky Bay, Stockdale Harbor, Port Chalmers, Zaikof Bay, Boulder Bay, Landlocked, Two Moon, St. Matthews, Olsen Bay

Table 2. Diver calibration model parameter estimates, 1994.

Diver (j)	Kelp Type (k)	Slope Estimate ($\hat{\beta}_{jk}$)	Standard Error
BB	1 = eelgrass	0.9905	0.0122
	2 = hair kelp	0.9618	0.0127
	3 = fucus	0.9672	0.0103
	4 = large brown kelp	0.9489	0.0091
EB	1 = eelgrass	0.9727	0.0103
	2 = hair kelp	0.9718	0.0140
	3 = fucus	0.9452	0.0140
	4 = large brown kelp	0.9531	0.0128
KB	1 = eelgrass	0.9616	0.0054
	2 = hair kelp	0.9635	0.0060
	3 = fucus	0.9503	0.0070
	4 = large brown kelp	0.9412	0.0060
BH	1 = eelgrass	0.9754	0.0082
	2 = hair kelp	0.9632	0.0081
	3 = fucus	0.9325	0.0072
	4 = large brown kelp	0.9433	0.0070
MM	1 = eelgrass	0.9688	0.0087
	2 = hair kelp	0.9721	0.0077
	3 = fucus	0.9269	0.0081
	4 = large brown kelp	0.9387	0.0068

Table 3. Diver calibration model parameter estimates, 1995.

Diver (j)	Kelp Type (k)	Slope Estimate ($\hat{\beta}_{jk}$)	Standard Error
BB	1 = eelgrass	0.9749	0.0137
	2 = hair kelp	0.9783	0.0129
	3 = fucus	0.9412	0.0146
	4 = large brown kelp	0.9293	0.0147
EB	1 = eelgrass	0.9618	0.0124
	2 = hair kelp	0.9532	0.0111
	3 = fucus	0.9345	0.0136
	4 = large brown kelp	0.9727	0.0159
KB	1 = eelgrass	0.9414	0.0080
	2 = hair kelp	0.9562	0.0074
	3 = fucus	0.9295	0.0090
	4 = large brown kelp	0.9450	0.0090
BH	1 = eelgrass	0.9692	0.0091
	2 = hair kelp	0.9443	0.0085
	3 = fucus	0.9073	0.0098
	4 = large brown kelp	0.9504	0.0100
MM	1 = eelgrass	0.9667	0.0088
	2 = hair kelp	0.9621	0.0070
	3 = fucus	0.9165	0.0080
	4 = large brown kelp	0.9259	0.0073

Table 4. Diver calibration model parameter estimates, 1996.

Diver (j)	Kelp Type (k)	Slope Estimate ($\hat{\beta}_{jk}$)	Standard Error
BH	1 = eelgrass	0.9764	0.0081
	2 = hair kelp	0.9656	0.0074
	3 = fucus	0.9347	0.0088
	4 = large brown kelp	0.9691	0.0094
KB	1 = eelgrass	0.9655	0.0070
	2 = hair kelp	0.9525	0.0060
	3 = fucus	0.9512	0.0079
	4 = large brown kelp	0.9426	0.0077
MM	1 = eelgrass	0.9750	0.0080
	2 = hair kelp	0.9796	0.0072
	3 = fucus	0.9309	0.0094
	4 = large brown kelp	0.9164	0.0077

Table 5. Diver calibration model parameter estimates, 1997.

Diver (j)	Kelp Type (k)	Slope Estimate ($\hat{\beta}_{jk}$)	Standard Error
BH	1 = eelgrass	0.9896	0.0087
	2 = hair kelp	0.9846	0.0077
	3 = fucus	0.9359	0.0091
	4 = large brown kelp	0.9665	0.0096
KB	1 = eelgrass	0.9559	0.0074
	2 = hair kelp	0.9701	0.0066
	3 = fucus	0.9605	0.0078
	4 = large brown kelp	0.9845	0.0087
MM	1 = eelgrass	0.9809	0.0073
	2 = hair kelp	0.9944	0.0075
	3 = fucus	0.9255	0.0078
	4 = large brown kelp	0.9269	0.0088

Table 6. Estimated mean weight and length and contributions of each age and year class to the run biomass of herring in Prince William Sound, Alaska, 1994.

Year Class	Age Class	Mean Weight (g)	Mean Standard Length (mm)	Biomass by Age Class			
				Weight (tonnes)	Percent by Weight	Number of Fish (x 1,000)	Percent by Number
1993	1			0.0	0.0	0.0	0.0
1992	2	34	147	0.0	0.0	105.3	0.1
1991	3	70	182	129.3	0.5	1,207.6	1.0
1990	4	88	194	2,068.2	8.0	14,062.4	11.5
1989	5	110	209	594.6	2.3	3,181.9	2.6
1988	6	125	215	16,416.0	63.5	78,437.0	63.9
1987	7	132	219	387.8	1.5	1,742.3	1.4
1986	8	155	231	904.8	3.5	3,502.7	2.9
1985	9	153	231	3,179.8	12.3	12,420.6	10.1
1984	10	160	232	2,094.0	8.1	7,876.6	6.4
1983	11	155	230	25.9	0.1	80.8	0.1
1982	12	186	244	51.7	0.2	174.8	0.1
1981	13+			0.0	0.0	0.0	0.0
Total		126	215	25,852.0	100.0	122,792.0	100.0

Table 7. Estimated mean weight and length and contributions of each age and year class to the run biomass of herring in Prince William Sound, Alaska, 1995.

Year Class	Age Class	Mean Weight (g)	Mean Standard Length (mm)	Biomass by Age Class			
				Weight (tonnes)	Percent by Weight	Number of Fish (x 1,000)	Percent by Number
1994	1			0.0	0.0	0.0	0.0
1993	2	20	163	65.0	0.2	767.4	0.5
1992	3	76	184	4,689.1	15.0	35,679.2	24.1
1991	4	96	197	920.5	2.9	5,597.4	3.8
1990	5	112	208	4,264.3	13.6	22,136.2	15.0
1989	6	133	218	830.3	2.7	3,636.5	2.5
1988	7	144	222	16,471.6	52.7	66,521.0	44.9
1987	8	164	229	293.8	0.9	1,038.4	0.7
1986	9	156	230	416.3	1.3	1,557.8	1.1
1985	10	168	234	1,419.3	4.5	4,906.9	3.3
1984	11	177	237	1,825.2	5.8	6,002.5	4.1
1983	12	166	236	49.5	0.2	173.0	0.1
1982	13+			0.0	0.0	0.0	0.0
Total		123	211	31,245.0	100.0	148,016.2	100.0

Table 8. Estimated mean weight and length and contributions of each age and year class to the run biomass of herring in Prince William Sound, Alaska, 1996.

				Biomass by Age Class			
Year Class	Age Class	Mean Weight (g)	Mean Standard Length (mm)	Weight (tonnes)	Percent by Weight	Number of Fish (x 1,000)	Percent by Number
1995	1			0.0	0.0	0.0	0.0
1994	2	45	156	133.3	0.4	2,144.7	1.0
1993	3	79	185	4,273.1	12.2	38,811.6	18.8
1992	4	101	200	9,718.2	27.7	68,630.8	33.3
1991	5	119	211	1,226.8	3.5	7,379.5	3.6
1990	6	133	217	3,736.1	10.7	20,082.9	9.7
1989	7	149	226	1,463.5	4.2	7,021.3	3.4
1988	8	164	230	12,357.3	35.3	53,949.9	26.1
1987	9	168	233	307.0	0.9	1,313.5	0.6
1986	10	179	236	373.1	1.1	1,495.7	0.7
1985	11	188	239	996.4	2.8	3,802.9	1.8
1984	12	180	236	436.2	1.2	1,733.1	0.8
1983	13+			0.0	0.0	0.0	0.0
Total		122	209	35,021.0	100.0	206,365.9	100.0

Table 9. Estimated mean weight and length and contributions of each age and year class to the run biomass of herring in Prince William Sound, Alaska, 1997.

				Biomass by Age Class			
Year Class	Age Class	Mean Weight (g)	Mean Standard Length (mm)	Weight (tonnes)	Percent by Weight	Number of Fish (x 1,000)	Percent by Number
1996	1			0.0	0.0	0.0	0.0
1995	2	39	149	73.6	0.3	2,072.5	1.1
1994	3	80	185	3,834.5	17.6	53,022.9	28.5
1993	4	109	203	2,608.8	11.9	26,278.5	14.1
1992	5	132	214	4,413.5	20.2	36,792.3	19.8
1991	6	147	222	603.8	2.8	4,522.5	2.4
1990	7	157	226	1,799.0	8.2	12,646.2	6.8
1989	8	171	232	1,090.4	5.0	7,028.1	3.8
1988	9	184	236	6,235.6	28.6	37,338.2	20.0
1987	10	182	238	159.8	0.7	966.6	0.5
1986	11	197	243	303.0	1.4	1,692.8	0.9
1985	12	200	242	405.9	1.9	2,227.4	1.2
1984	13+	209	244	311.0	1.4	1,640.4	0.9
Total		129	173	21,839.0	100.0	186,228.4	100.0

Table 10. Calculation of spawning herring biomass by project summary area from the spawn deposition surveys in Prince William Sound, Alaska, 1994.

Quantity Estimated	Symbol	Montague	Northeast	Southeast	Total
Statute miles of spawn		14.02	0.32	0.27	14.61
Kilometers of spawn		22.57	0.51	0.43	23.51
Number of possible transects	N	71350	1612	1359	74323
Number of transects sampled	n	55	7	3	65
Number of quadrats sampled	Σm_i	1249	45	31	1325
Proportion of transects sampled	f_1	0.00077	0.00434	0.00220	0.00087
Proportion of quadrats sampled	f_2	0.06324	0.06324	0.06324	0.06324
Average spawn patch width (m)		113.54	32.14	56.66	
Total area of spawn patches (km^2)		2.56	0.01	0.02	2.60
Unweighted average density (1000/m^2)		755.86	39.49	141.06	
Average total eggs per transect (K)	$\hat{y}$	28891.06	472.13	1697.40	
Total eggs in area (billions)	T	2061.39	0.76	2.30	2064.46
Average herring weight from AWL (g)	$\overline{W}$	126	126	126	
Average weight of females (g)	$\overline{W}_f$	129	129	129	
Number of females in AWL sample	q	1292	1292	1292	
Number of fish in AWL sample		2812	2812	2812	
Sex ratio	S	2.17	2.17	2.17	
Fecundity of average female	$F(W_f)$	21899.52	21899.52	21899.52	
Fecundity regression slope		184.44	184.44	184.44	
Fecundity regression intercept		-1893.24	-1893.24	-1893.24	
Tonnes per billion eggs	B'	12.52	12.52	12.52	
Estimated biomass in tonnes	B	25813.63	9.53	28.90	25852.07
Estimated biomass in short tons		28454.37	10.51	31.86	28496.74
Short tons per statute mile		2029.55	33.16	119.24	1951.28
Millions of pounds per statute mile		4.05	0.06	0.23	
Distribution (percent miles of spawn)		96.00	2.17	1.83	100.0
Distribution (percent biomass)		99.85	0.04	0.11	100.0

Table 11. Variance of calculations of spawning herring biomass from spawn deposition surveys by project summary area, Prince William Sound, Alaska, 1994.

Quantity Estimated	*Symbol*	Montague	Northeast	Southeast	Total
Egg Counts					
Variance - among transects	s_1^2	1.67×10^{9}	2.73×10^{5}	3.21×10^{6}	
Variance - within transects	s_2^2	6.39×10^{9}	1.34×10^{6}	7.25×10^{6}	
Variance - individual quadrats	s_3^2	1.29×10^{6}	59.74	94.22	
Variance of estimated total eggs	*Var(T)*	1.54×10^{6}	0.10168	1.97762	1.54×10^{6}
AWL Sampling					
Variance of average weight		961	961	961	
Variance of sex ratio	*Var(S)*	0.0019	0.0019	0.0019	
MSE from fecundity regression	s^2	1.48×10^{7}	1.48×10^{7}	1.48×10^{7}	
Mean weight in fecundity sample		134.3	134.3	134.3	
Number of fish in fecundity sample		340	340	340	
Variance of est. average fecundity		56388.68	56388.68	56388.68	
Variance of B′	*Var(B′)*	9.57	9.57	9.57	
Biomass Estimate					
Variance of biomass	*Var(B)*	6.34×10^{7}	20.52	3.42×10^{2}	6.34×10^{7}
Standard error of B	*SE(B)*	7967.04	4.53	18.49	7967.06
Coefficient of variation for B		0.3086	0.4751	0.6399	0.3081
95% confidence interval as % of B		60.50	93.1	125.43	60.40
Confidence limits on estimated biomass					
Lower 95% (tonnes)		10198.22	0.6558	-7.352	10236.62
Upper 95% (tonnes)		41429.04	18.41	65.16	41467.52
Lower 95% (short tons)		11241.50	0.7229	-8.105	11283.83
Upper 95% (short tons)		45667.23	20.29	71.82	45709.65

Table 12. Calculation of spawning herring biomass by project summary area from the spawn deposition surveys in Prince William Sound, Alaska, 1995.

Quantity Estimated	Symbol	Montague	Northeast	Southeast	Total
Statute miles of spawn		12.6	2.0	5.8	20.4
Kilometers of spawn		20.28	3.22	9.33	32.83
Number of possible transects	N	64124	10178	29517	103819
Number of transects sampled	n	54	10	29	93
Number of quadrats sampled	Σm_i	1626	238	800	2664
Proportion of transects sampled	f_1	0.00084	0.00098	0.00098	0.00089
Proportion of quadrats sampled	f_2	0.06324	0.06324	0.06324	0.06324
Average spawn patch width (m)		150.55	119.00	137.93	
Total area of spawn patches (km^2)		3.05	0.38	1.28	4.72
Unweighted average density ($1000/m^2$)		546.41	178.29	122.00	
Average total eggs per transect (K)	$\hat{y}$	28863.38	4171.05	3744.97	
Total eggs in area (G)	T	1850.83	42.45	110.54	2003.82
Average herring weight from AWL (g)	$\overline{W}$	123	154	118	
Average weight of females (g)	$\overline{W}_f$	130	160	121	
Number of females in AWL sample	q	835	544	303	
Number of fish in AWL sample		2223	1238	877	
Sex ratio	S	2.66	2.27	2.89	
Fecundity of average female	$F(W_f)$	21086.03	26643.20	19418.88	
Fecundity regression slope		185.23	185.23	185.23	
Fecundity regression intercept		-2995.04	-2995.04	-2995.04	
Tonnes per billion eggs	B'	15.52	13.15	17.58	
Estimated biomass in tonnes	B	28742.85	558.44	1944.19	31245.49
Estimated biomass in short tons		31683.25	615.57	2143.08	34441.91
Short tons per statute mile		2514.54	307.78	369.49	
Millions of pounds per statute mile		5.02	0.61	0.73	
Distribution (percent miles of spawn)		61.8	9.8	28.4	100.0
Distribution (percent biomass)		92.0	1.8	6.2	100.0

Table 13. Variance of calculations of spawning herring biomass from spawn deposition surveys by project summary area, Prince William Sound, Alaska, 1995.

Quantity Estimated	*Symbol*	Montague	Northeast	Southeast	Total
Egg Counts					
Variance - among transects	s_1^2	2.48×10^9	2.27×10^7	5.75×10^7	
Variance - within transects	s_2^2	1.34×10^{10}	2.47×10^8	4.17×10^8	
Variance - individual quadrats	s_3^2	1.87×10^6	2.45×10^4	4.72×10^4	
Variance of estimated total eggs	*Var(T)*	1.88×10^5	2.35×10^2	1.72×10^3	1.90×10^5
AWLS Sampling					
Variance of average weight		1369	1089	1521	
Variance of sex ratio	*Var(S)*	0.0052	0.0053	0.0180	
MSE from fecundity regression	s^2	1.78×10^7	1.78×10^7	1.78×10^7	
Mean weight in fecundity sample		139.49	139.49	139.49	
Number of fish in fecundity sample		311	311	311	
Variance of est. average fecundity		82136.61	105585.68	128872.41	
Variance of B′	*Var(B′)*	22.04	8.14	34.56	
Biomass Estimate					
Variance of biomass	*Var(B)*	1.16×10^8	5.35×10^4	8.97×10^5	1.17×10^8
Standard error of B	*SE(B)*	10812.84	231.48	947.24	10856.72
Coefficient of variation for B		0.3761	0.4145	0.4872	0.3357
95% confidence interval as % of B		73.73	81.24	95.49	68.10
Confidence limits on estimated biomass					
Lower 95% (tonnes)		7549.68	104.73	87.59	9966.32
Upper 95% (tonnes)		49936.02	1012.16	3800.79	52524.67
Lower 95% (short tons)		8322.01	115.44	96.55	10985.87
Upper 95% (short tons)		55044.48	115.70	4189.62	57897.94

Table 14. Calculation of spawning herring biomass by project summary area from the spawn deposition surveys in Prince William Sound, Alaska, 1996.

Quantity Estimated	Symbol	Montague	Northeast	Southeast	Total
Statute miles of spawn		14.6	10.0	2.4	27
Kilometers of spawn		23.49	16.09	3.86	43.44
Number of possible transects	N	74302	50891	12214	137407
Number of transects sampled	n	59	18	4	81
Number of quadrats sampled	Σm_i	1614	434	50	2098
Proportion of transects sampled	f_1	0.00079	0.00035	0.00032	0.00058
Proportion of quadrats sampled	f_2	0.06324	0.06324	0.06324	
Average spawn patch width (m)		136.77	120.55	62.50	
Total area of spawn patches (km^2)		3.21	1.94	0.24	5.39
Unweighted average density (1000/m^2)		647.20	145.73	169.08	
Average total eggs per transect (K)	$\hat{y}$	31782.06	5105.98	4563.53	
Total eggs in area (billions)	T	2361.47	259.85	55.73	2677.07
Average herring weight from AWL (g)	$\overline{W}$	120	136	130	
Average weight of females (g)	$\overline{W}_f$	125	145	130	
Number of females in AWL sample	q	763	1023	195	
Number of fish in AWL sample		1770	2090	447	
Sex ratio	S	2.31	2.04	2.29	
Fecundity of average female	$F(W_f)$	21001.76	24393.36	21849.66	
Fecundity regression slope		169.58	169.58	169.58	
Fecundity regression intercept		-195.74	-195.74	-195.74	
Tonnes per billion eggs	B'	13.25	11.39	13.63	
Estimated biomass in tonnes	B	31300.99	2959.82	760.20	35021.02
Estimated biomass in short tons		24503.08	3262.61	837.97	38603.68
Short tons per statute mile		2363.22	326.26	349.15	
Millions of pounds per statute mile		4.72	0.65	0.69	
Distribution (percent miles of spawn)		54.07	37.03	8.9	100.0
Distribution (percent biomass)		89.38	8.45	2.17	100.0

Table 15. Variance of calculations of spawning herring biomass from spawn deposition surveys by project summary area, Prince William Sound, Alaska, 1996.

Quantity Estimated	*Symbol*	Montague	Northeast	Southeast	Total
Egg Counts					
Variance - among transects	s_1^2	2.31×10^{9}	2.52×10^{7}	4.76×10^{7}	
Variance - within transects	s_2^2	3.94×10^{10}	9.76×10^{7}	1.61×10^{8}	
Variance - individual quadrats	s_3^2	7.47×10^{5}	4.01×10^{3}	1.26×10^{3}	
Variance of estimated total eggs	*Var(T)*	2.16×10^{5}	3.63×10^{3}	1.77×10^{3}	2.21×10^{5}
AWL Sampling					
Variance of average weight		1444	2304	1089	
Variance of sex ratio	*Var(S)*	0.0040	0.0020	0.0151	
MSE from fecundity regression	s^2	1.46×10^{7}	1.46×10^{7}	1.46×10^{7}	
Mean weight in fecundity sample		136.46	136.46	136.46	
Number of fish in fecundity sample		206	206	206	
Variance of est. average fecundity		96780.88	89145.81	148695.59	
Variance of B′	*Var(B′)*	17.78	16.24	12.58	
Biomass Estimate					
Variance of biomass	*Var(B)*	1.33×10^{8}	1.50×10^{6}	3.47×10^{5}	1.35×10^{8}
Standard error of B	*SE(B)*	11548.79	1228.65	589.26	11628.90
Coefficient of variation for B		0.3689	0.4151	0.7751	0.3320
95% confidence interval as % of B		72.31	81.36	151.92	65.08
Confidence limits on estimated biomass					
Lower 95% (tonnes)		8665.36	551.66	-394.75	12228.37
Upper 95% (tonnes)		53936.62	5367.98	1915.17	57813.68
Lower 95% (short tons)		9551.82	608.10	-435.14	13479.34
Upper 95% (short tons)		59454.34	5917.12	2111.09	63728.02

Table 16. Calculation of spawning herring biomass by project summary area from the spawn deposition surveys in Prince William Sound, Alaska, 1997.

Quantity Estimated	Symbol	Montague	Northern	Northeast	Southeast	Total
Statute miles of spawn		17.96	2.05	15.60	6.96	42.57
Kilometers of spawn		28.9	3.3	25.1	11.2	68.5
Number of possible transects	N	91402	10433	79391	35421	216647
Number of transects sampled	n	68	6	33	15	122
Number of quadrats sampled	Σm_i	1516	72	739	412	2739
Proportion of transects sampled	f_1	0.00074	0.00057	0.00041	0.00042	0.00056
Proportion of quadrats sampled	f_2	0.06324	0.06324	0.06324	0.06324	0.06324
Average spawn patch width (m)		111.47	60.00	111.96	137.33	
Total area of spawn patches (km^2)		3.22	0.19	2.81	1.53	7.76
Unweighted average density (1000/m^2)		417.39	87.68	67.62	222.86	
Average total eggs per transect (K)	$\hat{y}$	15170.37	1733.80	2586.52	10289.01	
Total eggs in area (G)	T	1386.60	18.08	205.34	364.44	1974.48
Average herring weight from AWL (g)	$\overline{W}$	120	130	130	130	
Average weight of females (g)	$\overline{W}_f$	128	138	138	138	
Number of females in AWL sample	q	1640	957	957	957	
Number of fish in AWL sample		3549	2157	2157	2157	
Sex ratio	S	2.16	2.25	2.25	2.25	
Fecundity of average female	$F(W_f)$	23846.66	25557.96	25557.96	25557.96	
Fecundity regression slope		171.13	171.13	171.13	171.13	
Fecundity regression intercept		1941.88	1941.88	1941.88	1941.88	
Tonnes per billion eggs	B'	10.88	11.46	11.46	11.46	
Estimated biomass in tonnes	B	15099.66	207.37	2354.21	4178.18	21839.43
Estimated biomass in short tons		16644.36	228.58	2595.05	4605.60	24073.61
Short tons per statute mile		926.74	111.50	166.34	661.72	
Millions of pounds per statute mile		1.85	0.22	0.33	1.32	
Distribution (percent miles of spawn)		42.19	4.82	36.64	16.35	100.0
Distribution (percent biomass)		69.14	0.95	10.78	19.13	100.0

Table 17. Variance of calculations of spawning herring biomass from spawn deposition surveys by project summary area, Prince William Sound, Alaska, 1997.

Quantity Estimated	*Symbol*	Montague	Northern	Northeast	Southeast	Total
Egg Counts						
Variance - among transects	s_1^2	3.42×10^8	1.66×10^6	1.54×10^7	7.10×10^8	
Variance - within transects	s_2^2	2.51×10^9	1.13×10^7	8.04×10^7	1.25×10^{10}	
Variance - individual quadrats	s_3^2	3.86×10^5	2.48×10^2	4.95×10^3	1.84×10^3	
Variance of estimated total eggs	*Var(T)*	4.20×10^4	3.0×10^1	2.94×10^3	5.94×10^4	1.04×10^5
AWLS Sampling						
Variance of average weight		1849	2304	2304	2304	
Variance of sex ratio	*Var(S)*	0.0015	0.0029	0.0029	0.0029	
MSE from fecundity regression	s^2	1.77×10^7	1.77×10^7	1.77×10^7	1.77×10^7	
Mean weight in fecundity sample		131.9	131.9	131.9	131.9	
Number of fish in fecundity sample		200	200	200	200	
Variance of est. average fecundity		100499.2	109299.3	109299.3	109299.3	
Variance of B′	*Var(B′)*	15.28	18.01	18.01	18.01	
Biomass Estimate						
Variance of biomass	*Var(B)*	3.37×10^7	9.3×10^3	1.09×10^6	9.13×10^6	4.39×10^7
Standard error of B	*SE(B)*	5807.94	96.55	1045.90	3022.00	6630.83
Coefficient of variation for B		0.384	0.465	0.444	0.723	0.3036
95% confidence interval as % of B		75.38	91.25	87.07	141.76	59.50
Confidence limits on estimated biomass						
Lower 95% (tonnes)		3716.08	18.13	304.24	-1744.94	8842.99
Upper 95% (tonnes)		26483.24	396.62	4404.19	10101.30	34835.87
Lower 95% (short tons)		4096.24	19.98	335.36	-1923.44	9747.63
Upper 95% (short tons)		29192.48	437.19	4854.73	11134.66	38399.58

Table 18. Summary of herring biomass estimates obtained from spawn deposition, aerial, and acoustic surveys by summary area, Prince William Sound, 1994-1997.

		Spawn Deposition Est.		Aerial Survey Est.		Acoustic Est.
Summary Area	Management Year	10% Egg Loss (tonnes)	Variable Egg Loss (tonnes)	Peak Biomass (tonnes) [a]	Shoreline Spawn (km) (tonnes) [b]	Pre-spawning Survey (tonnes)
Totals	1993-1994	15,485	25,852	17,817	12,248	
Montague		15,479	25,813	17,418	11,779	
Northeast		2	10	100	261	
Southeast		4	29	299	156	
Northern		0	0	0	0	
Naked Island		0	0	0	0	
Totals	1994-1995	18,163	31,245	6,453	17,095	13,284
Montague		16,464	28,743	4,853	10,580	13,284
Northeast		309	558	1,093	1,668	
Southeast		1,391	1,944	506	4,847	
Northern		0	0	0	0	
Naked Island		0	0	0	0	
Totals	1995-1996	25,101	35,021	9,699	22,827	4,546
Montague		21,964	31,301	8,537	12,248	4,546
Northeast		2,497	2,960	984	8,391	
Southeast		640	760	164	1,980	
Northern		0	0	14	156	
Naked Island		0	0	0	0	
Totals	1996-1997	19,069	21,839	9,850	35,700	22,985
Montague		11,501	15,100	7,167	15,062	17,689
Northeast		2,650	2,354	2,390	13,081	838
Southeast		4,656	4,178	277	5,837	4,458
Northern		262	207	16	1,720	
Naked Island		0	0	0	0	

[a] Largest single day aerial estimate of herring biomass.

[b] Total linear kilometers of spawn.

Table 19. Results from statistical tests (*p*-values) for a difference between herring biomass estimates obtained within each year from spawn deposition surveys using an air-exposure egg loss model and (1) spawn deposition surveys using a fixed 10% egg loss, (2) aerial survey estimates of shoreline kilometers of milt and (3) acoustic surveys on pre-spawning herring.

Year	Area	Spawn Deposition	Aerial	Acoustic
1994	PWS	<0.001	0.001	-
1995	PWS	<0.001	<0.001	-
1996	PWS	<0.001	<0.001	<0.001
1997	Montague	<0.001	0.500	0.165
1997	Southeast	0.123	0.295	0.326

Table 20. Summary of several variables relating to differences between biomass estimates obtained from spawn deposition, aerial and acoustic surveys.

Year	Mean Egg Density	Mean Patch Width (m)	Mean Depth of Eggs (m)	Mean No. Days to Survey
1994	794	113	-1.78	9
1995	425	149	-1.08	11
1996	497	134	-0.73	9
1997	254	116	-1.14	6

APPENDIX I: Herring egg loss report summary

Summary Report of Results from Prince William Sound Egg Loss Modeling

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INTRODUCTION - Summary

The Prince William Sound herring (*Clupea pallasi*) population did not support commercial harvests in 1993, 1994 and 1995 for reasons which are still unknown; however, a combination of physical and biological processes acting on egg stages may be involved. Physical variables, including habitat and substrate variables (e.g. exposure to waves, exposure to air, depth, substrate type), may induce inter-annual variability in egg loss and survival. Biological interactions may also be involved, as birds (glaucous-winged gulls, shorebirds), invertebrates (crabs, seastars), marine mammals and fish (salmonids, flatfishes, sculpins) are known to be predators of herring eggs and juveniles. Finally, the *Exxon Valdez* oil spill of 1989 may have affected herring adult and juvenile health, egg viability, and genetic composition.

In Prince William Sound estimates of the number of eggs spawned are used to estimate spawning biomass of the herring population. Because the survey occurs some days after spawning, some loss of eggs occurs, requiring a correction factor. In the past a correction factor of 10% has been used; however, recent research has suggested that egg loss is highly variable between years and locations.

Alaska Department of Fish and Game (ADF&G) conducted studies of egg loss for herring in Prince William Sound in 1990, 1991, 1994 and 1995. The focus of the 1990 and 1991 studies was to examine the effects of oil on egg loss. Analysis of covariance conducted with egg abundance as the dependent variable, transects and depth as factors, and days as the covariate, along with several interaction terms resulted in a model explaining about 70% of the variability in the data (Biggs-Brown and Baker 1993). Most of the variability was explained by transect-related parameters.

The focus of 1994 and 1995 egg loss sampling was to examine habitat variables associated with transects that may influence egg loss. This research was conducted as a cooperative project between ADF&G and University of Alaska Fairbanks. We also revisited the analyses of Baker and Biggs-Brown with the goal of explaining egg loss rates by physical and biological factors related to spawning habitat. Because transects represent specific locations, the previous analysis using transects as a factor did not provide an understanding of the possible mechanisms which affect egg loss rates. In this study, we obtained data on both physical and biological components and analyzed them to determine their individual contribution to egg loss. Physical variables included depth, time of exposure to air, spawning substrate, and wave action. Biological variables included predation by fish, predation by birds, and the effect of the type of vegetation upon which eggs are deposited. Finally we developed a model for predicting egg loss based on those variables found to be significant.

MATERIALS AND METHODS - Summary

Data sets from herring egg loss studies in 1990, 1991, 1994 and 1995 were acquired from Alaska Department of Fish and Game, in Cordova, Alaska. The variables depth, time of air exposure, vegetation type, wave exposure, and substrate type were available for all years. The 1994 and 1995 datasets came from transects located in previously oiled areas only, so a variable for presence or absence of oil was only used for the 1990 and 1991 data sets. Additional data collected in 1994 allowed classification of the data by the covariates average bird abundance, average glaucous-winged gull abundance and cumulative loose eggs observed at each transect. The 1995 data were analyzed using both of the bird abundance measurements, as well as an another covariate, fish predation measured by gillnetting.

Analyses of egg loss assume that the instantaneous rate of egg loss (*Z*) is constant over days. Reference day 0 is considered to be the beginning of the spawning period. If *N(t)* is the number of eggs at reference day *t* and N_0 is the number of eggs at reference day 0, then

$$N(t) = N_0 e^{-Zt} e^{\varepsilon}$$

where e is a random error term with mean 0 and constant variance. Taking the logarithm of this equation, one obtains

$$\ln N(t) = \ln N_0 - \mathrm{Z}t + \varepsilon$$

showing that a linear regression of ln(egg abundance) versus days can be used to estimate ln N_0 and *Z* from the y-intercept and slope respectively.

Modeling of habitat variables was carried out using the egg loss rates (Z). Egg loss rates were used as the dependent variable in analysis of variance models where

$$Z=m+a_i+b_j+g_k+(ab)_{ij}+....+e$$

The independent variables were the habitat factors, covariate terms and year. Factorial analyses of these variables were performed, sequentially removing factors that were insignificant. In most cases the resulting models explained a significant portion of the variability in egg loss rates.

Because of the unbalanced nature of the study design, various subsets of the data were modeled. For example, the substrate type "rocky" associated with the highest number of was analyzed independently and as part of the entire data set. This eliminated some noise associated with the substrate variable and allowed inclusion of the maximum number of interaction terms.

Data from individual years as well as combinations of years were analyzed to attain the best possible model of egg loss for Prince William Sound. The years 1990 and 1991 and years 1994 and 1995 were combined; in addition, data from Montague Island transects only were combined over all four years.

The best model resulting from the factorial analyses was then used to calculate the initial number of eggs and number of eggs at hatch for selected spawn deposition transects in 1995.

RESULTS - Summary

Egg loss rates (Z) in 1990 averaged 0.076, and about 61% of the linear regressions of ln(egg abundance) versus days since spawn were significant (Table 1). Egg loss rates obtained from each transect at each depth were used as dependent variables in analysis of variance models to determine habitat variables significantly affecting egg loss. Approximately 40.1% of the variability in egg loss rates in 1990 was explained by a model containing one habitat variable, the presence or absence of oil (Table 2). The average egg loss rate (Z) at oiled transects in 1990 was 0.108 while the average in unoiled transects was only 0.002.

In 1991 egg loss rates (Z) averaged 0.042, with about 58% of the linear regressions significant (Table 1). The best model of egg loss rates for 1991 explained 65.3% of the variability and contained two significant ($p<0.05$) habitat variables, depth and the wave-exposed/protected variable (Table 2). At wave-protected transects the average egg loss rate was 0.074, while at wave-exposed transects the average was -0.018. Egg loss rates were inversely related to depth and total time of air exposure, with higher egg loss rates occurring at higher depths relative to mean low water.

The average egg loss rate (Z) was 0.096 in 1994, and 90% of the regressions were statistically significant (Table 1). The best model of egg loss rates for the 1994 data explained 73.6% of the variability in the data and contained two terms, depth and the depth*average bird abundance interaction (Table 2). Egg loss rates decreased with both increased depth and increased bird abundance.

About 66% of the egg loss regressions were significant in 1995, with an average egg loss rate (Z) of 0.096 (Table 1). Factorial analysis of the 1995 egg loss rates leads to a model explaining 53.9% of the variability in egg loss rates, containing only the depth term (Table 2). As in previous years, the egg loss rate decreased with depth.

The same methods were used to analyze combined 1990 and 1991 data as were applied to the individual years. To model egg loss rates, the slopes of egg loss regressions for each transect in 1990 and 1991 were used as the dependent variable in factorial analyses to evaluate the effects of habitat variables.

The best model explained about 60.0% of the variability in egg loss rates for the combined years 1990 and 1991 (Table 3). Significant habitat variables included in the model were depth, wave-exposed/protected, oiled/unoiled and the interaction between oiled/unoiled and year. Depth and the interaction term accounted for the most variability in egg loss rates, suggesting that these two terms were the most important factors affecting egg loss in 1990 and 1991. The average egg loss rate decreased with increasing depth, and the average egg loss rate was higher for oiled transects (0.070, SE=0.016) than unoiled transects (0.052, SE=0.013) when both years are combined. Average egg loss rates were higher in oiled areas only in 1990, in 1991 egg loss rates were marginally higher in unoiled areas. Average egg loss rate is also higher for protected transects (0.077, SE=0.012) than for exposed transects (0.021, SE=0.018), a counterintuitive result since transects that were exposed to higher wave forces over the incubation period would be expected to have higher egg loss.

When egg loss rates from the combined years, 1994 and 1995, are subjected to a factorial analysis, a model explaining 52.4% of the data set variability results (Table 3). All transects were on rocky substrates, and the only significant term is depth. The model is very consistent with the previous analyses of egg loss rates, with egg loss rates decreasing with increasing depth.

Data from all four years for Montague Island transects were combined for a single analysis. This combination uses only data from one location, thus avoiding combining egg loss rates from the northern and southern areas of Prince William Sound. Factorial analysis of the combined Montague Island data from only rocky substrates results in the best model. This model explains 60.6% of the variability, and contains three significant terms, depth, wave-exposed/protected and year, with depth explaining the majority of the variation in egg loss rates (Table 3).

The average egg loss rate in protected areas was 0.115 (SE= 0.014) while in exposed areas the average was 0.078 (SE= 0.010), the opposite of the expected result. The year with the highest egg loss on Montague Island was 1990 (Z= 0.134, SE= 0.022), however, the following year had the lowest average egg loss (Z= 0.003, SE= 0.015). Results also show that as depth relative to mean low water increased, egg loss rates decreased, a consistent pattern within all the egg loss data.

For each of the datasets examined, total time of air exposure was calculated for each depth and used as a covariate in factorial analyses in place of depth. The resulting models were slightly less significant than models containing depth. To analyze whether there were significant differences between models containing depth and models containing air exposure, the contributions to sum of squares with either depth or air exposure included in the model were compared using an F-test. The conclusion was that the models with air exposure were not significantly different than those models using depth (P>0.50). This result was consistent for all data sets except 1994.

The benefit of using air exposure instead of depth is that it reduces the number of parameters estimated (one rather than five) without significantly increasing variation. The time of exposure to air increases exponentially as depth relative to mean low water decreases (Figure 1).

The R^2 values for habitat models developed from factorial analyses were compared to R^2 values for three other models for each dataset examined. The three models were: a model containing only the depth variable, a model containing only the time of air exposure covariate, and a model containing transect and depth. As expected, transect-depth models were consistently better at explaining variation in egg loss rates, with an average R^2 value of 0.751 (SE=0.024). Models from factorial analysis had an average R^2 value of 0.586 (SE=0.036), while average R^2 values from the depth only models and the time of air exposure models were 0.332 (SE=0.067) and 0.276 (SE=0.070). The last two models were heavily influenced by the first two years of data, in which depth was not very significant. When the depth and time of air exposure models were compared for just 1994 and 1995, they performed much better, with average R^2 values of 0.511 (SE=0.021) and 0.463 (SE=0.012) respectively.

To calculate the initial number of eggs spawned at spawn deposition transects for 1995 a model using only time of air exposure was used. Time of exposure to air can be calculated for 1995 spawn deposition transects at each depth using the equation

$$AE=(6.013697+1.696911*D)^2$$

where AE is the total time of air exposure over the incubation period in hours and D is depth in feet. The egg loss rate for each depth in 1995 can then be calculated using

$$Z=0.052357+0.000601*AE.$$

The initial abundance of herring eggs at each depth can be estimated from the number of eggs counted during spawn deposition surveys using the formula

$$N_0=N_t/e^{Zt}$$

where N_t is the observed egg count, N_0 is the number of eggs initially spawned at that depth, and t is the elapsed time between spawning and the survey.

The average eggs lost from the time of spawning to the time at which the spawn deposition survey took place was 6.69% per day at selected spawn deposition transects in 1995. Egg loss increased from 4.61% per day at subtidal depths to 21.61% per day at higher depths, which experienced more hours of air exposure. The percentage of eggs lost over the entire incubation period increased exponentially from 67.40% at subtidal depths to an asymptote at 100% at the shallower depths (Figure 2). The average percentage of eggs lost over the entire incubation period at all transects was 76.06%.

DISCUSSION - Summary

It is apparent that depth is probably the most important variable affecting egg loss. Depth was included in the best model for all datasets except 1990, and was the predominant variable in all models of 1994 and 1995 data. Time of air exposure is a good substitute for depth, reducing the number of parameters estimated without significantly decreasing the efficiency of the model.

The wave exposure variable produced a very interesting result in that egg loss was higher at protected transects than at exposed transects. This result is highly counter-intuitive and may reflect the presence of an undiscovered process driving egg loss in protected areas. Preliminary examination of data collected by wave sensors placed at three egg loss transects in 1995 indicate there may be a threshold wave energy level. Beyond this threshold wave forces may result in high levels of egg loss, while below this threshold energy level egg loss due to wave energy may be negligible.

Both substrate type and kelp type were found to be insignificant in most models of egg loss rates. Substrates other than rocky were not well represented in most years, so replication was not sufficient to provide robust analyses. The kelp type variable was confounded with the depth variable since large brown kelp typically did not occur at depths above mean low water. An analysis of variance of egg loss rates to address the problem of kelp type was performed on data from subtidal depths only. The results indicated that kelp type was highly insignificant in predicting the rate of egg loss.

Oiled/unoiled condition (location) seems to have also been very important, especially in 1990. The differences in physical and biological regimes between the north and south sound are probably responsible for the differences in egg loss observed between the two areas. In 1994 and 1995 this variable was not examined since the majority of spawn was located in the south sound at Montague Island.

Of the covariate terms used in the modeling (average bird abundance, average gull abundance, the fish predation index and cumulative loose eggs), only bird abundance was significant, and only in 1994. Increased bird abundance in 1994 resulted in increases in egg loss rates.

Based on the results of this egg loss study, a model including only time of air exposure over incubation is recommended for predicting the removal of eggs from spawning beds in the interval between spawning events and spawn deposition surveys. However, interannual variation in the strength of other habitat variables may increase or decrease their contribution to herring egg loss causing them to become significant, as was seen with average bird abundance in 1994. An air exposure based model will account for a significant proportion of egg loss in most years, without having to include transect based variation, as seen in egg loss rates from all years plotted time of air exposure (Figure 3).

Table 1. Number of egg loss rates sampled, mean egg loss rate, standard error, range and proportion of significant egg loss regressions for each year of the Prince William Sound egg loss study.

Year	n	Mean egg loss rate (Z)	SE	Range	Proportion significant (p<0.05
1990	41	0.076	0.011	0.244 to -0.025	0.61
1991	26	0.042	0.013	0.263 to -0.059	0.58
1994	30	0.096	0.012	0.242 to -0.112	0.90
1995	32	0.096	0.011	0.231 to -0.007	0.66

Table 2. Summary of egg loss model resulting from factorial analysis of Prince William Sound egg loss rates for each year.

Dataset	n	Term	Sum of Squares	DF	p-value	R^2
1990	26	Oiled/unoiled	0.064	1	0.001	0.401
		Error	0.095	24		
1991	26	Depth	0.025	4	0.036	0.653
		Wave exposed/protected	0.049	1	0.000	
		Error	0.040	20		
1994	30	Depth*Bird abundance	0.063	5	0.000	0.736
		Depth	0.047	5	0.002	
		Error	0.032	19		
1995	32	Depth	0.067	5	0.001	0.539
		Error	0.057	26		

Table 3. Summary of egg loss models resulting from factorial analysis of combined Prince William Sound datasets.

Dataset	n	Term	Sum of Squares	DF	p-value	R^2
1990-1991 combined	52	Year*Oiled/unoiled	0.043	1	0.000	0.600
		Depth	0.043	5	0.017	
		Wave exposed/protected	0.039	1	0.000	
		Oiled/unoiled	0.028	1	0.002	
		Error	0.118	43		
1994-1995 combined	41	Depth	0.076	8	0.001	0.524
		Error	0.069	32		
Montague Island combined	60	Depth	0.084	9	0.004	0.606
		Year	0.052	3	0.001	
		Wave exposed/protected	0.018	1	0.016	
		Error	0.130	46		

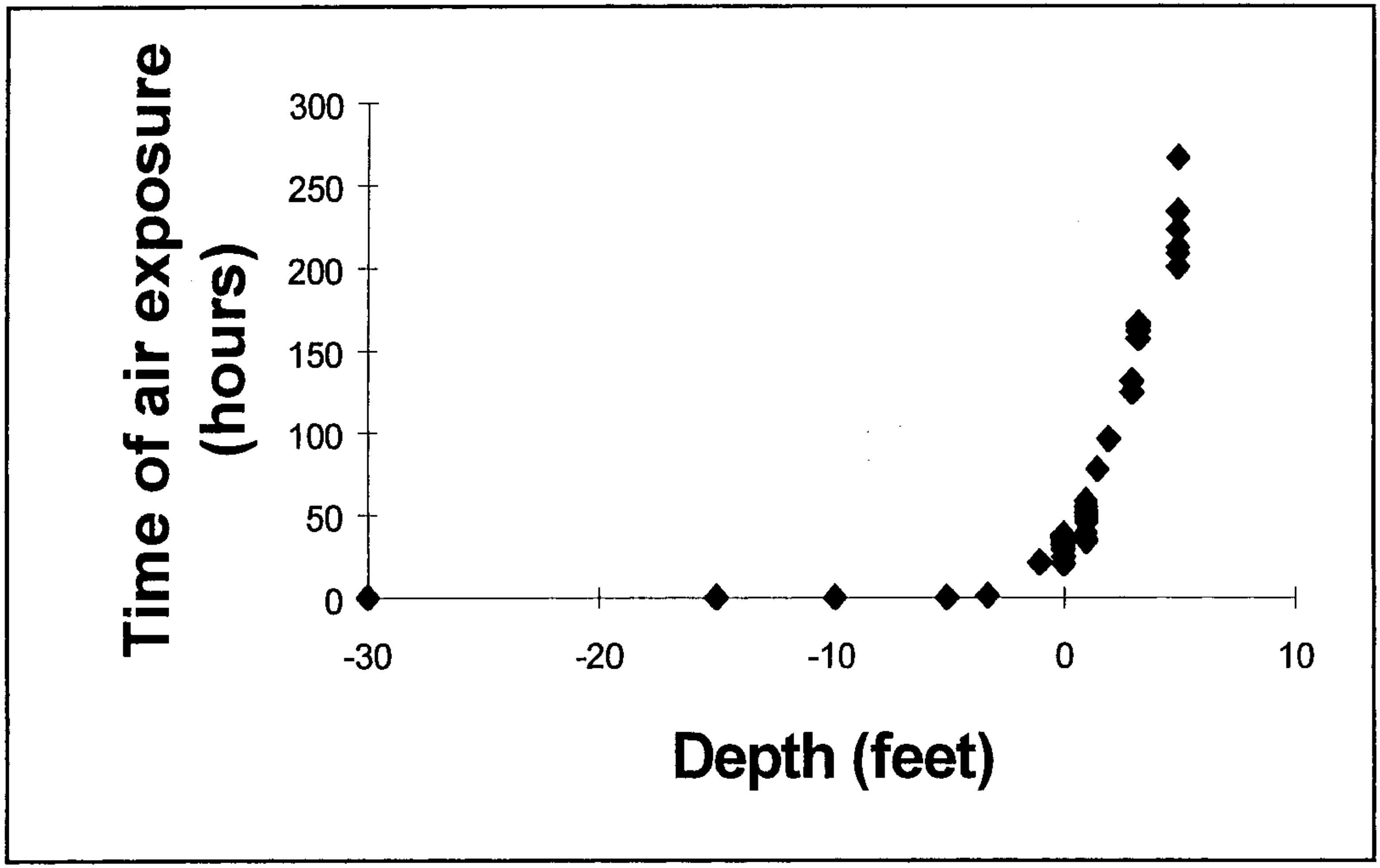

Figure 1. Total time of air exposure over the egg incubation period for each depth sampled at egg loss transects.

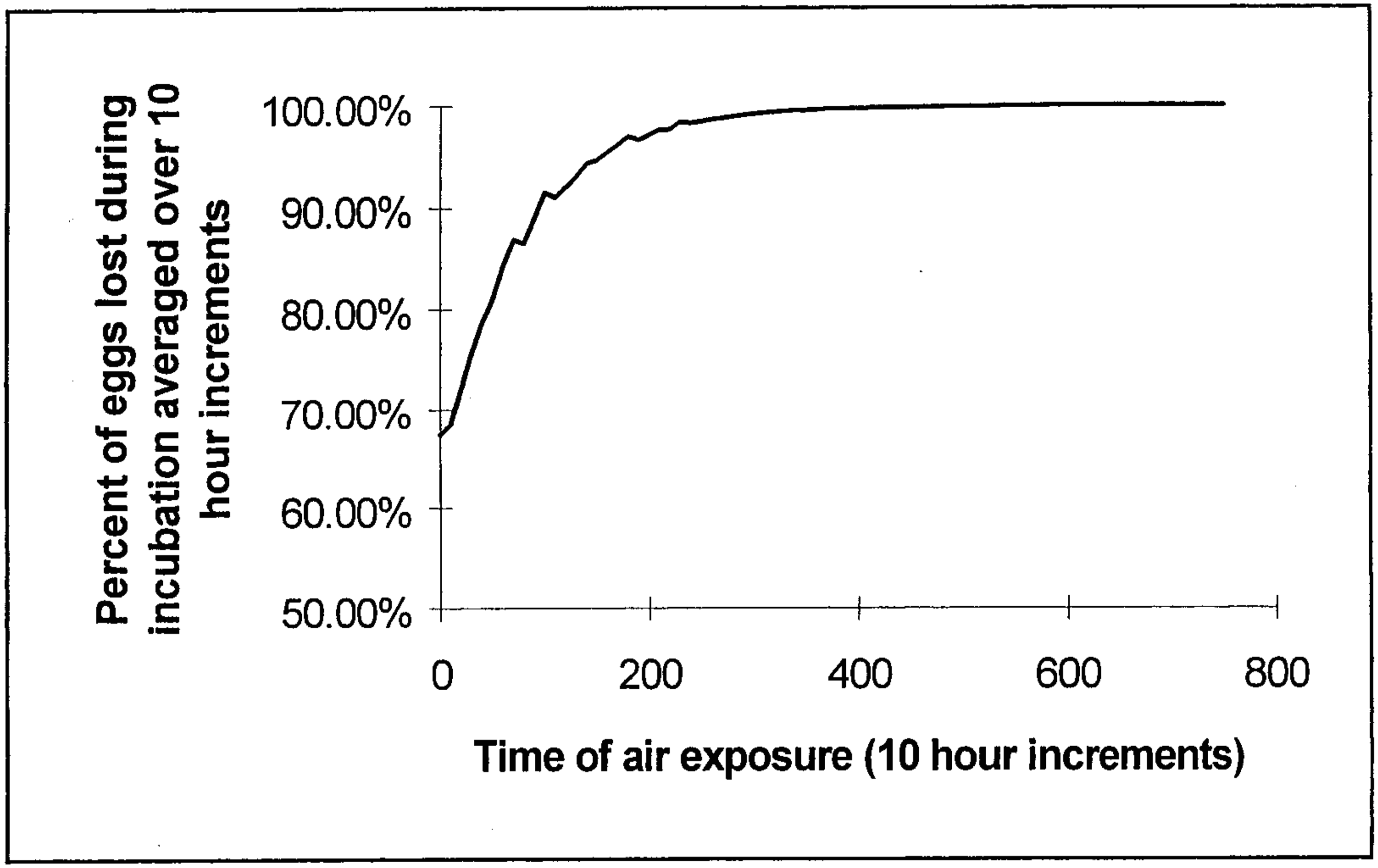

Figure 2. Percentage of eggs lost from time of spawning to time of hatching at spawn deposition transects in 1995, as predicted by the time of air exposure model.

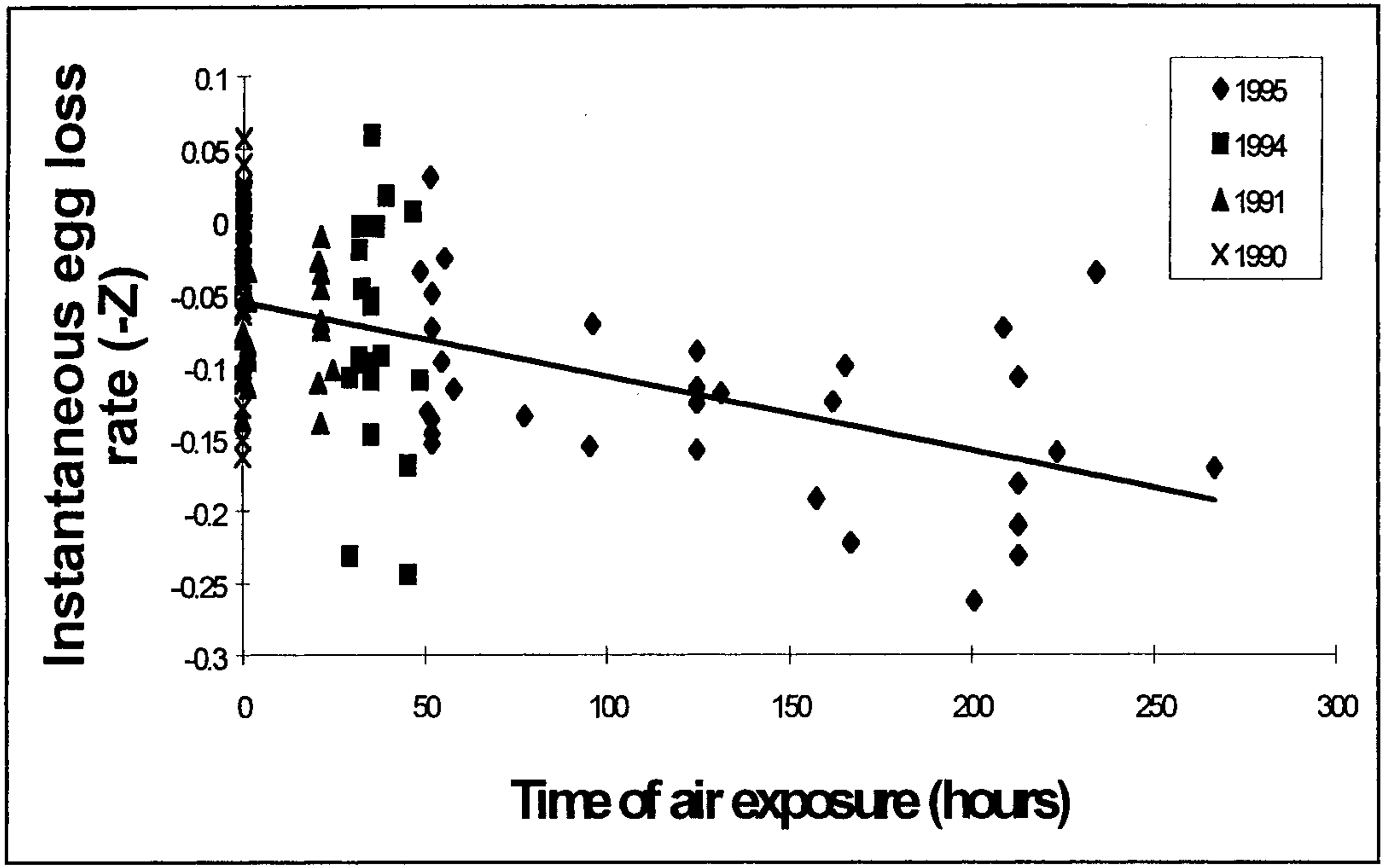

Figure 3. Instantaneous egg loss rate (-Z) versus time of air exposure for all years, from rocky and boulder substrates only.

INTERRELATIONSHIPS OF PACIFIC HERRING, CLUPEA PALLASI, POPULATIONS AND THEIR RELATION TO LARGE-SCALE ENVIRONMENTAL AND OCEANOGRAPHIC VARIABLES

By

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Date

INTERRELATIONSHIPS OF PACIFIC HERRING, CLUPEA PALLASI, POPULATIONS AND THEIR RELATION TO LARGE-SCALE ENVIRONMENTAL AND OCEANOGRAPHIC VARIABLES

A

THESIS

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DOCTOR OF PHILOSOPHY

By

Erik Hamilton Williams, B.S., M.S.

Fairbanks, Alaska

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Abstract

Recruitment estimates for Pacific herring, *Clupea pallasi*, populations in the Bering Sea and Northeast Pacific Ocean are highly variable, difficult to forecast, and crucial for determining optimum harvest levels. Age-structured population models for annual stock assessments of the sac-roe fisheries rely on fishery and survey age composition data tuned to an auxiliary survey of total biomass. In Chapter 1, the first age-structured model for Norton Sound herring was developed similarly to existing models.

Estimates of variability from age-structured stock assessment models for Pacific herring are often not calculated. In Chapter 2, a parametric bootstrap procedure using a fit of the Dirichlet distribution to observed age composition data was developed as a quick and easy method for computing error estimates of model estimates. This bootstrap technique was able to capture variability beyond that of the multinomial distribution. This technique can provide estimates of variability for existing population models with age composition data requiring little change to the original model structure.

Recruitment time series from Pacific herring stock assessment models for 14 populations in the Bering Sea and Northeast Pacific Ocean were analyzed for links to the environment. For some populations, recruitment series were extended backward in time using cohort analysis. In chapter 3, correlation and multivariate cluster analyses were applied to determine herring population associations. There appear to be four major herring groups: Bering Sea, outer Gulf of Alaska, coastal SE Alaska, and British Columbia.

These associations were combined with an exploratory correlation analysis of environmental data in chapter 4. Appropriate time periods for environmental variables were determined for use in Ricker type environmentally dependent spawner-recruit forcasting models. Global and local scale environmental variables were examined in

forecasting models, resulting in improvements in recruitment forecasts compared to models without environmental data. The exploratory correlation analysis and best fit models, determined by jacknife error prediction, indicated temperature data corresponding to the year of spawning resulted in the best forecasting models. The Norton Sound age-structured model, parametric bootstrap procedure, and recruitment forecasting models serve as enhancements to the decision process of managing Pacific herring fisheries.

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Preface

Pacific herring, *Clupea pallasi*, is a commercially and ecologically important fish species throughout most of its range (Hay 1985). It is found in abundance along the shores of Japan and along the Alaskan and Canadian coasts. Historically, Pacific herring have been harvested by man for thousands of years, and their use has ranged from basic subsistence to expensive gourmet food (Pete 1991). Within the Northeast Pacific Ocean, commercial fishing for Pacific herring began in the 1890's when fish were salted and pickled. At the beginning of the1920's, reduction fisheries for Pacific herring meal and oil began to operate in Southeast Alaska and British Columbia. Around the late 1960's the reduction fisheries stopped in Southeast Alaska and British Columbia because of the availability of cheaper Peruvian anchoveta. Bering Sea herring experienced some exploitation from various foreign fleets during this time. In the early 1970's the modern day sac-roe fisheries started in the Bering Sea and Northeast Pacific Ocean and continue to this day. In the past few years the Alaskan herring harvest has averaged 48,000 tons and has been valued at nearly 15 million dollars (Alaska Department of Fish and Game 1997). The sac-roe fishery primarily exists to serve the Japanese market for herring roe, which demands a relatively high price.

Fisheries science seeks to obtain the optimum benefits, typically by harvesting a resource, for society from the aquatic environment. In order to obtain "optimum benefits," a thorough knowledge of the resource and its environment is required. Harvesting practices involve removing surplus production from a particular population. The amount of surplus production available for harvest each year can be highly variable and is most dependent on the population dynamics of the stock. Integral to managing a population harvest is the understanding of mechanisms that govern population fluctuations and the ability to predict future population sizes. Despite the vast amount of published material on herring, a basic understanding of the causes of population fluctuations remains elusive.

Herring population sizes, like most fish species, are determined by three primary controlling factors: recruitment, growth, and mortality. Recruitment is the number of new fish added to the measured portion of the population. This measured portion can be age of first reproduction, minimum size of commercial utilization, or any other life stage of a fish. In any case, recruitment is the starting and ending point by which population fluctuations are studied. Growth and mortality are the forces that act on the individuals of the population and ultimately determine the probability that an individual will survive and move into the next life stage.

Recruitment prediction is one of the most important concerns for fisheries managers. Pacific herring have a relatively short life span and high degree of recruitment variability, making an understanding of recruitment dynamics crucial to management (Quinn et al. 1990). Many scientists have attempted to model growth and mortality processes in order to make better predictions of recruitment. Both biological and physical factors have been implicated as forces that determine recruitment. For herring, biological factors alone have shown little promise in improving recruitment predictions. Density-dependent spawner-recruit models explain very little of the total variation in annual recruitment of Pacific herring. In many cases Pacific herring spawner-recruit relationships seem non-existent, indicating that density-independent factors in the environment may be more important.

Pacific herring populations are modeled by the Alaska Department of Fish and Game (ADF&G) and the Department of Fisheries and Oceans (DFO), Canada using age-structured analysis (Funk et al. 1992; Schweigert and Stocker 1988). These models use catch-age composition data from commercial and survey catches along with an auxiliary estimate of biomass, typically in the form of an aerial or spawn deposition survey. Age-structured models for Pacific herring data are available from stocks located in the Bering Sea and Northeast Pacific Ocean. In order to extend the geographic range of Pacific herring data, an age-structured model of Norton Sound, Alaska herring was developed in Chapter 1.

In order to interpret fully the results from age-structured models, estimates of parameter variability are required. Obtaining error estimates of estimated parameters is often accomplished most easily by the incorporation of a bootstrap procedure. Typically, a parametric bootstrap procedure is used in which a statistical distribution, usually the multinomial distribution, is fit to the age composition residuals. Use of the multinomial distribution often requires manipulation of the sample size. In an attempt to obtain more objective error estimates, an alternate parametric bootstrap procedure was developed in Chapter 2 that can easily be adapted for existing age-structured models.

Age-structured models are primarily used for analyzing fishery data, but also serve as an excellent means of assimilating data from various surveyed sources. Recruitment, spawning biomass and weight-at-age data are available from the age-structured models used by ADF&G and DFO. Historical age composition, weight-at-age, and total catch data were recorded by the National Marine Fisheries Service during the reduction fisheries in Kodiak, Prince William Sound, and Southeast Alaska (Reid 1971).

Pacific herring population data from the Bering Sea and Northeast Pacific Ocean were assimilated from the sources mentioned above for use in an analysis of herring population interrelationships. Some series were extended backward in time using data from reduction fisheries in cohort analysis. Previous studies have indicated herring recruitment fluctuations are often synchronous and correlated (Hollowed et al. 1987; Zebdi and Collie 1995; Zheng 1996). Similarities in recruitment time series for Pacific herring suggests populations may be grouped into large-scale associations. Chapter 3 contains investigations of Pacific herring population associations in the Bering Sea and Northeast Pacific Ocean. An analysis of the associations could indicate deviations, possibly caused by local disturbances, natural or man induced. Large-scale associations could be the result of herring populations responding to similar large-scale environmental influences.

In order to investigate the possibility that Pacific herring populations are being influenced by the environment, recruitment time series from the data sources mentioned above were analyzed in order to determine important correlations with large-scale and local environmental variables. Since spawner-recruit models seem inadequate in many cases for herring recruitment prediction, environmentally dependent Ricker type, spawner-recruit models were used to model and forecast Pacific herring recruitment in Chapter 4. The addition of environmental information should enhance the ability to forecast herring recruitment for use in population models and the management of herring fisheries in general.

The chapters in this thesis have been formatted for submission to scholarly journals. Chapter 1 has been published in the *Alaska Fisheries Research Bulletin* (Williams and Quinn 1998). Chapter 2 is in the format for publication in the proceedings from the Lowell Wakefield Symposium (Williams and Quinn *in press*). Chapters 3 and 4 have been formatted for submission to the journals *Fisheries Oceanography* and the *Canadian Journal of Fisheries and Aquatic Sciences*, respectively.

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Chapter 1. Age-Structured Analysis of Pacific Herring from Norton Sound, Alaska[1]

1.1 Abstract

For many exploitable Pacific herring *Clupea pallasi* stocks in Alaska, age-structured assessment models are used to forecast the abundance of returning herring. The purpose of this study was to develop such a model for Norton Sound herring. Commercial catch and sampling data for Norton Sound herring were obtained from the Alaska Department of Fish and Game. Natural mortality estimates were obtained from analysis of life history parameters. Initial starting values for the age-structured model were obtained from cohort analysis. Better results were obtained when age-composition data for age 10 and older were pooled into a plus group. A parametric bootstrap analysis using a beta distribution by incorporating variability from the age-composition residuals provided standard errors of the estimates. The analysis suggested that aerial surveys underestimated actual biomass in the early 1980s. However a sensitivity analysis suggested that higher natural mortality in those years could have produced similar results. The fit of this model to the data was comparable to that obtained with age-structured assessments of other Alaska herring stocks. We believe this model can be used as a stock assessment tool for management of Norton Sound herring.

1.2 Introduction

Commercial harvest of Pacific herring *Clupea pallasi* from Norton Sound, Alaska (Figure 1.1) has been recorded as far back as 1916. Until World War II, the product was mostly salt cured. After World War II the demand for herring dropped, and limited roe herring harvests were documented from 1964 to 1978. After passage of the Magnuson Act in 1978, a large-scale herring sac roe fishery began to develop. In 1979, purse seiners

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[1] An earlier version of this chapter was published (Williams and Quinn 1998).

began working in Norton Sound; local fishers, using gillnets and beach seines, could not compete with them. The Alaska Board of Fisheries recognized this and implemented regulations that prevented purse seining north of the Togiak fishery. Since 1981, only gillnets and beach seines could be used to harvest herring in Norton Sound (Lean 1989). In 1992, the gillnet fishery for herring in Norton Sound could not be opened due to late thawing of the pack ice.

The Alaska Department of Fish and Game (ADF&G) performs annual stock assessments of Norton Sound herring based on information from commercial catch samples, aerial surveys, and test fishing (done with a variable mesh gillnet operated by ADF&G personnel). Herring sampled from commercial and test fishery catches are used to estimate age, sex, size, and sexual maturity. Aerial surveys are flown annually to estimate biomass based on observed herring school surface area and miles of spawn (Lebida and Whitmore 1985). Quality of aerial survey estimates varies and in some cases herring abundance cannot be determined. Herring forecasts are calculated by projecting spring biomass estimates forward to the next year while accounting for growth, natural mortality, harvests, and recruitment. Forecasts are used to set harvest levels for the upcoming year (Funk 1993).

Harvest levels are limited to a maximum exploitation rate of 20% of the spawning population. A threshold level, below which harvests are not allowed, has been established to ensure a minimum stock size of 7,000 tons is maintained. Exploitation rates may be lowered if stock sizes decline to levels near threshold level (Funk 1993). The occurrence and length of fishing periods is managed through emergency order authority. The Board of Fisheries has established regulations that allocate 10% of the preseason projected harvest to beach seine and 90% to gillnet gear (Funk 1993).

For many exploitable herring stocks, ADF&G uses age-structured assessment models to forecast the abundance of returning herring (Funk et al. 1992; Brannian et al. 1993; Yuen et al. 1994). These models incorporate auxiliary information, similar to models developed by Deriso et al. (1985). The purpose of this study was to develop an age-structured assessment model for Norton Sound herring that would allow assimilation of available data, provide standard error estimates, and could be used by ADF&G for forecasting purposes.

1.2.1 Data

Annual sampling reports with records of weight-at-age for Norton Sound herring and a spreadsheet-based, age-structured analysis model used for the analysis of herring from Togiak Bay were obtained from ADF&G (Brannian et al. 1993; F. Funk, ADF&G, Juneau, personal communication; Figure 1.1). We also obtained ADF&G age-based data for Norton Sound herring beach seine catches, gillnet catches, total-run estimates, and aerial biomass survey results (H. Hamner, ADF&G, Anchorage, personal communication).

The beach seine and gillnet age-composition data are based on samples taken from the respective commercial fisheries. Total-run age-composition is based on the test fishery. Aerial survey biomass estimates are based on the survey results, timing of peak biomass in the survey, and timing of the fishery. These data sets were then input into a spreadsheet-based model that uses the beach seine catches (Figure 1.2), gillnet fishery age compositions (Figure 1.3), total-run age compositions (Figure 1.4), and aerial survey biomass estimates (Figure 1.5) as its data sources. Visual analysis of the year class data in Figures 1.2-1.4 suggests that 4 strong year classes were recruited to the fishery and persisted a number of years: 1977 year class persisted 1982-1985, 1979 year class persisted 1984-1987, 1982 year class persisted 1989-1991, and 1988 year class persisted 1993-1995. The observed aerial biomass in Figure 1.5 indicates a small increase in biomass from 1981 to 1988, a larger increase from 1989 to a peak in 1992, and then a decrease from 1992 to 1995.

1.3 Methods

An estimate of natural mortality is required for use in cohort analysis and age-structured analysis. Typically, for lack of a better estimate, natural mortality is assumed to be 0.2. For Pacific herring, natural mortality has been shown to range from 0.1 to 0.4 based on catch curve analyses, the rate decreasing northward (Trumble and Humphreys 1985; Wespestad 1991). Southeast Alaska and British Columbia estimates of herring natural mortality range from 0.33 to 0.46 for age-4 fish and 0.79 to 0.85 for age-8 fish, based on a mark-recapture experiment and catch curve analyses (Skud 1963; Tester 1955). Hence, the overall potential range of natural mortality for Norton Sound herring is 0.10 to 0.85.

We assume a single value for instantaneous natural mortality (*M*) for all ages and years, while recognizing that this value might actually change. It is difficult to estimate a single value for natural mortality, let alone a series of values, in catch-age analysis (Schnute and Richards 1995). Nevertheless, we do explore the sensitivity of the model to different values of *M*.

Several estimators of natural mortality are based on life history parameters such as the Brody growth coefficient, *K*, of the von Bertalanffy growth curve. Gulland (1965) and Beverton and Holt (1957) provided estimates of natural mortality for clupeoids as 1.5*K* and 1.2*K*, respectively. Other methods of estimating natural mortality include the Alverson and Carney (1975), Pauly (1980), Gunderson and Dygert (1988), and Jensen (1997) methods.

For these methods, estimates of growth parameters are necessary. A von Bertalanffy growth curve for body weight was fitted to Norton Sound herring weight-at-age data from 1989 to 1994 using a nonlinear least squares technique. An estimate of the allometric growth parameter, $\beta = 3.48$, for spawning fish from Norton Sound was obtained from Wespestad (1991). The results from the fit of the equation were $W_\infty =$ 382.9 g and $K = 0.29$. The Alverson-Carney method for estimating instantaneous natural mortality uses the age of maximum biomass of the fish stock. Based on an empirical regression analysis, Alverson and Carney (1975) determined the age of maximum biomass was positively correlated to the maximum age of the fish. The maximum observed age for Norton Sound herring is 17, which is based on age samples collected pre- and post-fishery. Since a fishery has the effect of decreasing the age of maximum biomass and maximum age, a conservative estimate of 18 years was used for the maximum observed age for Norton Sound herring. For the Pauly method, the mean water temperature experienced by the stock was set at 4°C based on Wespestad's (1991) research of Eastern Bering Sea herring stocks. The results from this analysis were then used to calculate estimates for natural mortality.

The Gunderson and Dygert (1988) method exploits an apparent relationship of the GSI (gonadal somatic index) to natural mortality. In this technique the ratio of gonad weight to somatic weight is computed. The somatic weight must be calculated with the stomach contents removed. Since the fishery is targeting the sac-roe, roe percentages estimated during the fishery may serve as approximations of the GSI. Since the roe percentage calculation performed by the industry includes the weight of the stomach contents, the GSI will be slightly biased towards lower estimates. Historical roe percentages for Norton Sound herring range from 9-11% of the total catch, which should correspond to roughly 18-22% for females, assuming a 50:50 sex ratio. Based on these estimates the natural mortality may range from 0.33 to 0.39 and may be higher based on the bias created by the weight of stomach contents.

Cohort analysis was performed on the Norton Sound herring catch data in order to obtain initial starting values for use in the age-structured analysis. The available Norton Sound herring data involved catches from 2 gear types, beach seine and gillnet, which were pooled for the cohort analysis. The data covered years 1981 to 1995 and included ages 3 through 16. As mentioned earlier there was no gillnet fishery in 1992. Age-specific gear-selectivity values were based on a logistic function, which resulted in full selection at ages 12 and higher. Terminal fishing mortality was set at 0.35 based on the level of catches compared to survey estimates of total abundance. Instantaneous fishing mortality (F) for younger years was calculated by multiplying terminal fishing mortality by an age-specific gear-selectivity value obtained from the Togiak Bay herring fishery. Numbers of fish at age a and year t were estimated by the following formulae:

$$N_{a,t} = N_{a+1,t+1}\, e^{M} + C_{a,t}\, e^{M/2}$$

and for terminal values,

$N_{A,t}$, t=1,..., T(last year) and $N_{a,T}$, a=1,..., A(last age)

$$= \frac{C_{a,t}}{\frac{F_{a,t}}{Z_{a,t}}\left(1 - e^{-Z_{a,t}}\right)},$$

where $C_{a,t}$ is the total catch at age a and time t, and total instantaneous mortality is, $Z_{a,t} = M + F_{a,t}$.

The age-structured model used in this analysis was based on a model currently in use by ADF&G (Brannian et al. 1993). The model calculates pre-fishery abundance at age and aerial survey abundance at age using beach seine and gillnet catch data supplemented with total-run and aerial survey data. The following notation is used in the formula for the age-structured analysis:

S_a = annual survival at age a,
$W_{a,t}$ = weight at age a and year t in g,
$s_{a,g}$ = gillnet gear vulnerability at age a,
$s_{a,r}$ = total-run gear vulnerability at age a,
$C_{t,g}$ = total gillnet catch at year t in millions of fish,
$C_{a,t,s}$ = beach seine catch at age a and year t in millions of fish,
$\Theta'_{a,t,g}$ = observed gillnet age-composition at age a and year t,

$\Theta_{a,t,g}$ = estimated gillnet age-composition at age a and year t,

$X_{t,g}$ = exploitable abundance relative to gillnets in millions of fish,

$\Theta'_{a,t,r}$ = observed pre-fishery total-run age-composition at age a and year t,

$\Theta_{a,t,r}$ = estimated pre-fishery total-run age-composition at age a and year t,

$X_{t,r}$ = surveyed abundance relative to the total-run in millions of fish,

$N_{a,t}$ = estimated total pre-fishery population abundance at age a and year t in millions of fish,

B'_t = observed total aerial survey biomass in tonnes,

$B_{a,t}$ = estimated aerial survey biomass for age a in tonnes,

$B_{t,q}$ = adjusted total aerial survey estimate in tonnes.

Some of the assumptions of the model are:

1) Beach seine catch and gillnet total catch are measured without error.

2) Catch occurs instantaneously at the start of the year, and natural mortality occurs during the entire year.

3) Gillnet selectivity is constant over time and can be modeled with a logistic function.

4) The survey may take place either before the fishery or after, but the survey selectivity is assumed constant over time.

All necessary data were entered into the spreadsheet by year and age. Pre-fishery total population abundance, $N_{a,t}$, was calculated by the following formula, where $a = 4$ to 16 and $t = 1982$ to 1994:

$$N_{a,t} = S_a \left[N_{a-1,t-1} - (C_{a-1,t-1,s} + \Theta_{a-1,t-1,g} C_{t,g})\right]$$

$N_{a,1981}$ and $N_{3,t}$ were the initial starting values obtained from cohort analysis. The estimated gillnet age-composition in the model was calculated as follows:

$$\Theta_{a,t,g} = s_{a,g} N_{a,t} / X_{t,g} ,$$

$$s_{a,g} = 1 / (1 + e^{-[b+(c\ a)]}) \text{ and}$$

$$X_{t,g} = \sum_{a=1}^{A} s_{a,g} N_{a,t}$$

where *b* and *c* are parameters of the logistic function. Gillnet residuals are $\Theta'_{a,t,g} - \Theta_{a,t,g}$. The estimated total-run age-composition in the model is as follows:

$$\Theta_{a,t,r} = s_{a,r} N_{a,t} / X_{t,r} ,$$

$$s_{a,r} = 1 / (1 + e^{-[d+(e\ a)]}), \text{ and}$$

$$X_{t,r} = \sum_{a=1}^{A} s_{a,r} N_{a,t} ,$$

where *d* and *e* are parameters of the logistic function. Total-run residuals are $\Theta'_{a,t,r} - \Theta_{a,t,r}$. The estimated aerial survey biomass in the model is as follows:

$$B_{a,t} = W_{a,t} s_{a,r} N_{a,t} ,$$

$$B_t = \sum_{a=1}^{A} B_{a,t},$$

and the adjusted aerial survey biomass is:

$$B_{t,q} = B_t q_t,$$

where q_t is a survey calibration parameter. The survey underestimates, is unbiased for, or overestimates true abundance when q_t is less than, equal to, or greater than 1, respectively. The aerial survey residuals are $B'_t - B_{t,q}$.

The solver function in the Microsoft Excel spreadsheet program, which is based on a quasi-Newton optimization algorithm (Chong and Zak 1996), was then used to minimize total sums of squares, SSQ_{total}, which consisted of the 3 components: (1) gillnet age compositions (SSQ_g), (2) total-run age compositions (SSQ_r), and (3) aerial survey biomass estimates (SSQ_b). Each represents the sum of the squared residuals:

$$SSQ_g, SSQ_r, SSQ_b = \sum (residual)^2 .$$

To keep the magnitude of the sums of squares similar, each component was multiplied by a weighting term, λ, such that

$$SSQ_{total} = \lambda_g SSQ_g + \lambda_r SSQ_r + \lambda_b SSQ_b .$$

A bootstrap analysis was performed to obtain standard errors of the estimates from the age-structured model. At first, an ordinary bootstrap of the aerial survey and age-composition residuals, a random sample with replacement of residuals added to predicted values, was performed (Efron 1982; Efron and Tibshirani 1993). This technique worked for the aerial survey residuals, but resulted in negative age compositions because of the presence of negative residuals and many observed age compositions of low to zero value. Alternatively, the age-composition data could be fitted to a multinomial distribution and age compositions generated based on this fit, but this method requires subjective determination of the effective sample sizes; we observed that residual variation was larger than what would be expected for a multinomial distribution.

Our purpose in performing a bootstrap exercise was to obtain quick and easy estimates of the standard errors that could be obtained from the observed residual variation in age composition. We developed an alternative approach by performing a parametric bootstrap based upon a fit of the age compositions to a beta distribution (Efron 1982; Efron and Tibshirani 1993), details of which we intend to publish elsewhere (Williams and Quinn, in press). The beta distribution utilizes the beta function, which is a U-shaped curve with 2 shape parameters *v* and *w*, given by

$$B(v,w) = \int_0^1 u^{v-1}(1-u)^{w-1} d\,.$$

The beta function is related to the gamma function (Evans et al. 1993). The gamma function and its interrelationship with the beta function are as follows:

$$\Gamma(c) = \int_0^\infty \exp(-u)u^{c-1} d\,,$$

and

$$B(v,w) = \frac{\Gamma(v)\Gamma(w)}{\Gamma(v+w)} = B(w,v)\,.$$

It is assumed that the observed age compositions, $\Theta'_{a,t}$, follow the beta distribution with parameters $v_{a,t}$ and $w_{a,t}$, given by:

$$v_{a,t} = z\,\Theta_{a,t} \text{ and } w_{a,t} = z\,(1 - \Theta_{a,t})$$

where $z = v_{a,t} + w_{a,t}$ and the beta distribution variance of $\Theta_{a,t}$ is

$$var(\Theta_{a,t}) = v_{a,t}\,w_{a,t} / [z^2\,(z + 1)]\,.$$

The parameter z represents a common variance and allows age compositions across years to be modeled by the same overall distribution. The z parameter is inversely related to the amount of variation in the age-composition residuals. Given the above information, the beta distribution was fitted to the observed gillnet and total-run age-composition data by maximizing the log likelihood with respect to z:

$$\ln L\left(z \middle| \{\Theta'_{a,t}\}\right) = \sum \left[(v_{a,t} - 1)\ln\Theta'_{a,t} + (w_{a,t} - 1)\ln(1 - \Theta'_{a,t}) - \ln B(v_{a,t}, w_{a,t})\right],$$

where

$$\ln B(v_{a,t}, w_{a,t}) = \ln\Gamma(v_{a,t}) + \ln\Gamma(w_{a,t}) - \ln\Gamma(z)\,.$$

A bootstrap analysis was performed by using the log-likelihood fitted beta function parameters $v_{a,t}$ and $w_{a,t}$ in a visual basic program, modified from Cheng (1978), to generate beta distributed random age compositions. Efron and Tibshirani (1993) suggest a bootstrap sample of 50-200 be used for standard error estimates. We anticipated a few convergence failures and therefore chose a bootstrap sample of 110 for this exercise. The nature of this log-likelihood function does not allow for zero-valued observed age compositions to be estimated. For the Norton Sound data the observed gillnet ages that were unrepresented (zero) include all ages for 1992, age 3 for all years, age 4 for 1988-1995, and age 5 for 1991 and 1995; in the observed total-run only age 3 in 1994 and 1995 was unrepresented. These zeros were left alone in the bootstrap procedure.

Two sensitivity analyses were performed to determine the sensitivity of model parameters and output to changes in model specifications. The first sensitivity analysis was performed to examine the effect of changes in aerial survey sums of squares weighting on survey calibration coefficients (q_t) and biomass estimates. A second sensitivity analysis was performed to determine how changes in natural mortality (M) affect q_t.

1.4 Results

The Alverson-Carney estimate of natural mortality resulting from the analysis of growth parameters was 0.16 (Table 1.1). This estimate was chosen for use in the cohort analysis because Trumble and Humphrey's (1985) and Wespestad's (1991) research indicated natural mortality for Pacific herring decreases to the north and could be as low as 0.10 in the Eastern Bering Sea.

Estimates of abundance obtained from cohort analysis are shown in Figure 1.6. The results from the cohort analysis provided initial starting values for use in the age-structured analysis. Specifically, the estimated abundances for age 3 (all years) and year 1981 (all ages) were used as starting values for the age-structured analysis.

A total of 35 parameters were estimated in the optimization function in order to minimize the total sums of squares of the residuals, SSQ_{total}. The estimated total population abundance, N, for all ages in 1981 and all years except 1995 at age 3 accounted for 27 parameters. The logistic parameters of gear-selectivity functions for gillnet in years 1981-1990, gillnet in years 1991-1995, and for sampling gear added an additional 6 parameters. Lastly, the survey calibration coefficients for the aerial survey estimates for years 1981 to 1984 and 1985 to 1990 accounted for 2 parameters. The years 1991-1995 were assumed to have total aerial survey coverage, and therefore, there was no survey calibration parameter for these years.

At first the survey calibration coefficients were not used in the analysis. Initial solver runs revealed undesirable patterns in the residuals. In an attempt to obtain a better fit of the model to the data, several weighting schemes were used for the various sums of squares. The aerial survey residuals for years 1982 and 1989 were removed from the total sums of squares calculation due to poor viewing conditions during these years. Initial runs of the age-structured analysis also revealed poor fitting of the gear-selectivity functions, especially for later ages. Analysis of catch curves revealed peaks in catches averaging around age 8-9; therefore, gear vulnerability was fixed to 1 (indicating full vulnerability) for all ages >7 in years 1981-1990 and ages 8 in years 1991-1995.

The results of various weighting schemes revealed that when more weight was placed on a particular sum of squares, the results tended to conform to the more heavily weighted data set and bias appeared in the residual patterns for the other data sets. The weighting runs revealed an apparent contradiction in the data between the gillnet age-composition data and the aerial survey data. The question then became: which data set was more reliable? The aerial biomass survey experienced changes in coverage throughout its history. Changes in the amount of area flown, sometimes resulted in minimal biomass estimates and variation in viewing conditions introduced subjectivity (C. F. Lean, Alaska Department of Fish and Game, Nome, personal communication). Two survey calibration coefficients were added for years 1981-1984 and 1985-1990 to compensate for incomplete aerial survey biomass estimates. These 2 intervals were chosen after several runs with various combinations of 1 and 2 survey calibration coefficients.

The age-structured model was optimized as a function of 35 parameters. The resulting values for these parameters are shown in Table 1.2. The values of the survey calibration coefficients indicate the aerial survey was overestimating the biomass in 1981-1984 and underestimating the biomass in 1985-1990. An analysis of the residuals was used to reveal whether the model was a good fit to the data. In the later years for the gillnet and total-run age-composition data there is an apparent bias in the model fit (Figures 1.8, 1.9) that was not apparent in the biomass data (Figure 1.7). This bias is a direct result of unrepresented older ages in the early years of these data sets (Figures 1.3, 1.4). As the years progress, older fish begin to appear in the data set. This apparent trend of older fish being captured in the gillnet fishery can partly be explained by a shift in the fishery to targeting older fish, which began around 1990 (C. F. Lean, Alaska Department of Fish and Game, Nome, personal communication). However, this does not explain the absence of older fish in early years for the sampling gear, which remains a mystery.

A pooled age group or plus group for ages 10-16 was added to the age-structured analysis to eliminate bias in the model fit for the older ages. This reduced the number of parameters being estimated by the optimization function to 29. Several weighting schemes were tested, but it became apparent that changes in the weighting affected the outcome greatly, often causing initial starting values to go to zero. The contradiction between the gillnet and aerial survey data sets seen in the non-pooled analysis was also apparent in this analysis. The final set of weighting schemes was determined by the minimum aerial survey weight necessary to obtain acceptable residual patterns. Based on this analysis, it appeared that the best weighting scheme was $2 \cdot 10^{-9}$ for the aerial survey and 1 for the gillnet and total-run sums of squares. Another minor change for the pooled group analysis was to set the sum of squares weight for age 3 in the gillnet data to zero, based on the fact that most of the observed age compositions are zero.

The resulting parameter estimates for the age-structured model with the pooled age group are shown in Table 1.3. As in the previous analysis, the estimates of the survey calibration parameters indicate the aerial survey overestimated biomass in 1981-1984 and underestimated biomass in 1985-1990. In the pre-fishery estimates, several recruitment year classes can be seen moving through time as the years progress (Figure 1.10). The first strong year class, 1977, appeared in 1981 followed by an equally strong year class, 1979, in 1983. In 1986 a moderate year class, 1982, was apparent, and there was not another apparent year class until 1990 when a relatively weak year class, 1986, became visible. In 1992 another strong year class, 1988, was apparent in the estimates. The input data revealed the same year classes, except for the 1988 year class, which first appeared in 1992 at age 4 (Figures 1.2, 1.3, 1.4). This year class was not noticeable until 1995 in the gillnet age-composition data (Figure 1.3). This is a direct result of older fish being targeted in the gillnet fishery, as mentioned earlier. In the aerial survey biomass estimates the year classes are difficult to distinguish (Figure 1.11), resulting from the differences in abundance and biomass. For these estimates the pooled age group predominated the biomass, particularly in later years.

The aerial survey biomass estimates have a similar residual pattern to the first analysis (Figure 1.7). The bias in age-composition residuals for older ages in the first analysis disappeared (Figure 1.12, 1.13). The residuals appear well distributed, except for some possible outliers for the pooled age group, but nevertheless indicate a good overall fit of the age-structured model. The gear vulnerability functions for the gillnet catch and the total-run sampling gear provided a reasonable fit (Figure 1.14). The increased age of vulnerability in the later years for the gillnet fishery followed the management changes that occurred in the early 1990s.

To obtain standard error estimates, a beta distribution was fitted to the age compositions. For both sets of age compositions, the beta distribution fits appear adequate and may actually be a bit high (Figure 1.15). The 110 bootstrap replicates required approximately 15 h of computing time using a 100 MHz computer. The majority of this computing time was involved in the optimization function in the Excel spreadsheet program. It must be noted that 6 optimization trials either failed to converge or settled on unreasonable solutions and were removed from the analysis. Because this technique for bootstrapping was only performed as a means of getting rough estimates of variation, failure to converge with a reasonable solution is probably inconsequential to the final results. From the bootstrap samples the standard error was calculated for pre-fishery abundance estimates, aerial survey biomass estimates, gear vulnerability function parameters, and aerial survey calibration coefficients.

The standard errors for pre-fishery abundance and aerial survey biomass estimates were converted to coefficients of variation. In Figures 1.10 and 1.11 the coefficient of variation appears to increase as the estimates approach zero. This is a common phenomenon for coefficients of variation, and the extreme result can be seen for age 9 in 1982 in both figures. Aside from this extreme example, the majority of the coefficients of variation appear to range from 20-60%. The standard deviations for the gear vulnerability function parameters and aerial survey calibration coefficients are shown in Table 1.3. The coefficients of variation for these parameters was relatively small, ranging from 7 to 17%.

1.4.1 Sensitivity Analysis to Changes in Aerial Survey Weighting

As mentioned earlier, several aerial survey sums of squares weights were tested for their effects on residual patterns. Changes in the aerial survey sums of squares weights also affected the biomass and survey calibration estimates. A weighting range of $2 \cdot 10^{-7}$ to $2 \cdot 10^{-11}$ for the aerial survey sums of squares indicated that increasing weight resulted in biomass estimates which increasingly conformed to observed values (Figure 1.17). The aerial survey weighting values were positively correlated with the 1981-1984 survey calibration parameter, while the 1985-1990 survey calibration parameter were not (Figure 1.18). Nevertheless, the trend in biomass estimates appeared robust, despite the large weighting range used in this analysis.

1.4.2 Sensitivity Analysis to Changes in Natural Mortality

A range for *M* of 0.16 to 0.60, which corresponds to an annual survival rate (*S*) of 0.85 to 0.55, was placed in the model for the year groupings corresponding to aerial survey calibration groupings and all model parameters were re-estimated. A positive correlation occurs between q_t for 1981-1984 and *M* for the same years. Increases in *M* resulted in increases in the aerial survey calibration parameter, which approached 1, indicating changes in *M* may explain the changes in surveyability in the aerial survey in the years from 1981-1984. The other aerial survey parameters for years 1985-1990 did not vary much with *M*. Changes in *M* for years 1985-1990 did not affect the corresponding aerial survey calibration coefficient, but increases in *M* in years 1985-1990 resulted in decreases in the aerial survey calibration parameter for years 1981-1984.

1.5 Conclusions

It appears that the pooled group age-structured analysis produced a better fit to the data than the non-pooled age-structured analysis. The addition of the pooled age group eliminated the bias being caused by the lack of representatives of older ages in early years of the gillnet and total-run age-composition data sets. One explanation for this lack of older fish in the early years for the gillnet fishery is related to the timing of the fishery relative to the timing of the run. Norton Sound herring, like many herring stocks, will begin their spawning run with the initial arrival of the older fish followed later by the younger fish. The fishery may have been targeting the end of the spawning run in early years and gradually there may have been a shift to target the early part of the run in recent years. The manager for Norton Sound has in the last few years attempted to target the early part of the run, as mentioned earlier. However, this management change does not explain the lack of older fish in the early years of the total-run age compositions, so the total explanation remains a mystery.

The bootstrap analysis chosen for this data and model did not utilize sample size or the sampling scheme used to collect the data, but rather used the variation in residuals of age-composition. The method is, however, easily performed without the complications of sample size or major changes in the model structure. The parametric beta distribution provided a concise synthesis of the variability found in the age-composition data. The estimates of variation are probably sufficient for most uses. To date ADF&G does not calculate any type of variance estimate for their age-structured assessments of exploitable herring stocks. The bootstrapping technique provided here might prove useful for other age-structured herring assessments.

The sensitivity analysis to changes in aerial survey sums of squares weighting indicates the biomass estimates are fairly robust to large changes in weighting values. However, increases in the aerial survey weight resulted in biomass estimates conforming to observed values, which coincided with bias in the age composition residuals. These weighting changes also affected the survey calibration parameters, particularly the 1981-1984 parameter. The residual bias and inflated survey calibration parameter are indicators of a data conflict.

Changes in the aerial survey calibration parameters in this age-structured model suggest that the influence of age-composition data tends toward lower biomass in years 1981-1984 and higher biomass in 1985-1990 than the aerial survey data. This data conflict could have arisen from 3 different causes: (1) a change in the aerial surveyability, (2) a change in ageing error bias, and/or (3) a change in the natural mortality rate. If this age-structured model is to be used in future assessments and forecasts by ADF&G for Norton Sound herring, reasons for the data conflict will need to be explored further.

The data conflict in this model was treated by the incorporation of aerial survey calibration parameters. Factors affecting biomass estimates from aerial surveys include surveyor bias, changes in herring biomass to school surface area ratios, changes in viewing conditions, and/or changes in area covered. Given the high degree of subjectivity and variability involved, we believe the aerial survey data is a likely candidate for impropriety.

If the data conflict arose from changes in ageing error bias, then the bias had to be toward younger ages in 1981-1984 and older ages in 1985-1990. The lack of older aged fish in the early years of the age composition datasets suggests an underageing bias. Given the available information, it is difficult to make any further conjectures regarding ageing error bias in Norton Sound herring. The best means of understanding ageing error bias in Norton Sound herring would come from a re-analysis of the scale samples by ADF&G. A change in scale readers could be the simplest cause for any ageing error bias.

Changes in survival rate were explored in the first sensitivity analysis. It appears natural mortality and the survey calibration coefficients are confounded. Higher natural mortality in the early years seems to explain the data conflict, as indicated by the correlation between changing survival rates and the 1981-1984 survey calibration parameter (Figure 1.16). However, the lack of any relationship between survival rate and the 1985-1990 survey calibration parameter (Figure 1.16) indicates this does not fully explain the data conflict. Furthermore, ageing error in the early data could create the perception that natural mortality (*M*) changed. Until ageing error is resolved, the conclusion of a change in *M* remains speculative.

Overall, age-structured stock assessment techniques, such as the type presented here, are among the best methods available to fisheries managers. This type of analysis is very useful in synthesizing much information and providing estimates that are in line with the available data. As shown in this analysis, age-structured techniques can also highlight contradictions among data sets. The evaluation of the goodness of fit for this model by graphical techniques of residuals indicated that the model provided a fairly good fit. The residuals were randomly distributed and did not show any patterns relating to age, year, or year class. The fit of this model to the data was comparable to previous age-structured assessments for Alaska herring stocks (Brannian et al. 1993). We believe this model should be used in future Norton Sound herring assessments and forecasts.

1.6 Acknowledgments

Fritz Funk provided the spreadsheet based age-structured model upon which this model was based and much insight and help with the subsequent analysis. Helen Hamner provided the age-based commercial catch and survey data for Norton Sound herring. Charlie Lean provided insight into the aerial survey data and history of the fishery. Both Fritz Funk and Dave Bernard provided critical reviews of this paper. This research was sponsored by Alaska Sea Grant with funds from the National Oceanic and Atmospheric Administration, Office of Sea Grant, Department of Commerce, under grant no. NA90AA-D-SG066, project number R/07-16, from the University of Alaska with funds appropriated by the state. The U.S. Government is authorized to produce and distribute reprints for government purposes, notwithstanding any copyright notation that may appear hereon.

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TABLE 1.1. Four estimates of natural mortality for Norton Sound herring; M = 0.16 (Alverson-Carney method) was selected for use in this study.

Method	Estimate of *M*
1.5*K*, Gulland (1965)	0.44
1.2*K*, Beverton and Holt (1957)	0.35
Alverson and Carney (1975)	0.16
Pauly (1980)	0.31

TABLE 1.2. Parameter estimates for Norton Sound herring from the non-pooled age-structured model.

Initial Cohort Sizes

Year	Age	Parameter Estimate (millions of fish)	Year	Age	Parameter Estimate (millions of fish)
1981	3	73.5133	1981	4	123.6259
1982	3	127.9579	1981	5	18.8811
1983	3	58.3050	1981	6	0.8600
1984	3	98.0477	1981	7	6.0544
1985	3	119.0715	1981	8	1.6593
1986	3	65.0653	1981	9	1.0670
1987	3	63.5074	1981	10	0.4910
1988	3	15.8540	1981	11	0.5680
1989	3	39.5981	1981	12	0.3430
1990	3	3.0684	1981	13	0.6342
1991	3	117.8595	1981	14	0.6569
1992	3	0.2907	1981	15	0.6727
1993	3	0.3414	1981	16	0.7488
1994	3	0.3142			

Gear Vulnerability Function Values

Gear	Years	Parameter	Estimate
Gillnet	1981-1989	*a*	-6.907
Gillnet	1981-1989	*b*	1.0412
Gillnet	1990-1995	*a*	-12.302
Gillnet	1990-1995	*b*	1.5574
Sampling	all	*a*	-4.5595
Sampling	all	*b*	0.6683

Aerial Survey Calibration Coefficients

Years	Coefficient Value
1981 to 1984	1.9162
1985 to 1990	0.7826

TABLE 1.3. Parameter and bootstrap standard deviation estimates for Norton Sound herring from the pooled age-structured model.

Initial Cohort Sizes

Year	Age	Parameter Estimate (millions of fish)	Year	Age	Parameter Estimate (millions of fish)
1981	3	75.2905	1981	4	134.4280
1982	3	128.6008	1981	5	22.9469
1983	3	55.1008	1981	6	2.4164
1984	3	98.4900	1981	7	8.1430
1985	3	108.1296	1981	8	2.3919
1986	3	41.0858	1981	9	1.7709
1987	3	42.5257	1981	10+	1.5745
1988	3	12.0766			
1989	3	38.7258			
1990	3	1.4502			
1991	3	113.9561			
1992	3	10.7807			
1993	3	17.2471			
1994	3	27.7576			

Gear Vulnerability Function Values

Gear	Years	Parameter	Estimate	Standard Deviation
Gillnet	1981-1989	*a*	-6.6600	0.7334
Gillnet	1981-1989	*b*	1.0140	0.1370
Gillnet	1990-1995	*a*	-15.0118	1.4534
Gillnet	1990-1995	*b*	1.9373	0.2342
Sampling	all	*a*	-4.2435	0.5525
Sampling	all	*b*	0.6154	0.0886

Aerial Survey Calibration Coefficients

Years	Coefficient Value	Standard Deviation
1981 to 1984	1.7064	0.1262
1985 to 1990	0.7395	0.0746

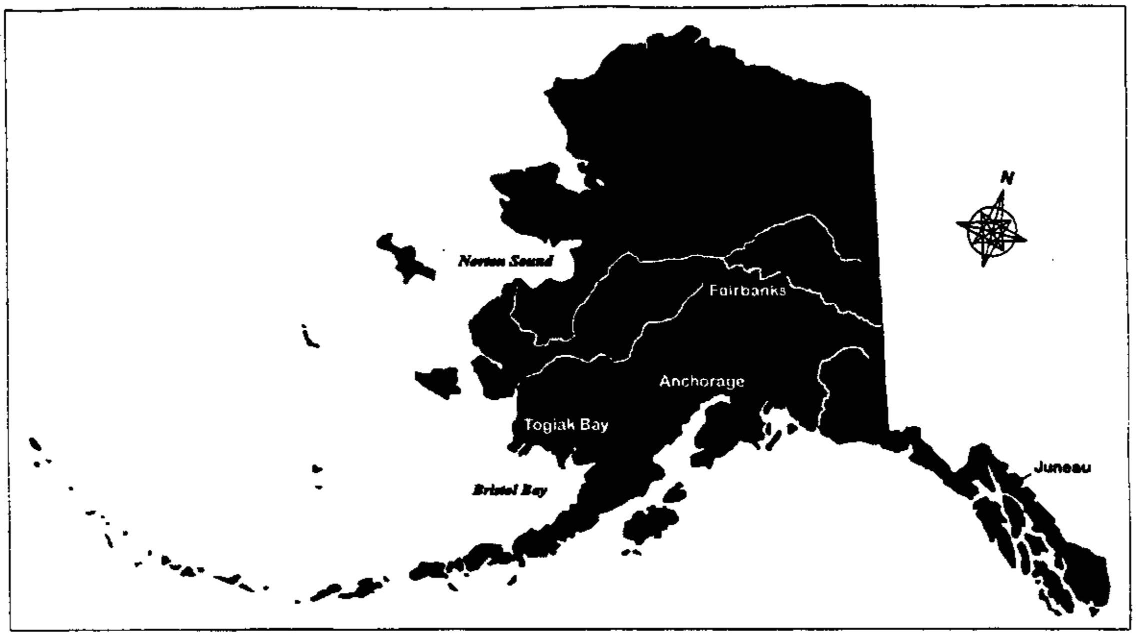

Figure 1.1. Map of Alaska showing the location of Norton Sound and Togiak Bay.

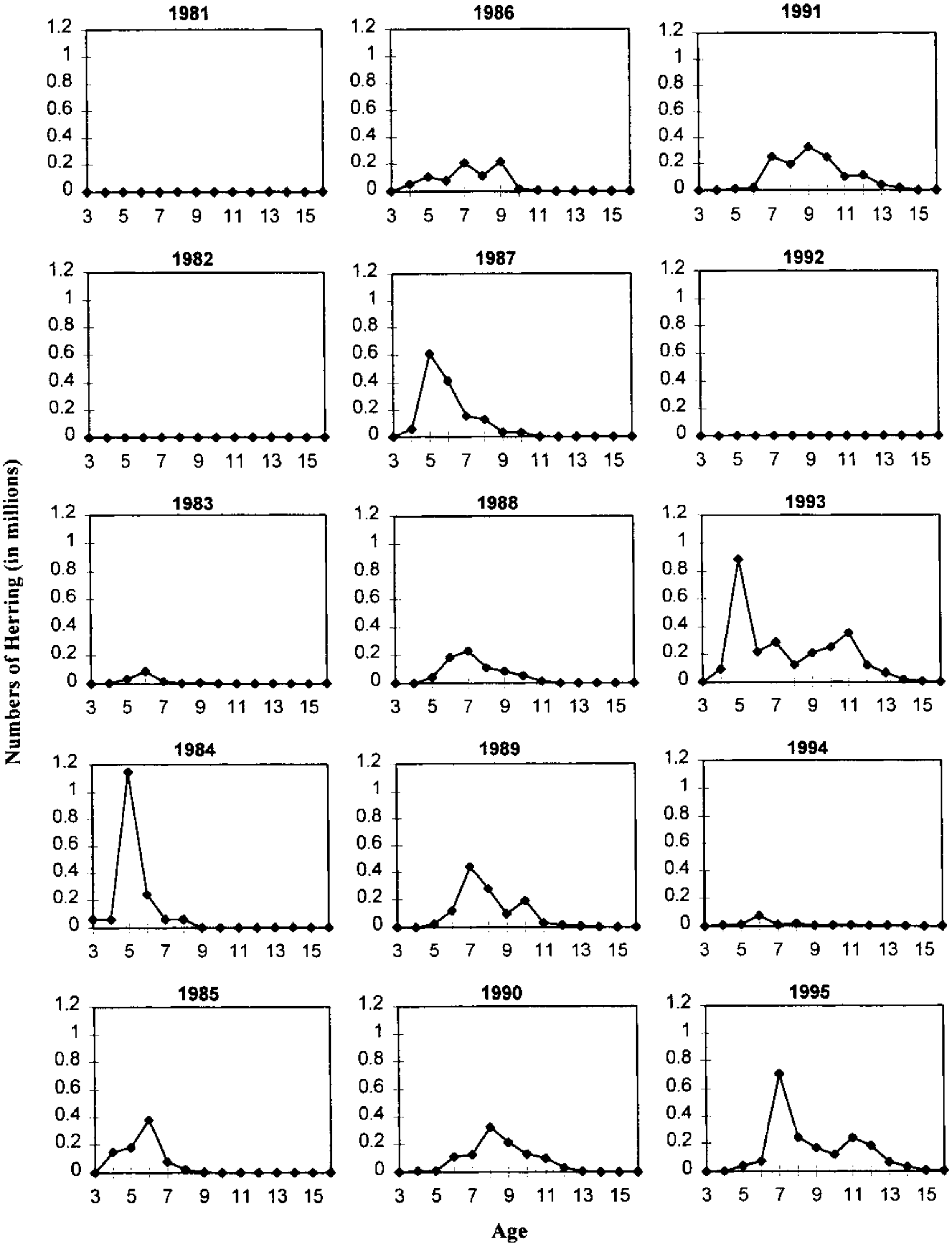

FIGURE 1.2. Yearly (1981-1995) observed beach seine catches of Pacific herring from Norton Sound for ages 3 to 16.

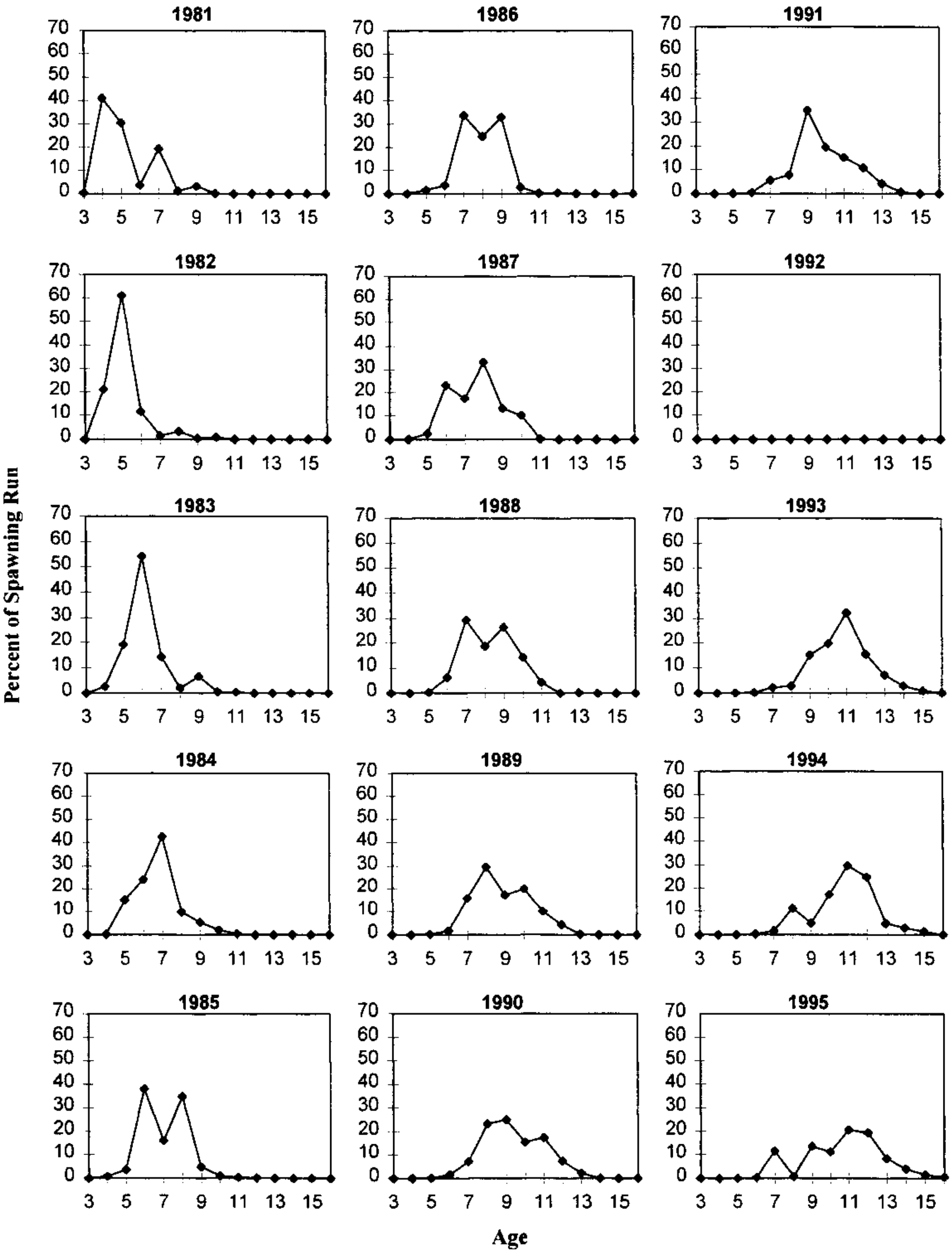

FIGURE 1.3. Yearly (1981-1995) observed gillnet age compositions of Pacific herring from Norton Sound for ages 3 to 16.

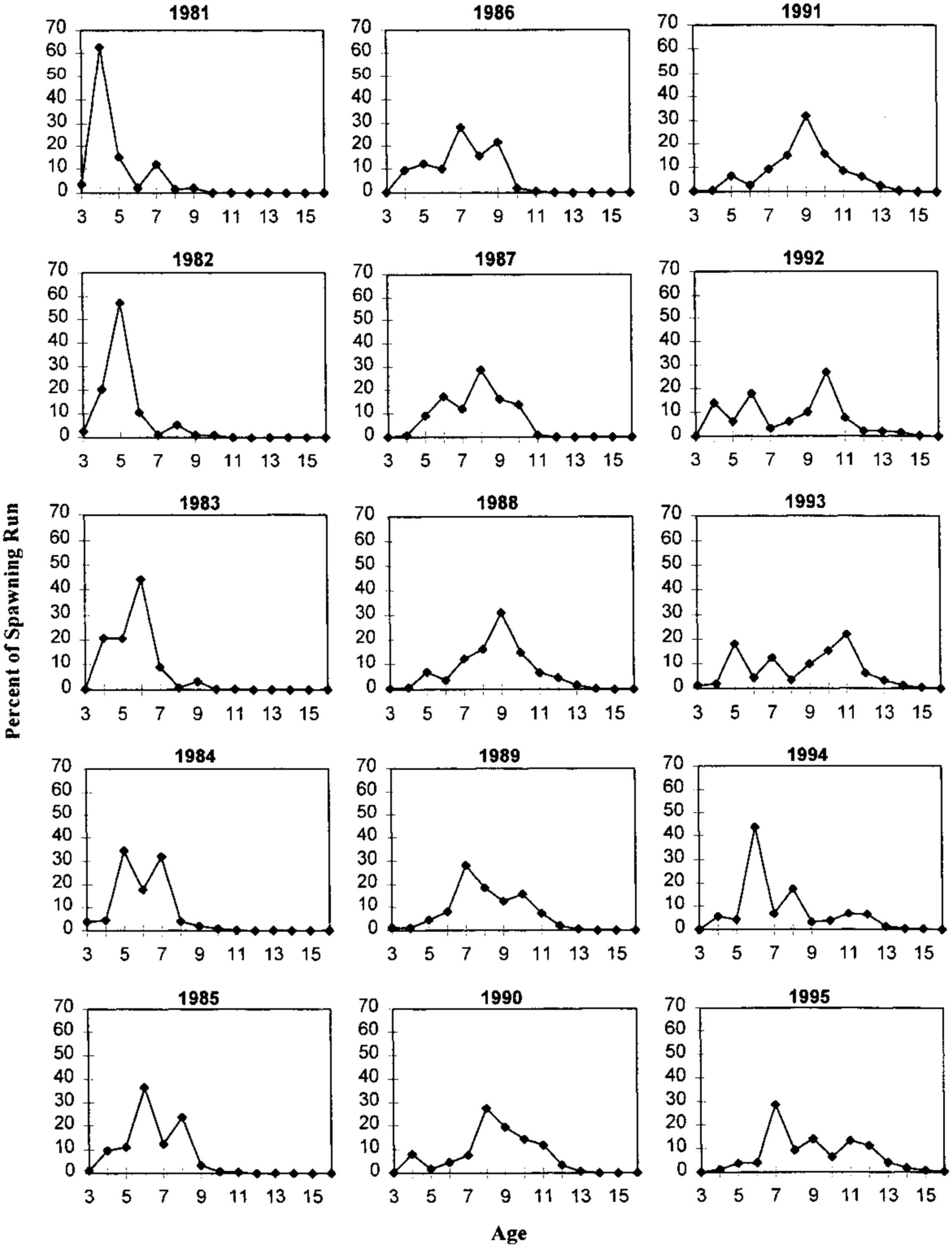

FIGURE 1.4. Yearly (1981-1995) observed total-run age compositions of Pacific herring from Norton Sound for ages 3 to 16.

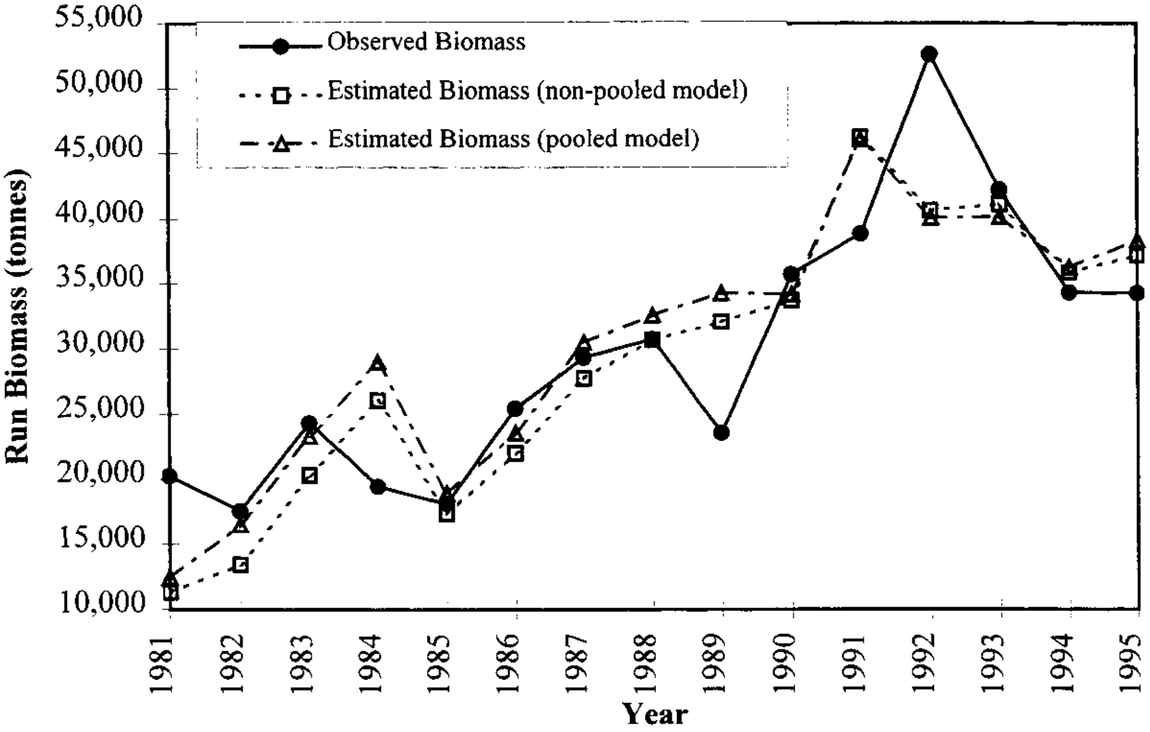

FIGURE 1.5. Yearly (1981-1995) observed and estimated aerial survey run biomass for Pacific herring from Norton Sound. The 1982 and 1989 observed values were removed from the analysis.

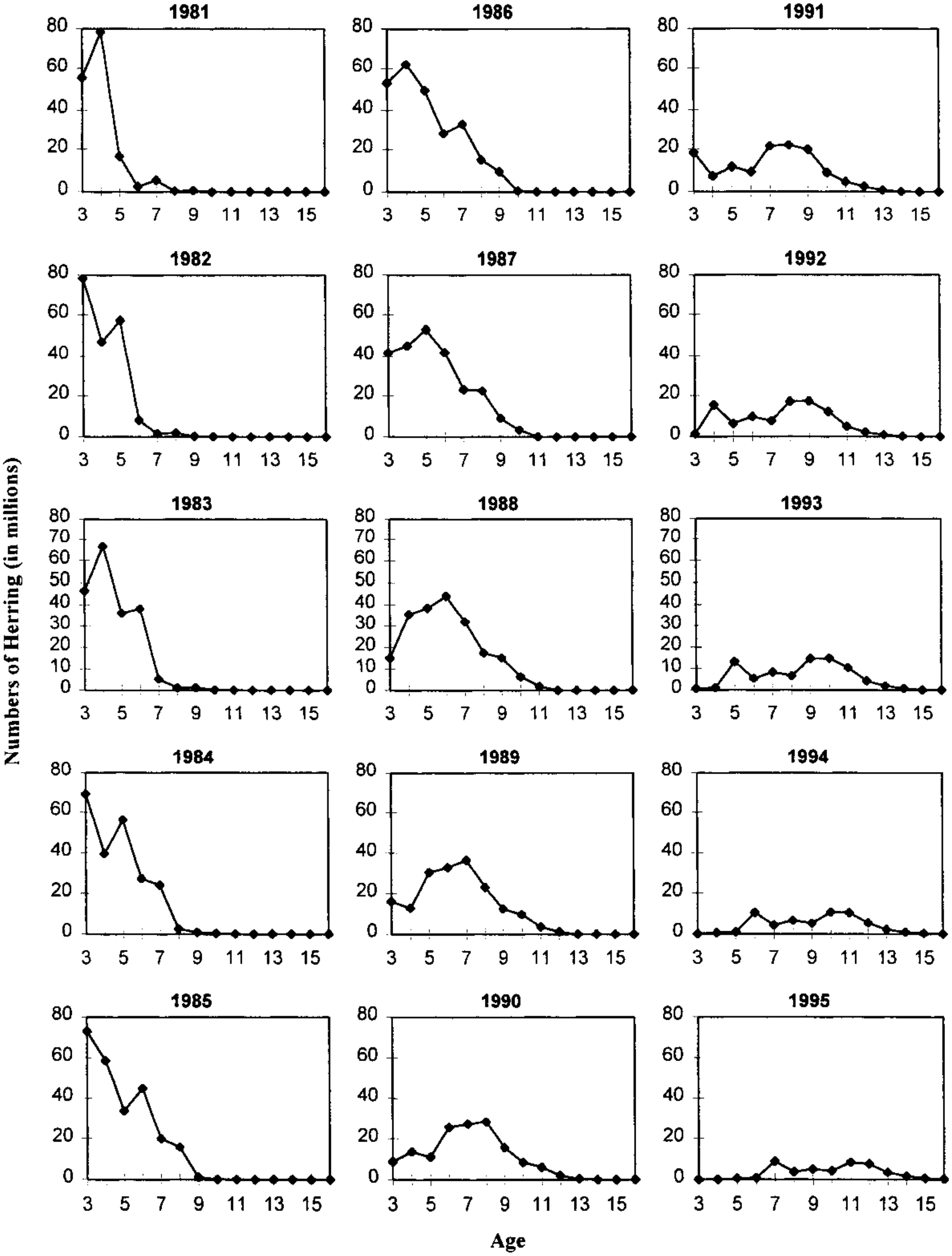

FIGURE 1.6. Yearly (1981-1995) estimated abundance of Norton Sound herring from cohort analysis for ages 3 to 16.

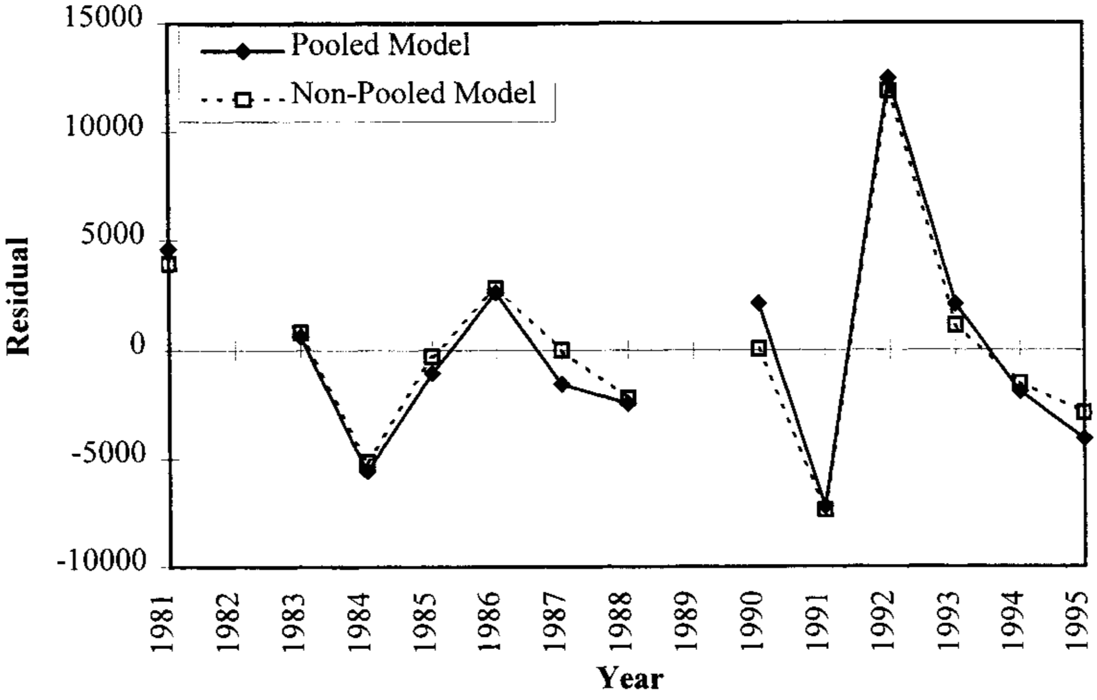

FIGURE 1.7. Aerial survey biomass residuals from the pooled and non-pooled age-structured models for Norton Sound herring.

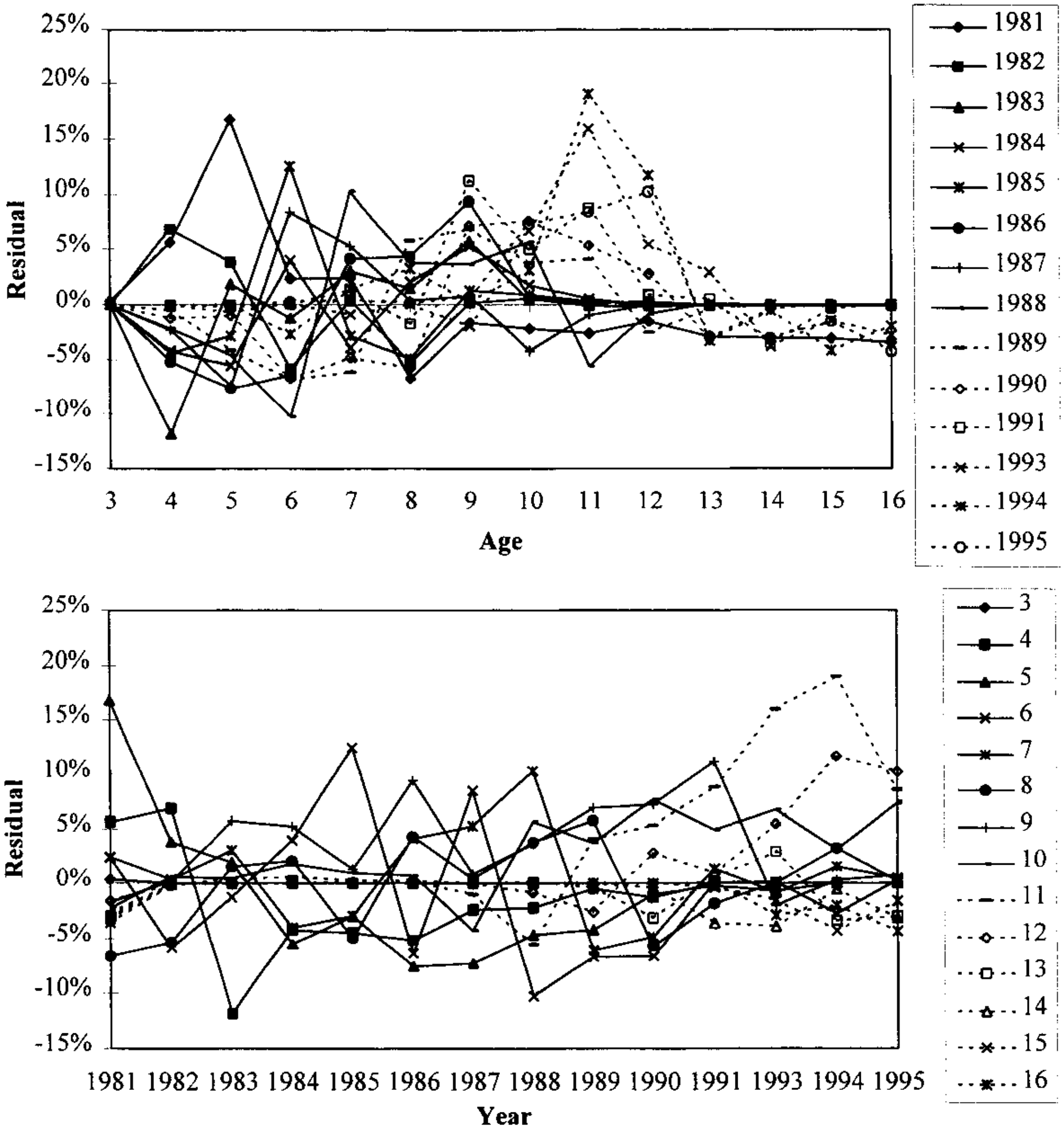

FIGURE 1.8. Gillnet age composition residuals from the non-pooled age-structured model for Norton Sound herring.

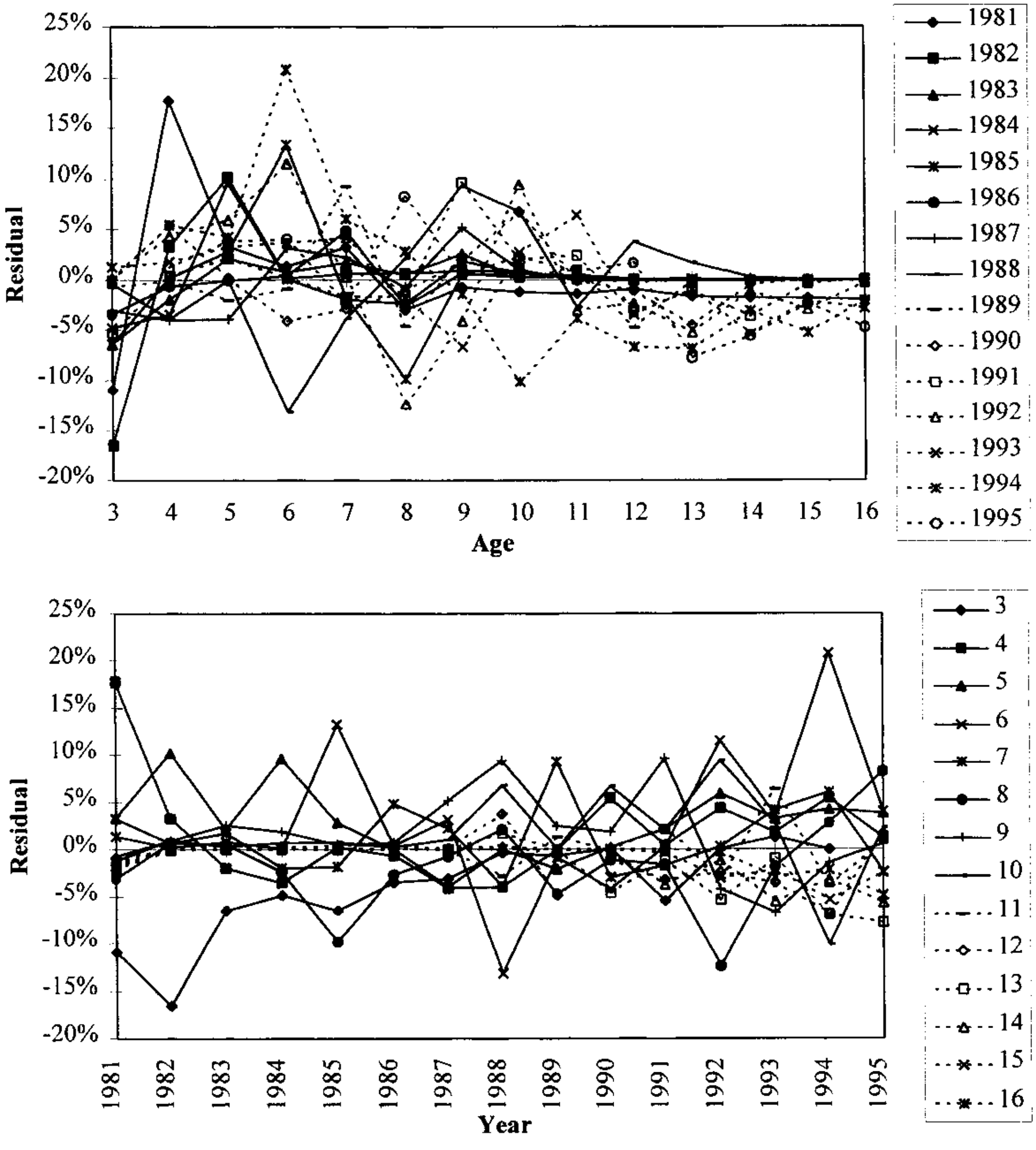

FIGURE 1.9. Total-run age composition residuals from the non-pooled age-structured model for Norton Sound herring.

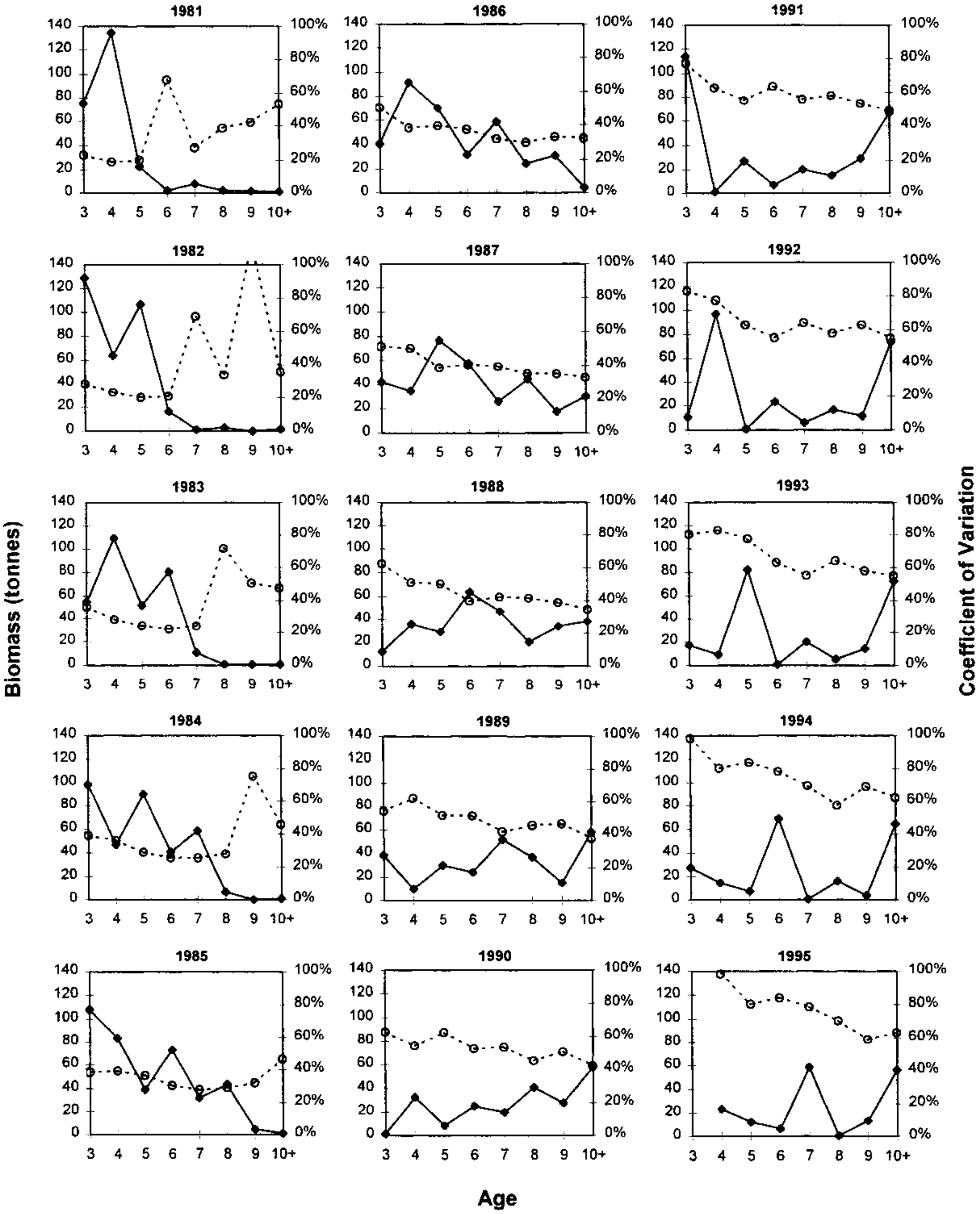

FIGURE 1.10. Yearly estimated pre-fishery abundance of Norton Sound herring from the pooled age-structured model in tonnes (marked as diamonds) and bootstrap estimates of coefficients of variation (percentages marked as circles) for ages 3 to 10+.

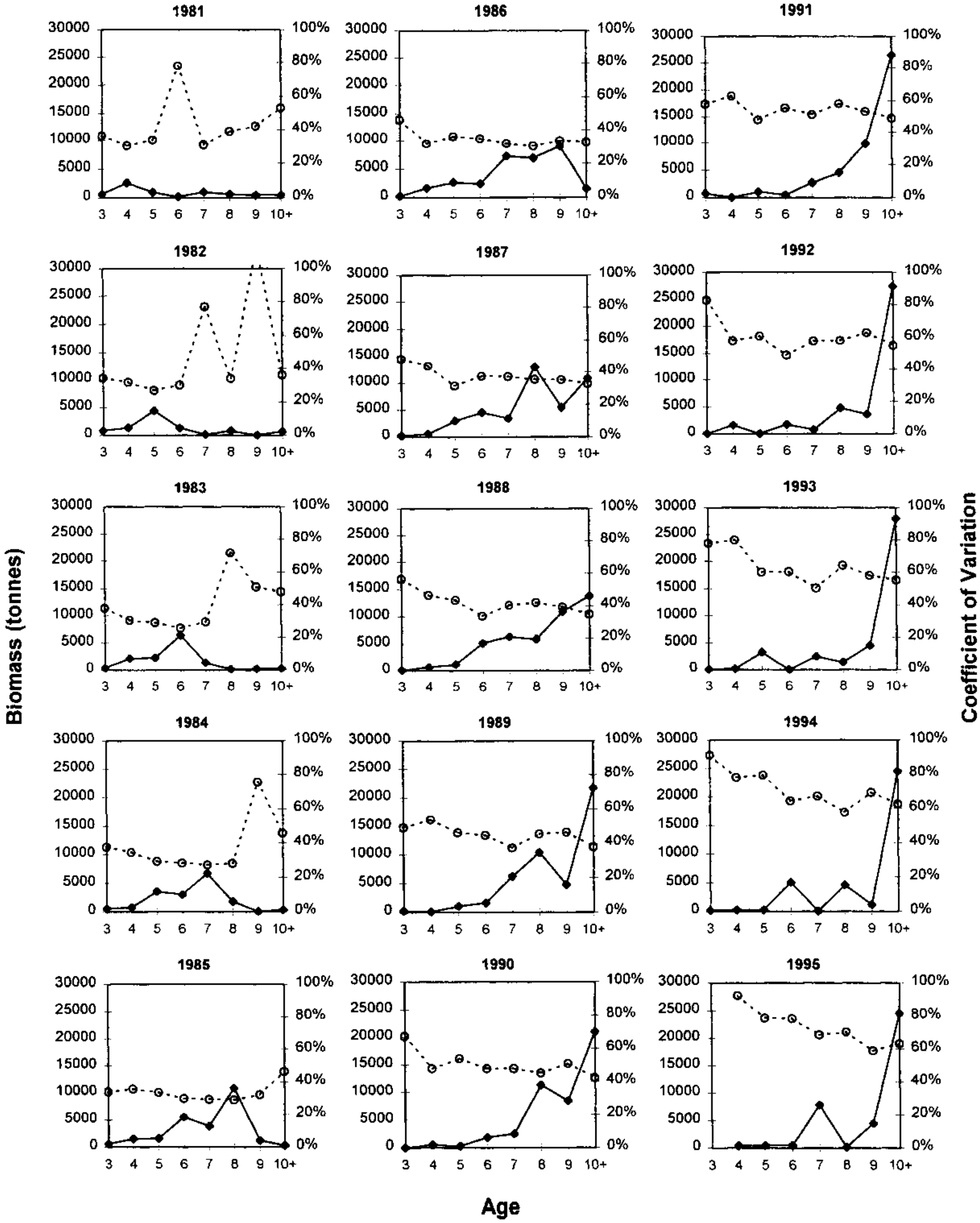

FIGURE 1.11. Yearly estimated aerial survey biomass of Norton Sound herring from the pooled age-structured model in tonnes (marked as diamonds) and bootstrap estimates of coefficients of variation (percentages marked as circles) for ages 3 to 10+.

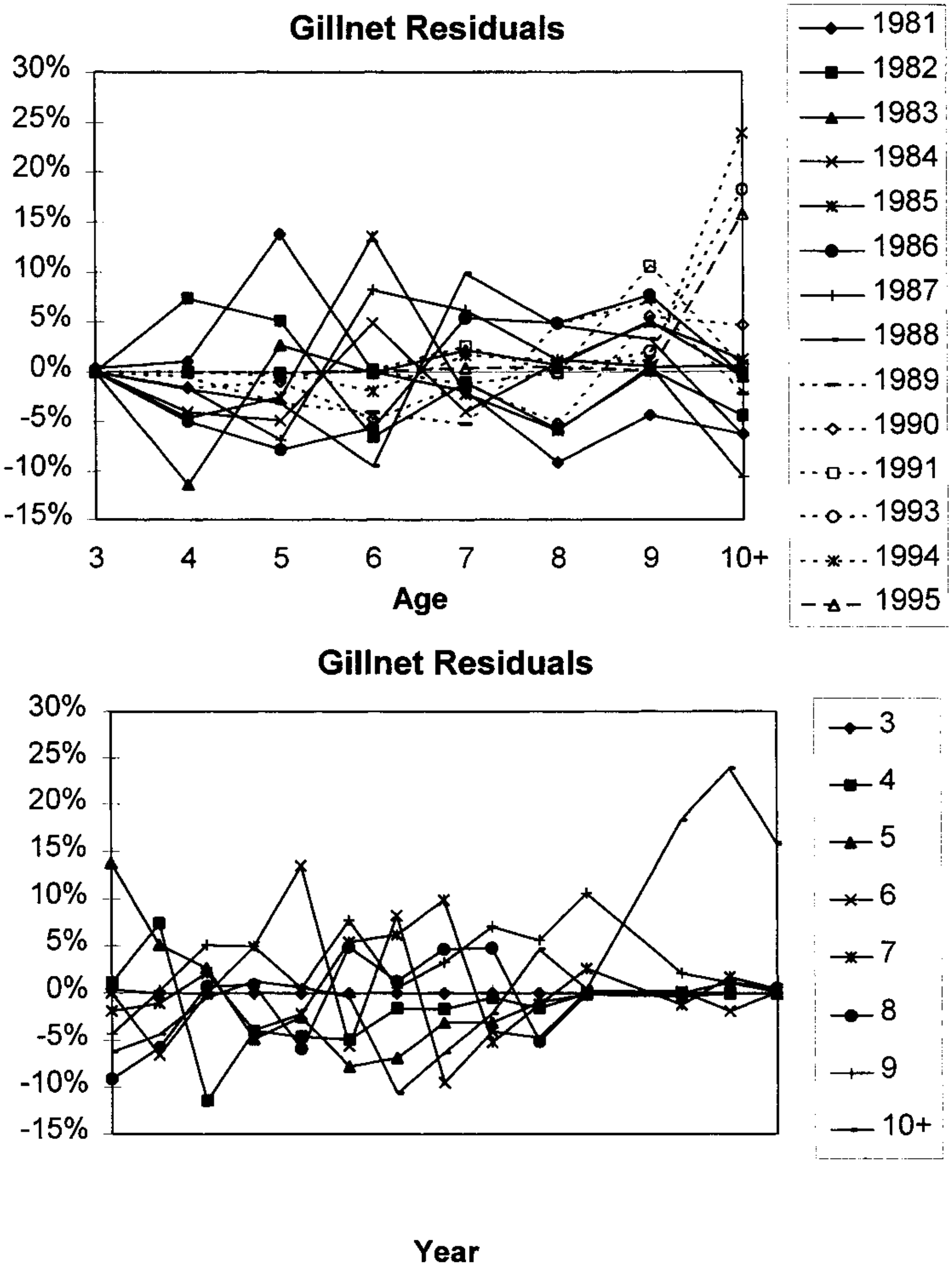

FIGURE 1.12. Gillnet age composition residuals from the pooled age-structured model for Norton Sound herring.

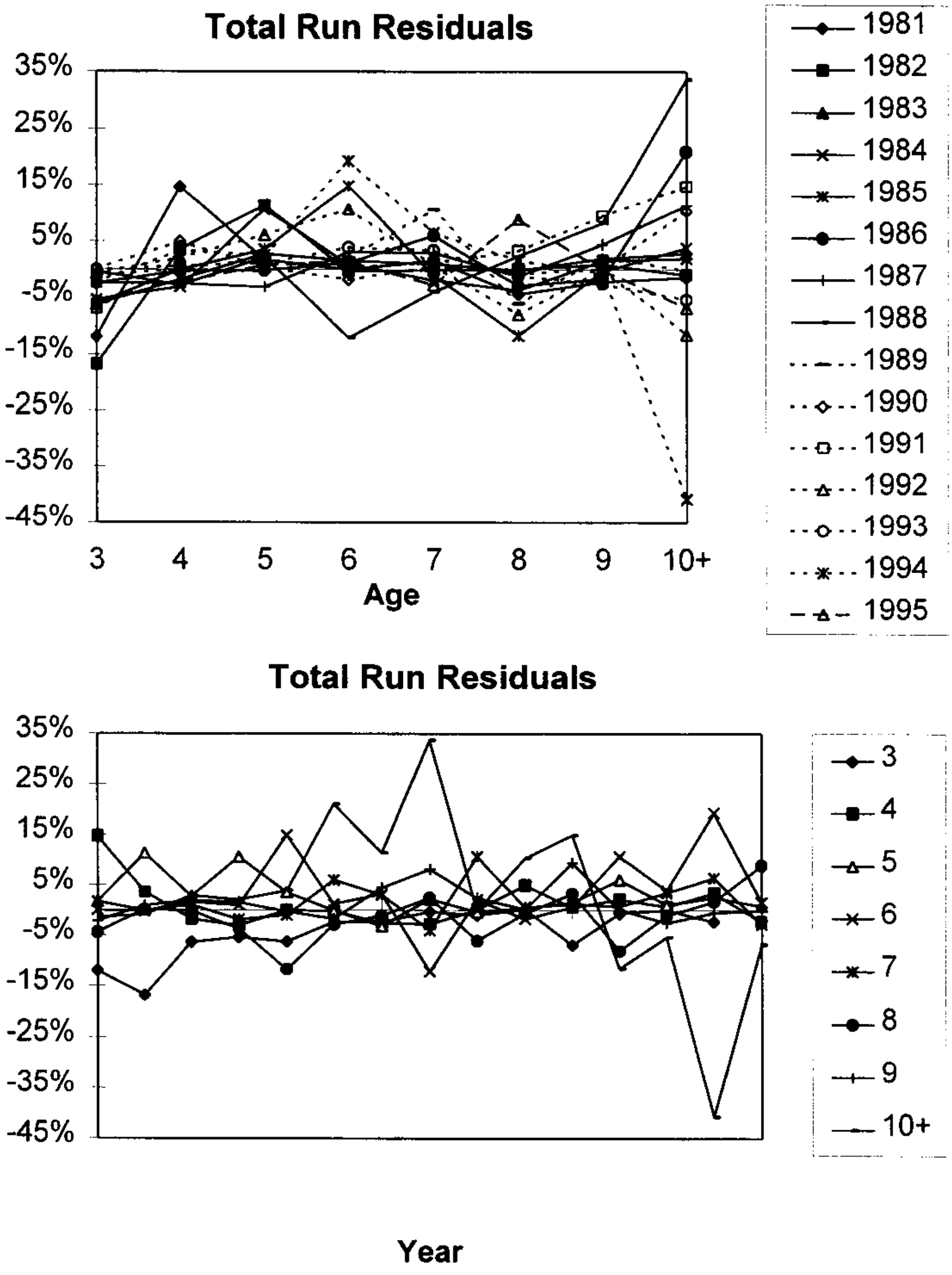

FIGURE 1.13. Total-run age composition residuals from the pooled age-structured model for Norton Sound herring.

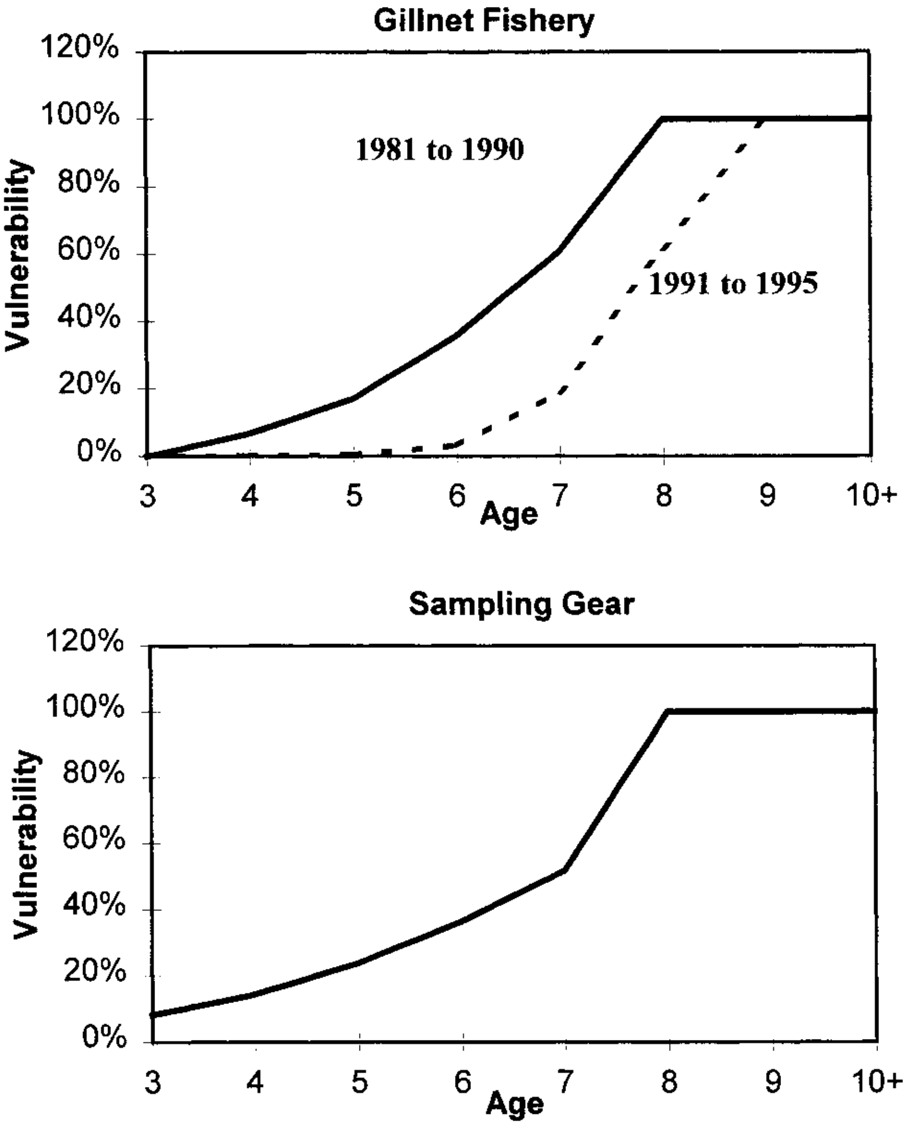

FIGURE 1.14. Fishing and sampling-gear vulnerabilities estimated from the pooled age-structured model for Norton Sound herring.

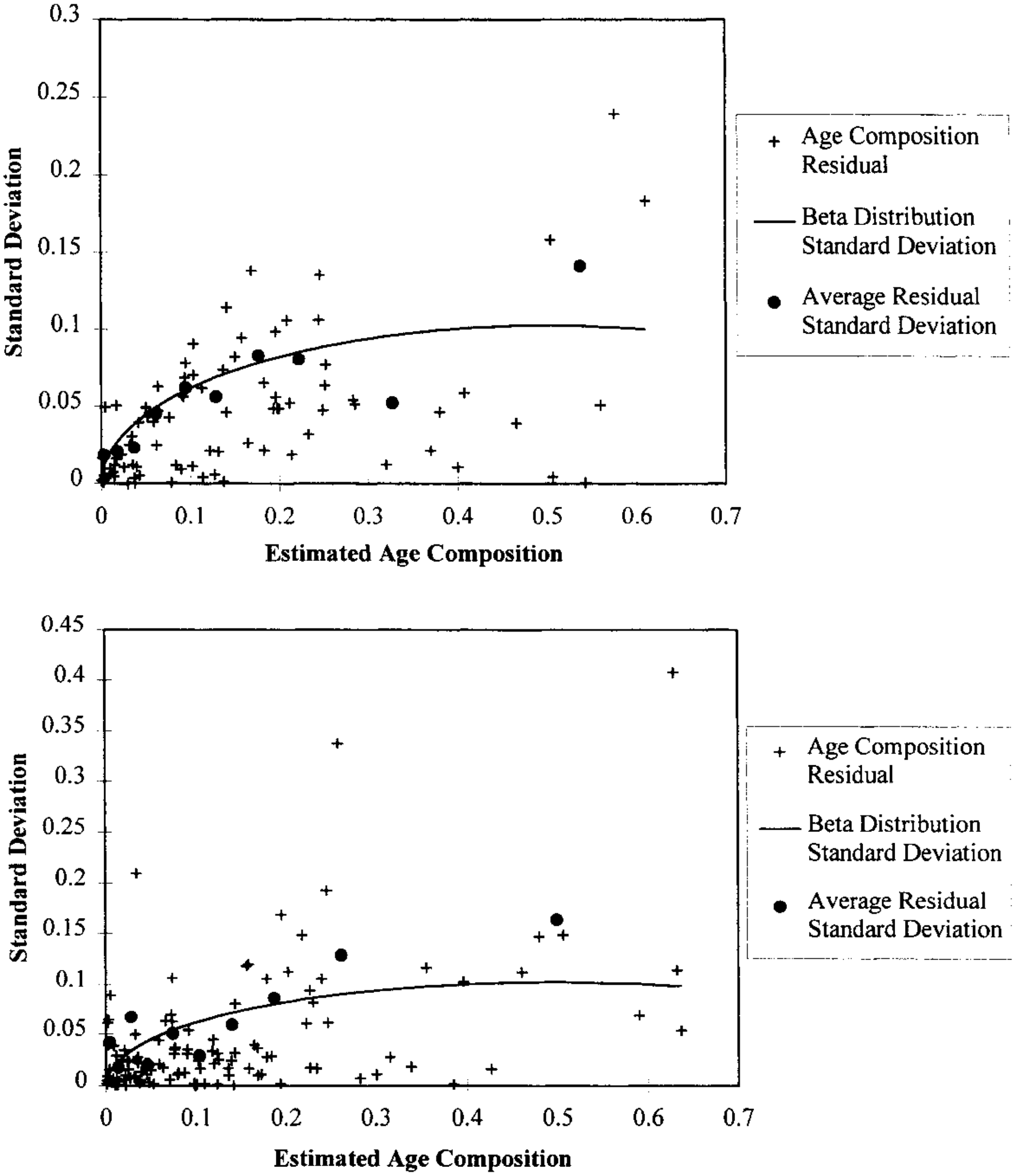

FIGURE 1.15. Beta distribution fit to Norton Sound herring gillnet (top) and total-run (bottom) age compositions.

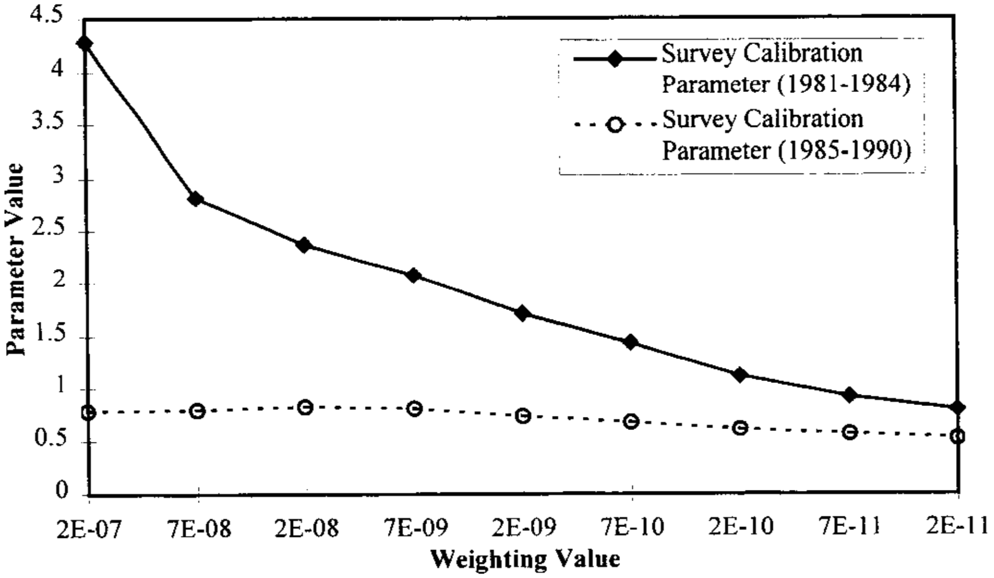

FIGURE 1.16. Effects of changes in aerial survey sums of squares weighting on the survey-calibration parameter values in the pooled age-structured model for Norton Sound herring.

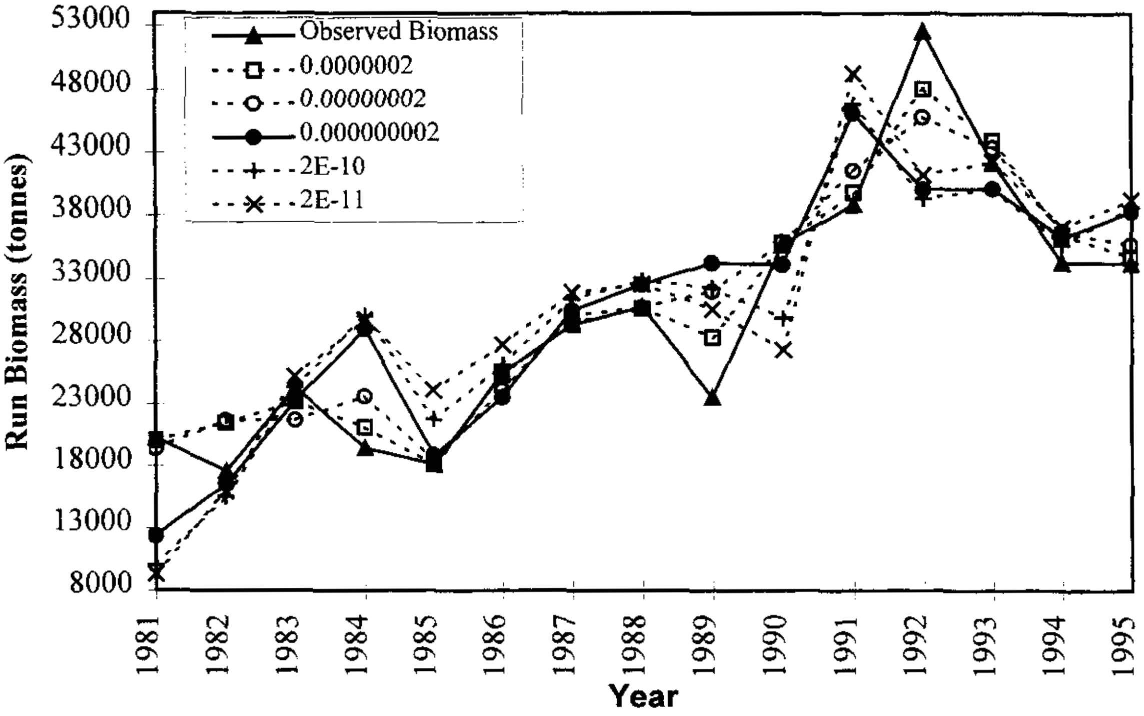

FIGURE 1.17. Effects of changes in aerial survey sums of squares weighting on the estimated run biomass in the pooled age-structured model for Norton Sound herring.

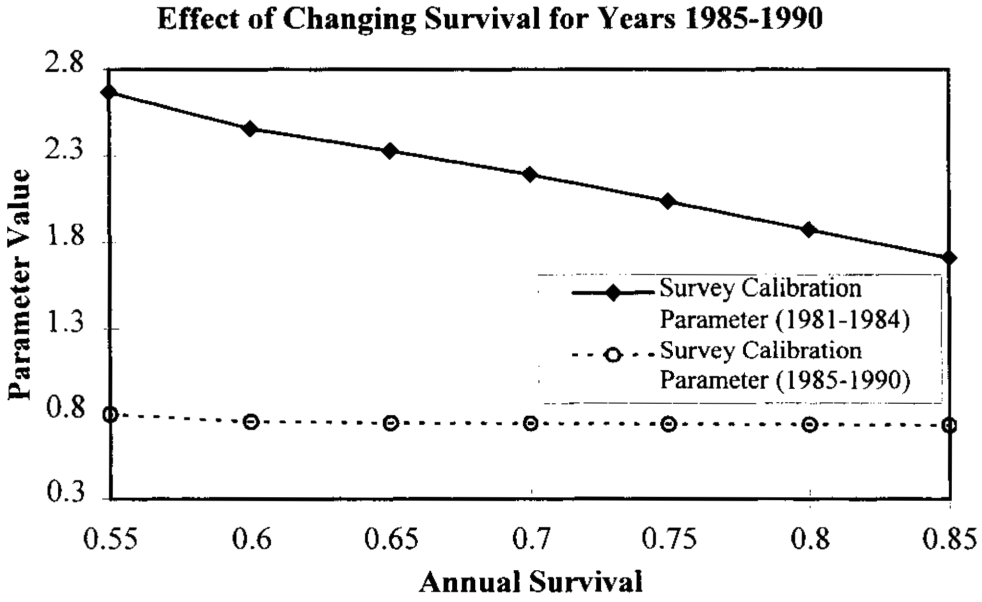

FIGURE 1.18. Effects of changes in annual survival on the aerial survey calibration parameters in the pooled age-structured model for Norton Sound herring.

Chapter 2. A Parametric Bootstrap of Catch-Age Compositions Using the Dirichlet[2] Distribution

2.1. Abstract

Stock assessment models that incorporate catch or survey age compositions and indices of abundance are commonly used for managing fisheries. Obtaining error estimates for estimated parameters in these models can be difficult. Many models incorporate a bootstrap procedure for estimating errors. In order to perform a bootstrap procedure, age compositions can be modeled by some type of statistical distribution and are often assumed to follow a multinomial process. However, the multinomial distribution is based on the assumption that a simple random sample of ages is taken from the catch, which in practice is rarely true and can lead to underestimation of error. In some applications, a smaller "effective sample size" is substituted for the actual sample size in a subjective manner. We developed an *a posteriori* method to model observed age compositions with the Dirichlet distribution, using the estimated age compositions from the stock assessment model. A parametric bootstrap procedure using the fitted Dirichlet distribution provided error estimates for estimated stock assessment parameters. We illustrate this technique by application to an age-structured model for Pacific herring (*Clupea pallasi*) from Norton Sound, Alaska. The Dirichlet procedure properly accounted for the variation in observed age compositions compared to those estimated by the stock assessment model. The effective sample sizes from the Dirichlet procedure were lower than the actual sample sizes, suggesting that a comparative multinomial bootstrap procedure underestimated the variance.

2.2. Introduction

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[2] An earlier version of this chapter is in press (Williams and Quinn, in press).

Fisheries managers commonly utilize stock assessment models which incorporate catch or survey age compositions and indices or estimates of abundance (Hilborn and Walters 1992, Quinn and Deriso in press). These catch-age or age-structured assessment models are among the best techniques for analysis available to fisheries managers. To fully interpret the parameter estimates from catch-age analysis, estimates of parameter variability are required. Obtaining error estimates of estimated parameters in these models can be awkward and sometimes subjective. Many catch-age models incorporate a bootstrap procedure for estimating errors (Quinn and Deriso in press, Efron 1982, Efron and Tibshirani 1993).

A nonparametric bootstrap procedure, as applied to catch-age analysis, involves randomly sampling age composition residuals with replacement and adding them to the original estimated values, giving a new set of observed values (Deriso et al. 1985). The new observed values are then used to estimate the parameters of the model resulting in a bootstrap replicate. The standard deviation of the bootstrap replicates is an estimate of the standard error of the estimate (Efron 1982, Efron and Tibshirani 1993). In the case of age composition data, large negative residuals relative to the smallest estimated value results in unrealistic negative "observed" values during the bootstrap procedure.

An alternative method of performing a bootstrap of age composition residuals in catch-age analysis which may be more accurate is to fit a parametric model, usually in the form of some type of statistical distribution, to the observed age compositions. The most commonly employed model for age composition data is the multinomial distribution (Fournier and Archibald 1982; Kimura 1990). However, incorporating a multinomial process into a bootstrap procedure may require manipulation of the sample size and assumes simple random sampling with known sample sizes. Fournier and Archibald (1982) and Methot (1986) suggested that there is variability other than that due to multinomial sampling alone. For this reason, they suggested the sample size for estimating age composition be limited to $n = 400$, even though the actual sample size is often much larger. In order to accurately apply the multinomial sampling distribution to catch-age analysis, the sample size may be adjusted in an *ad hoc* fashion so that the resulting error matches the expected level of variance.

Alternatively, an objective method is to determine the error structure empirically by examination of the observed and estimated age compositions. We propose to fit *a posteriori* the Dirichlet distribution to the set of observed age compositions for implementation in a parametric bootstrap procedure for estimation of standard errors of parameter estimates. We apply this technique and compare it to the multinomial bootstrap procedure using an age-structured model for Pacific herring (*Clupea pallasi*) from Norton Sound, Alaska (Williams and Quinn 1998).

2.3. Methods

The Dirichlet distribution is a multivariate statistical distribution for a set of random variables that take on values between 0 and 1, and sum to 1 (Evans et al. 1993). The beta distribution, a special case of the Dirichlet distribution, for a single variable (or more precisely, two variables summing to 1), is a flexible statistical distribution with two parameters v and w. It is appropriate for modeling proportions, because it takes on values between 0 and 1 and its density function can assume many shapes: U-shaped ($v = w$, $v < 1$, $w < 1$), J-shaped ($v >$ or $< w$), or unimodal ($v = w$, $v > 1$, $w > 1$). The probability density function of the Dirichlet distribution for a set of k proportions $\{\theta_a, a = 1, \ldots, k\}$ utilizes the gamma function, $\Gamma(\gamma) = \int_0^\infty \exp(-u) u^{\gamma-1} du$, and is given by

$$(1) \qquad \frac{\Gamma(\gamma)}{\prod_{a=1}^{k} \Gamma(\gamma_a)} \prod_{a=1}^{k} \theta_a^{\gamma_a - 1}, \text{ such that } \sum_{a=1}^{k} \theta_a = 1 \text{ and } \gamma = \sum_{a=1}^{k} \gamma_a .$$

We identify γ and $\{\gamma_a, a = 1,\ldots, k\text{-}1\}$ as the parameters of the distribution and obtain γ_k by subtraction as $\gamma_k = \gamma - \sum_{a=1}^{k-1} \gamma_a$. Note that γ_k is not a free parameter of the distribution, as a consequence of the proportions of the distribution summing to 1.

Let $\theta_{a,t}$ = true proportional age composition at age a in year t, $\theta'_{a,t}$ = observed proportional age composition from a sample and $\hat{\theta}_{a,t}$ = estimated proportional age composition from the stock assessment model. Because age composition data are available over several years, the Dirichlet distribution is initially parameterized for each year t. The observed proportions, $\theta'_{a,t}$, are assumed to follow the Dirichlet distribution with parameters γ_t and

(2) $\gamma_{a,t} = \gamma_t\theta_{a,t}$, $a = 1,\ldots, k\text{-}1$, where $\sum_{a=1}^{k} \theta_{a,t} = 1$.

(For the last age group, $\gamma_{k,t} = \gamma_t - \sum_{a=1}^{k-1} \gamma_{a,t}$.)

The parameters $\{\gamma_{a,t}\}$ are assumed proportional to $\{\theta_{a,t}\}$ in order to connect the data to common parameters across years. The variance of $\theta_{a,t}$ is given by

$$\mathrm{var}(\theta'_{a,t}) = \gamma_{a,t}(\gamma_t - \gamma_{a,t}) / [\gamma_t^2(\gamma_t + 1)] = \gamma_t\theta_{a,t}[\gamma_t(1 - \theta_{a,t})] / [\gamma_t^2(\gamma_t + 1)]$$
$$= \theta_{a,t}(1 - \theta_{a,t}) / (\gamma_t + 1).$$

Thus, the Dirichlet distribution variance is related to the variance of proportions, given by $p(1\text{-}p) / n$, with $\gamma_t = n - 1$ and $\theta_{a,t} = p$, where n is the sample size (Zar 1984). Therefore, the parameter γ_t of the Dirichlet distribution represents an "effective sample size". Intuitively, the γ_t parameter is inversely related to the amount of variance in the age composition data.

In this application, the sets of observed and estimated age compositions, $\{\theta'_{a,t}\}$ and $\{\hat{\theta}_{a,t}\}$, are the only information sources available for estimating the variance. The fit of the Dirichlet distribution to the age composition data is based on the probability density function (1). The observed age compositions, $\{\theta'_{a,t}\}$, from the age-structured model are used in a log likelihood function, for k age groups and j years, given by

$$\text{(3)} \qquad \ln L(\{\gamma_t\} \mid \{\theta'_{a,t}\}) = \sum_{t=1}^{j} \left[\ln \Gamma(\gamma_t) - \sum_{a=1}^{k} \ln \Gamma(\gamma_{a,t}) + \sum_{a=1}^{k} (\gamma_{a,t} - 1) \ln(\theta'_{a,t}) \right]$$

with $\gamma_{a,t} = \gamma_t \hat{\theta}_{a,t}$ from (2). By maximizing (3), estimates of the Dirichlet parameters $\hat{\gamma}_t$ and $\{\hat{\gamma}_{a,t}, a = 1, \ldots, k\text{-}1\}$ are obtained. (For the last age group, $\hat{\gamma}_{k,t} = \hat{\gamma}_t - \sum_{a=1}^{k-1} \hat{\gamma}_{a,t}$.) The larger the discrepancies between the observed and estimated age compositions, the smaller $\hat{\gamma}_t$ should be. A possibly more parsimonious model may be warranted in which a single effective sample size $\gamma_t = \gamma$ is used.

The parametric bootstrap analysis is performed by using the maximum likelihood estimates, $\{\hat{\gamma}_{a,t}\}$, to generate Dirichlet distributed random age compositions. Some methods of generating Dirichlet random age compositions are to use the $\hat{\gamma}_{a,t}$ Dirichlet parameters to calculate (1) random gamma variates (using a common scale parameter and $\{\hat{\gamma}_{a,t}\}$ for the shape parameters), (2) beta variates (with parameters $\{\hat{\gamma}_{a,t}\}$ and $\{\hat{\gamma}_t - \hat{\gamma}_{a,t}\}$) or (3) chi-squared variates (with $\{2\hat{\gamma}_{a,t}\}$ degrees of freedom) (Evans et al. 1993). In order to follow the Dirichlet distribution, the random age compositions must be adjusted to sum to one by dividing by the sum of the variates across ages for that year.

The Dirichlet random age compositions are then used in place of the observed age compositions in the model and the parameters re-estimated to produce one bootstrap sample. Efron and Tibshirani (1993) suggest a bootstrap sample size of no less than 1000 for accurate standard errors and confidence intervals. Figure 2.1 illustrates the algorithm for fitting the Dirichlet distribution to age composition data and the procedure for bootstrapping the model for error estimates.

The nature of this log-likelihood function does not allow for observed age compositions of 0 or 1 to be used, as seen in the log likelihood equation (3). If not too many observed proportions of zero occur, then essentially they can be ignored in the likelihood estimation of the γ_t's. Note that if $\gamma_{a,t} = 1$, then its likelihood contribution is zero; this is one of the few cases of the Dirichlet distribution with a nonzero probability for $\theta_a = 0$. In the bootstrap replications, there is no problem with zeros, because the $\hat{\gamma}_{a,t}$'s are based on estimated proportions $\{ \hat{\theta}_{a,t} \}$ that are usually nonzero. If there are quite a few zeros, then it might be best to pool ages to eliminate the zeros.

2.4. Application to Pacific Herring

We used an age-structured model for Pacific herring from Norton Sound, Alaska developed by Williams and Quinn (1998). This model incorporates catch and total-run age composition data and aerial survey estimates of abundance for years 1981 to 1996 and ages 3 to 10+, similar to other age-structured models for Pacific herring (Funk et al. 1992; Brannian et al. 1993; Yuen et al. 1994). Sample sizes for the gillnet and total run age compositions were usually large, ranging from about 400 to over 6000 (Table 2.1). A method for determining the variability associated with age-structured model estimates for Pacific herring could prove useful for herring management, because no variance estimates are currently calculated by the Alaska Department of Fish and Game (F. Funk, Alaska Department of Fish and Game, personal communication).

We fitted two Dirichlet distributions to the observed catch and total-run age-composition data: one with constant γ for each age composition data set, the other with annual γ_t. Estimates were obtained by maximizing the log likelihood function (3) in an Excel spreadsheet (available from the authors), which utilizes a quasi-Newton optimizer. Estimates of γ and γ_t for the gillnet and total run age compositions are given in Table 2.2, along with log likelihood statistics. The fit using annual γ_t parameters for the gillnet data set was significantly better than using a constant γ (likelihood ratio test: $\chi^2 = 38.97$, P < .001), while the annual γ_t parameterization for the total run data set was not significantly different ($\chi^2 = 9.16$, P = 0.87). Note that the estimates of γ in Table 2.2 are smaller than the sample sizes in Table 2.1, showing that effective sample size is smaller than actual sample size.

In order to evaluate the annual γ_t parameterization fits of the Dirichlet distribution, we calculated the empirical standard deviation for each year in each data set. These values are compared to the analytical standard deviation based on the Dirichlet variance formulae given above. Figure 2.2 indicates the Dirichlet standard deviation based on the computed effective sample sizes is comparable to the empirical standard deviation from the age-structured model.

As mentioned earlier, zero-valued observed age compositions cannot be estimated by the Dirichlet distribution. For this application there were some unrepresented (zero) ages, due to a closed fishery in 1992 and selective fishing pressure on older fish. In the bootstrap procedure these values were left at zero. A standard non-parametric bootstrap procedure was used for the aerial survey biomass data. A bootstrap sample of 1000 was chosen for this exercise.

For comparison to the Dirichlet distribution bootstrap procedure, a multinomial bootstrap procedure was performed with the Norton Sound herring age-structured model using the sample sizes in Table 2.1. The objective function of the Norton Sound herring model is a simple combination of sums of squares, which does not follow a multinomial process. The multinomial bootstrap procedure was only intended as a comparison to the Dirichlet distribution bootstrap procedure and therefore changing the objective function is not warranted.

2.5. Bootstrapping Results

One of the 1000 bootstrap samples for the annual γ_t case of the Dirichlet distribution failed to converge by settling on unrealistic, negative valued estimates. This failure suggests some evidence of model instability but is inconsequential to the final results, so we ignored this replication. All the bootstrap samples for the constant γ case of the Dirichlet distribution and for the multinomial distribution appeared to be realistic (no zero or negative valued estimates).

From the bootstrap samples the coefficient of variation (*cv*, bootstrap standard deviation divided by original estimate), a relative measure of uncertainty, was calculated for estimated total biomass (Figure 2.3), pre-fishery abundance estimates for recruitment age herring (age 3) (Figure 2.4), and selectivity and catchability parameters in the model (Figure 2.5). In general, the multinomial distribution resulted in lower *cv* estimates as compared to the two Dirichlet distribution estimates, suggesting that use of the multinomial understates actual variability. The error estimates for the total biomass and aerial survey parameters are similar for all three bootstrap procedures, probably because these quantities are determined more from aerial survey information than from age composition information. The *cv*'s for the fishery and sampling gear selectivities indicate larger *cv*'s for the two Dirichlet bootstrap procedures, particularly for the sampling gear selectivity parameters for the last six years. The recruitment *cv*'s indicate the difference among the three bootstrap procedures increases in more recent years. The annual γ_t case for the Dirichlet bootstrap procedure seems to result in the highest *cv*'s in the most recent years.

2.6. Discussion

The residuals from an age-structured model include both measurement and process error. The true sample size in a multinomial distribution bootstrap procedure is limited to representing the measurement error in the model under simple random sampling and has been suggested to be an inappropriate representation of the true estimation error (Fournier and Archibald 1982; Methot 1986). The multinomial bootstrap error estimates in this application are useful for comparison to the Dirichlet distribution bootstrap error estimates. Since the Dirichlet distribution fit is based on the observed and estimated age compositions from the model, the resulting *cv*'s for most cases were higher than those for the multinomial. This result indicates that the Dirichlet distribution is capturing variation in the estimates that is unaccounted for by the multinomial distribution. Otherwise the estimates of effective sample size would have been much closer to the actual ones. The multivariate logistic model is an alternative approach for incorporating greater variability into stock assessment models (Schnute and Richards 1995).

The annual γ_t case produced higher *cv*'s than the constant γ case, unexpectedly, since the maximum likelihood result in Table 2.2 indicated a better fit for the γ_t case. The reason for this is probably due to the lower effective sample sizes in the last three years for the total run data and the last year for the gillnet data for the annual γ_t case relative to the constant γ case. Since the nature of age-structured analysis is to track cohorts through time, poor fits in the last few years will affect estimates in earlier years. So, even though the constant γ case involves less parameterization, it resulted in lower *cv*'s in later years, because it smoothed over the high variability in the last years of the age-structured model.

Coefficients of variation for total biomass and the aerial survey catchability parameters from the Dirichlet method were much closer to the multinomial estimates as compared to the abundance and selectivity parameter estimates. Since the total biomass estimates and catchability parameters depend primarily on the aerial survey abundance data, the similarity of *cv*'s for all three bootstrap methods suggests these portions of the model are relatively unaffected by changes in sample size for the age composition data. The similarity of *cv*'s is consistent with the aerial survey abundance component in all three bootstrap procedures being computed by the same non-parametric procedure. This result suggests that the recommendation to limit age composition samples to 400 observations (Fournier and Archibald 1982; Methot 1986) in order to prevent age composition from dominating the likelihood does not have a strong rationale. Indeed, since effective sample size can be much smaller than actual sample size, a re-evaluation of sample size requirements in age-structured models is needed.

Overall, the Dirichlet distribution appears to be a statistical distribution which allows for fairly easy and objective bootstrap estimates of error for stock assessment models which utilize age composition data. It provides a means to utilize the observed variation in the model without having to resort to making unrealistic assumptions about the error distribution. An implicit assumption in this approach is that the underlying stock assessment model is correct. If not, the estimated proportions $\{\hat{\theta}_{a,t}\}$ may be biased, which would lead to bias in the Dirichlet parameter estimates.

We also note that this approach is an approximation to a true bootstrap, in which the original objective function for age composition would be based on the Dirichlet distribution. Equations (1) and (3) for the Dirichlet distribution would then be incorporated directly into the objective function of the stock assessment model. Dirichlet parameters would be estimated jointly with the other model parameters, which would avoid the necessity of fitting the Dirichlet distribution *a posteriori* as we did. Further study is necessary to determine if the additional model complexity presents difficulties in estimation, but such an approach would lend greater consistency to the stock assessment. We did not do so here because we were looking for a quick and simple procedure to generate standard errors after being satisfied with the basic stock assessment results.

Indeed, the major strength of bootstrap procedures in general is their ability to provide measures of uncertainty for all key variables of interest in a straightforward manner and with a minimum of assumptions. Our procedure should be generally applicable to stock assessment models with observed and estimated proportions.

Finally, the concept of effective sample size need not invoke the Dirichlet distribution. An empirical estimate of effective sample size can be made from the observed and estimated age compositions for a given year and gear type (McAllister and Ianelli 1997). If θ'_a and $\hat{\theta}_a$ are the observed and estimated age compositions for a given year (omitting the time subscript for clarity), then an estimate of the mean squared error is $\sum_a^k \left(\theta'_a - \hat{\theta}_a\right)^2 / k$. The average estimated variance of observed proportions from the multinomial distribution is $\sum_a^k \theta'_a(1-\theta'_a)/(kn)$, where n is sample size (Alternatively, the estimated $\hat{\theta}_a$'s could be used). By equating these two quantities and solving for n, the estimated effective sample size is $n = \sum_a \theta'_a(1-\theta'_a) / \sum_a (\theta'_a - \hat{\theta}_a)^2$. A bootstrap procedure could be performed utilizing these effective n's across years with the multinomial distribution. However, the approach utilizing the Dirichlet distribution is more rigorous, and is based on simultaneous analysis of all the information. The Dirichlet approach tends to give lower effective sample sizes, because it explicitly accounts for the extra variance due to the use of observed or estimated proportions.

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Table 2.1. Annual sample sizes for age composition of Norton Sound, Alaska herring.

Year	Gillnet Fishery	Total Run
1981	1084	4244
1982	637	2163
1983	994	3570
1984	671	2056
1985	1265	3550
1986	927	2981
1987	408	1595
1988	388	1100
1989	622	1593
1990	555	2586
1991	914	3704
1992	0[a]	1197
1993	1410	3968
1994	789	2626
1995	1645	6159
1996	1372	4231

[a] No fishery occurred in 1992.

Table 2.2. Maximum likelihood estimates γ and γ_t for gillnet and total run age compositions, along with maximum log likelihood values.

	Gillnet	Total Run
$\hat{\gamma}$	21.57	26.33
$\hat{\gamma}_t$		
1981	7.39	17.11
1982	41.38	17.23
1983	21.52	24.95
1984	22.42	45.24
1985	29.78	25.17
1986	11.66	42.92
1987	22.13	19.93
1988	19.61	18.87
1989	22.12	91.77
1990	34.07	80.41
1991	86.22	20.27
1992		18.71
1993	279.01	54.35
1994	129.28	11.57
1995	150.37	23.74
1996	11.51	20.23
Log Likelihood		
$\hat{\gamma}$	118.11	177.42
$\hat{\gamma}_t$	137.59	182.00

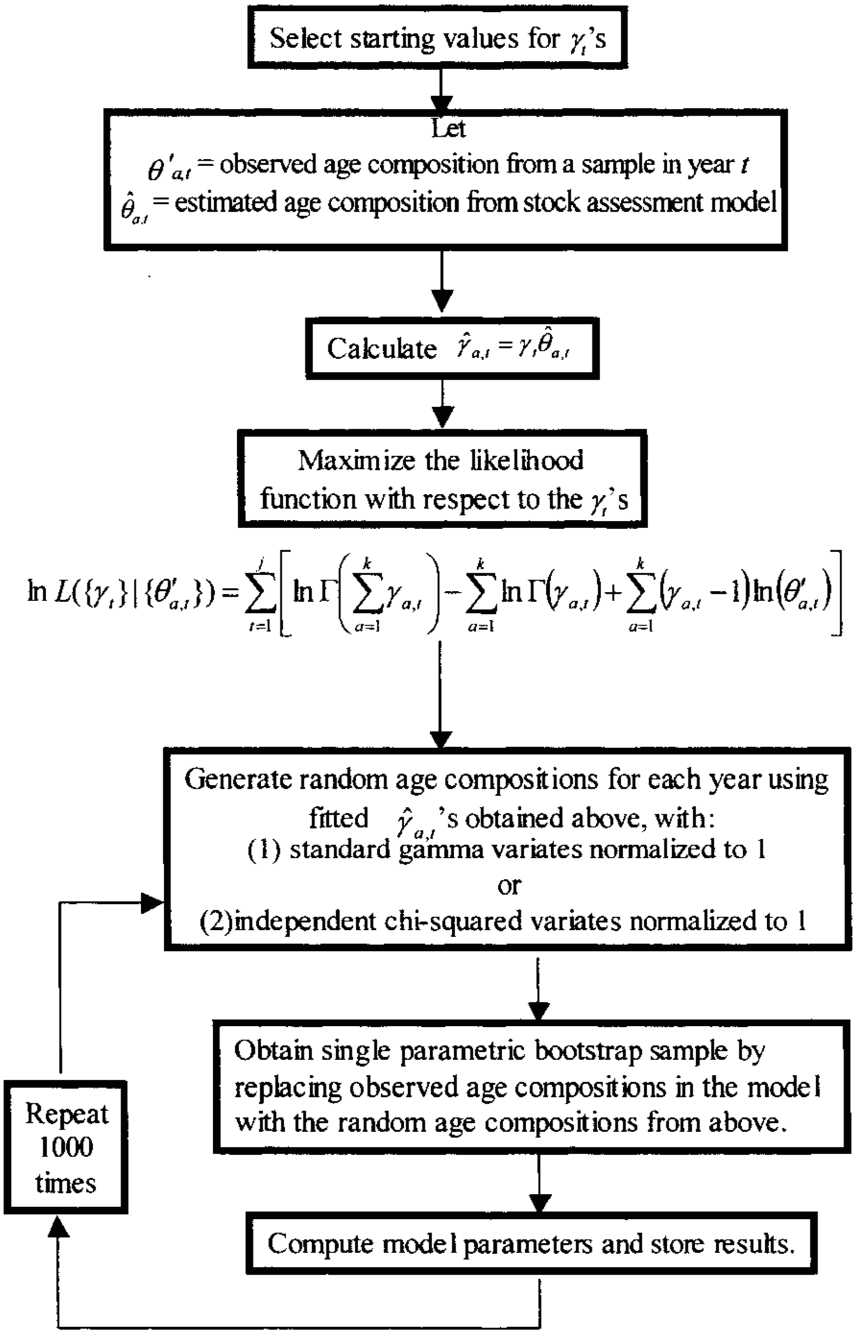
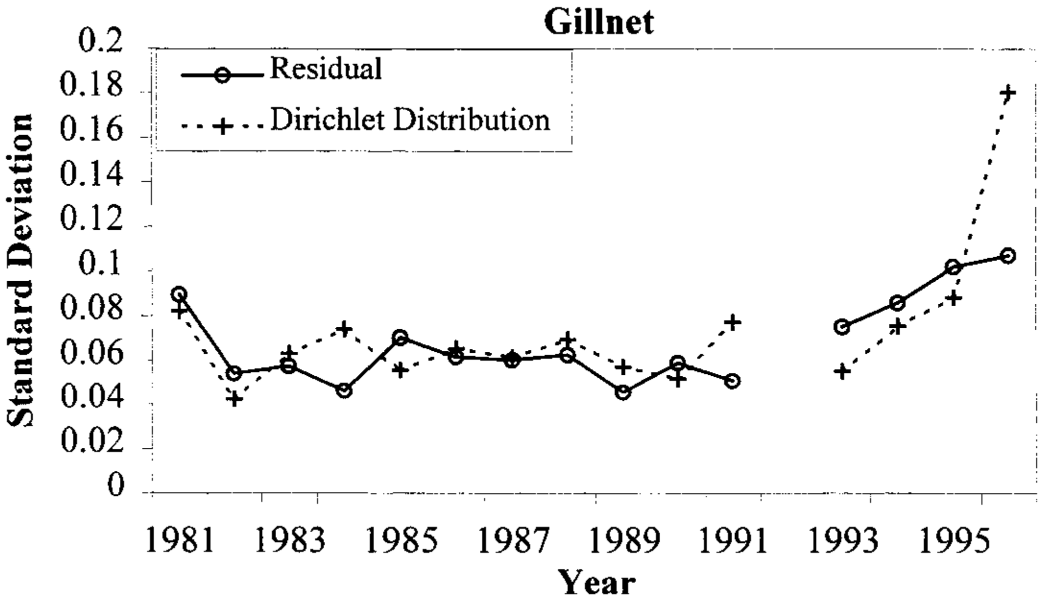


FIGURE 2.1. Flow chart of the methodology for applying the Dirichlet distribution bootstrap procedure to an age-structured model with age composition data.



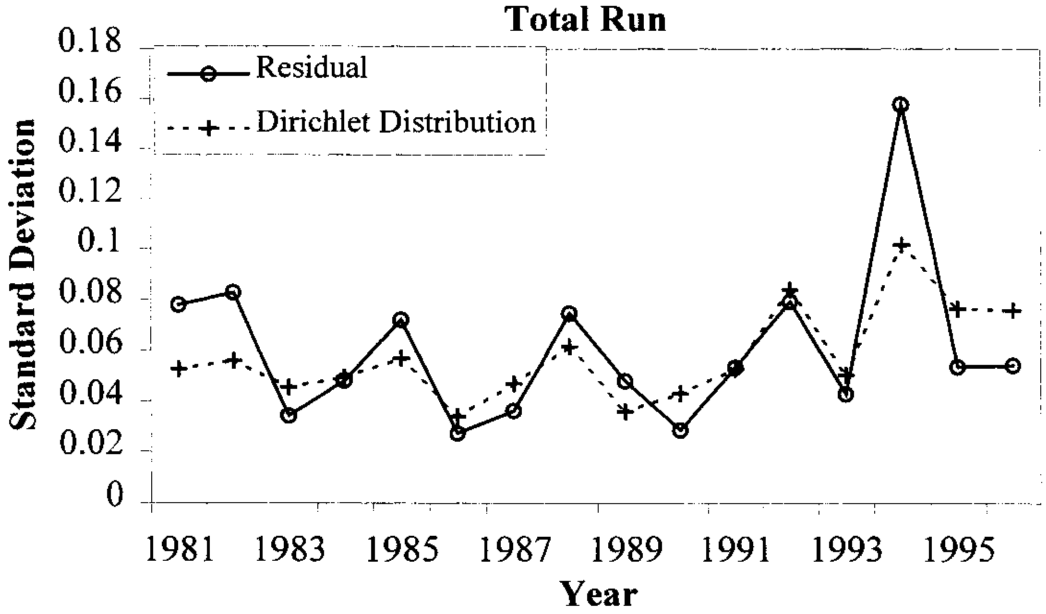


FIGURE 2.2. Standard deviations from the residuals and annual γ_t case of the Dirichlet distribution fit of the Norton Sound herring age-structured model.

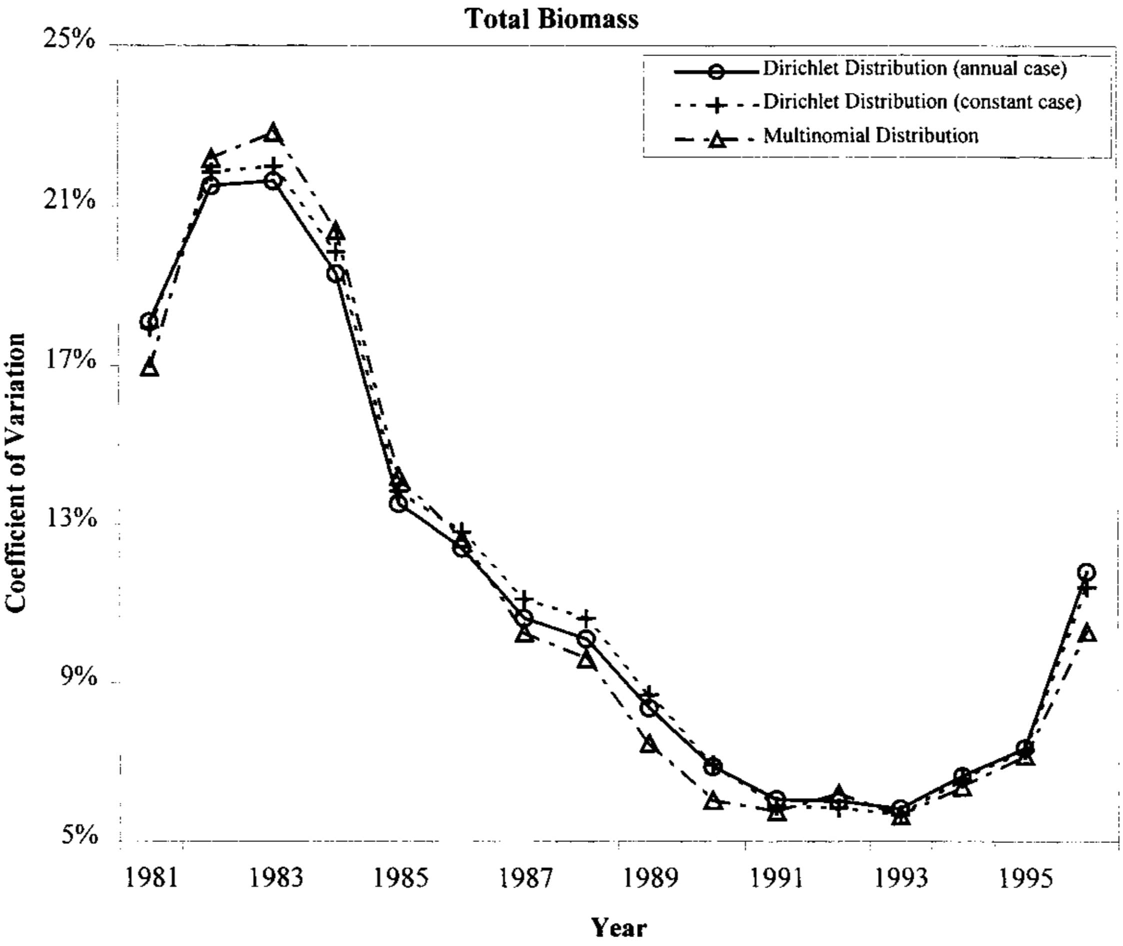


FIGURE 2.3. Annual percent error estimates for total biomass from 1000 bootstrap samples of three different procedures for the Norton Sound herring age-structured model.

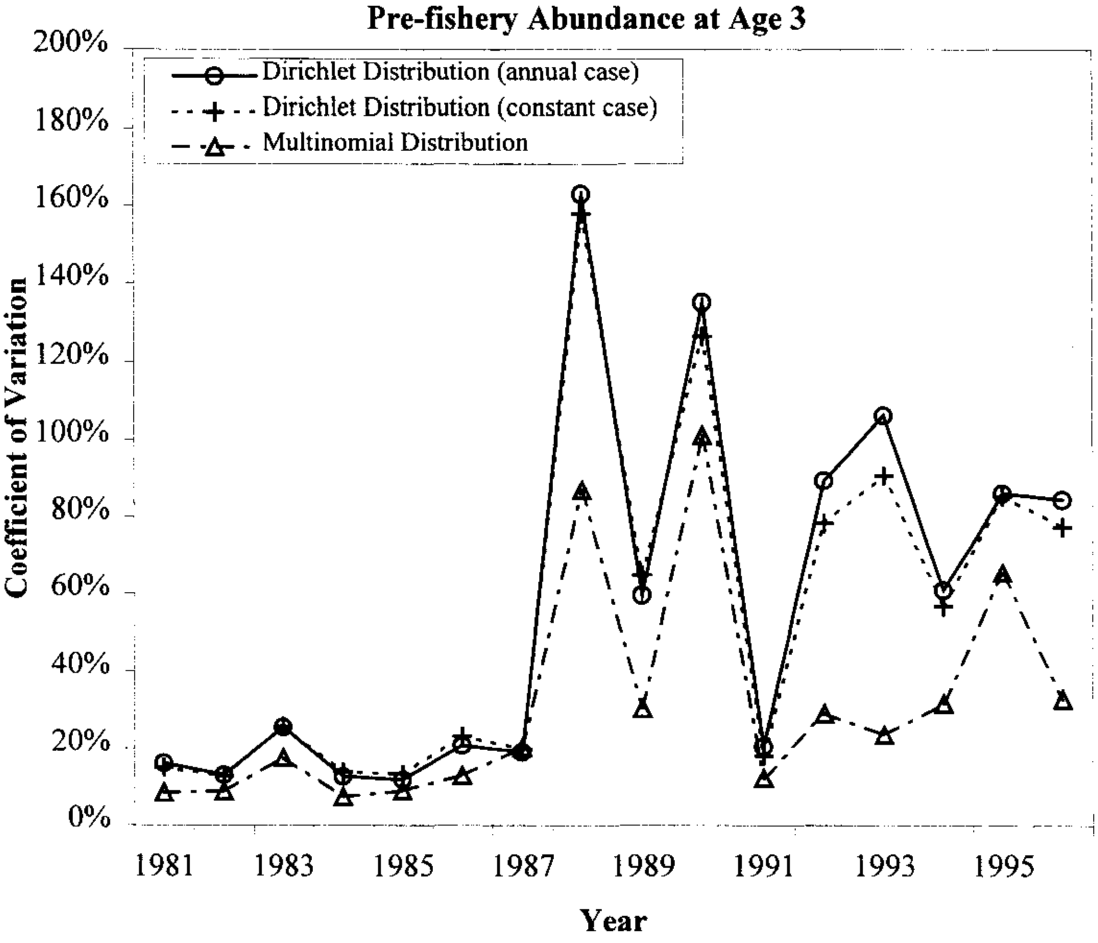


FIGURE 2.4. Annual percent error estimates for pre-fishery abundance at age 3, the age of recruitment, from 1000 bootstrap samples of three different procedures for the Norton Sound herring age-structured model.

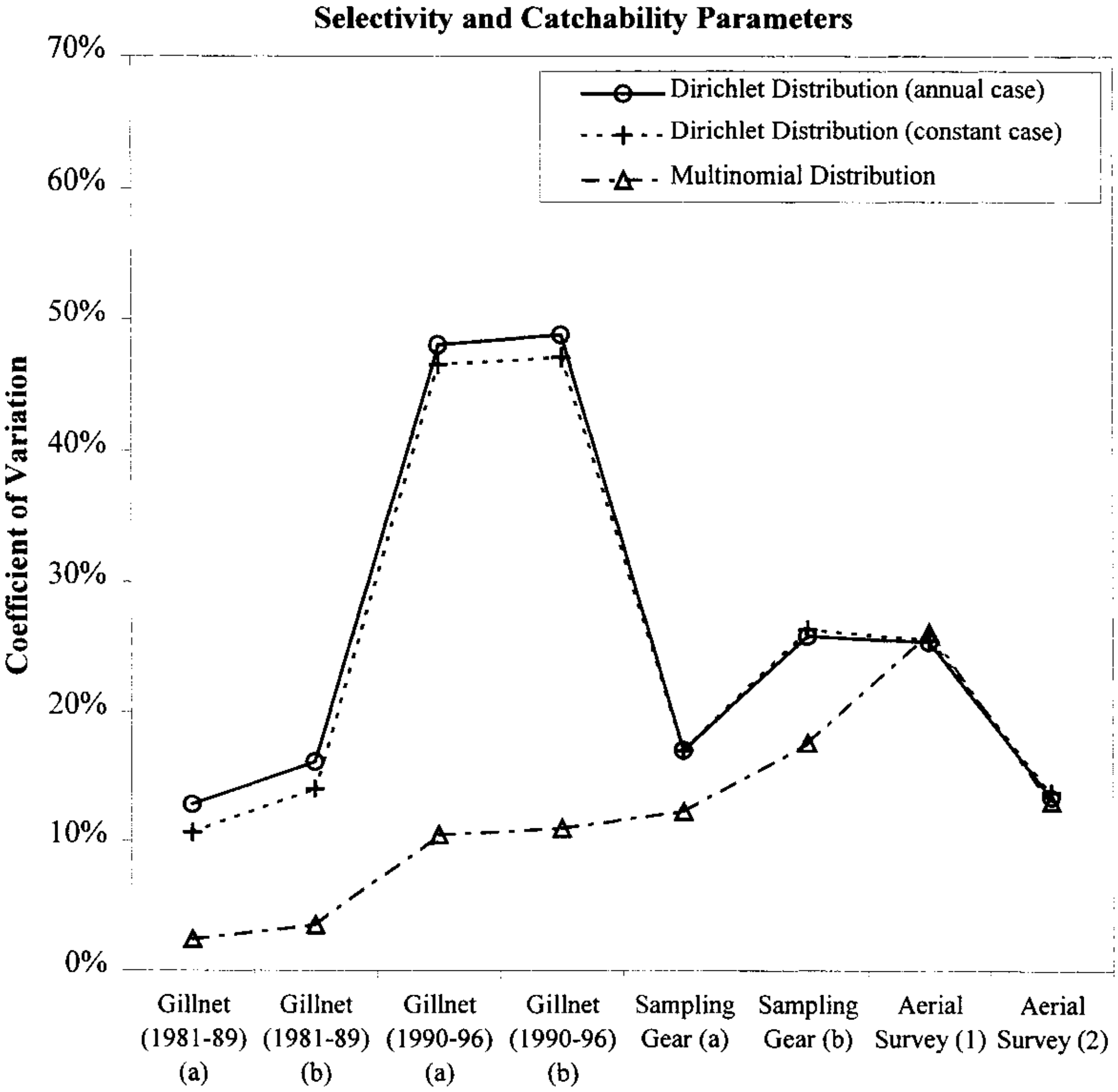


FIGURE 2.5. Percent error estimates for gillnet fishery, sampling gear, and aerial surveyability parameters from 1000 bootstrap samples of three different procedures

Chapter 3. An exploratory analysis of Pacific herring, *Clupea pallasi*, population[3] interrelationships in the Bering Sea and Northeast Pacific Ocean.

3.1. Abstract

We examined the similarities in recruitment and average weight-at-age time series for Pacific herring (*Clupea pallasi*) populations from the Bering Sea and Northeast Pacific Ocean. Statistical correlation and multivariate clustering methods indicated Pacific herring populations form large-scale associations. Large year-class events occur synchronously among several Pacific herring populations. Multivariate cluster analyses of recruitment and weight-at-age data indicated that Bering Sea herring populations are distinct compared to Northeast Pacific Ocean populations. Within the Northeast Pacific Ocean there appears to be three groups of herring populations: a British Columbia group, a Southeast Alaska coastal group, and an outer Gulf of Alaska group. Jacknife and randomization tests indicate these associations are robust and not the result of random chance. Deviations from observed herring population associations were examined for indications of man-induced perturbations. The Prince William Sound herring populations did not show any strong deviations corresponding to the oil spill of 1989. There might not yet be enough data since the spill to detect changes in the recruitment or weight-at-age data since that time, particularly if oil spill effects were concentrated on the early life history stages.

Key Words: Pacific herring, Bering Sea, Northeast Pacific Ocean, multivariate cluster analysis, recruitment, year-class strength, weight-at-age.

3.2. Introduction

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[3] This chapter is in the format for submission to the journal *Fisheries Oceanography*.

Pacific herring, *Clupea pallasi*, is a commercially and ecologically important fish species throughout most of its range (Hay, 1985). It is found in abundance along the shores of Japan and along the Alaskan and Canadian coasts. Populations of Bering Sea herring are larger, longer-lived, and genetically distinct from Northeast Pacific herring (Grant and Utter, 1984; Wespestad, 1991). Bering Sea herring are believed to migrate over 1,000 miles to offshore wintering grounds, while Northeast Pacific herring are thought to move less than 100 miles from spawning to wintering grounds. Historically, Pacific herring have been harvested by man for thousands of years and their use has ranged from basic subsistence to expensive gourmet food (Pete, 1991). Catches of Pacific herring can be relatively large. In the past few years the Alaskan herring harvest has averaged 48,000 tons, most of which ends up in the Japanese market (F. Funk, Alaska Department of Fish and Game, personal communication).

A thorough understanding of the recruitment dynamics of herring is essential to determining optimal harvesting strategies (Quinn et al., 1990). The clupeoids are notorious for their large population fluctuations, which seem to be the result of cycles possibly driven by density-independent processes (Cushing, 1982). A study of 59 fish population recruitment patterns, including Pacific herring, in the North Pacific Ocean indicated that recruitment success is synchronous and strongly influenced by environmental conditions (Hollowed et al., 1987). Zebdi and Collie (1995) indicated a 4-year cycle in strong year-classes for Alaskan and British Columbia herring populations in the Northeast Pacific, which suggested similarities in recruitment among populations located within the same oceanographic domains.

Similarities in recruitment time series suggest that populations may be grouped into large-scale associations. These associations may be the result of populations responding to similar large-scale environmental influences. Previous studies have indicated that Pacific herring recruitment time series are highly correlated and have eluded to population associations in the Northeast Pacific Ocean herring populations (Zebdi and Collie 1995, Zheng 1996). An analysis of recruitment associations could indicate deviations, possibly caused by local disturbances, natural or man- induced. A study of population associations could include population characteristics in addition to recruitment, such as body size, growth, or mortality.

We investigated associations among Pacific herring populations (Figure 3.1) through statistical analysis of recruitment and average weight-at-age time series. Herring spawning occurs in aggregations in nearshore areas where their adhesive eggs are deposited on subtidal and intertidal rocks and vegetation (Hay, 1985; Hay, 1990). These spawning aggregations are the basis for defining herring populations and management units (Haegele and Schweigert, 1985; Hourston, 1982). One of the motivating factors for this study is the Prince William Sound oil spill of 1989. For herring populations in the Bering Sea and Northeast Pacific recruitment is defined by the age of first reproduction, generally age 3. Results from this study could indicate if the Prince William Sound herring population has responded differently than the rest of the major Pacific herring populations

3.2.1. Data

Time series of Pacific herring recruitment and average weight-at-age were assembled from the Bering Sea and Northeast Pacific Ocean. The available herring data span seven decades and two fishery types. Reduction fishery data from years 1920-1966 for catch-age composition and weight-at-age exists for populations in Kodiak, Prince William Sound, and Southeast Alaska (Reid, 1971). Modern sac-roe fishery data include populations at locations shown in Figure 3.1. Recruitment and spawning biomass estimates for all populations except Norton Sound were obtained from age-structured analyses performed by the Alaska Department of Fish and Game and the Division of Fisheries and Oceans, British Columbia (Funk et al., 1992; Schweigert and Stocker 1988). Estimates for Norton Sound came from a similar age-structured analysis (Williams and Quinn, 1998). Recruitment estimates to be used in this study from the age-structured analyses are for age 3 fish for all the populations, except for Togiak, which are for age 4 fish.

Inclusion of the reduction fishery data was undertaken to extend the time series backward in time. To obtain recruitment and spawning biomass estimates for the reduction fisheries, the age composition data was analyzed using cohort analysis (Quinn and Deriso, 1999). Resulting population abundance estimates were converted to biomass using annual weight-age data. Terminal fishing mortality in the cohort analysis was estimated as the difference between an estimate of total mortality from a catch-curve analysis and natural mortality from the modern sac-roe fishery. Based on the distribution of catches in the reduction fishery, the Kodiak reduction fishery data were combined with the Kamishak Bay sac-roe fishery data, and a series for Southeast Alaska was extended using a summation of Sitka and Craig data (Reid, 1971).

Estimates of survival in these age-structured models were used to back-calculate older age compositions in the first year back to the time of recruitment, in order to extend the time series by a few more years (Table 3.1). In Table 3.1 it is apparent that the recruitment estimates obtained from back-calculation only extended the series slightly. The final result is 14 time series of recruitment and weight-at-age data dating back to the 1920's. However, the short length of the Alaskan herring time series limits some of the analyses which can be performed.

Weight-at-age data span ages 3-8 for each herring population and date back to the 1920's. For the Togiak stock there is no age 3 weight information and for other stocks the weight-at-age data for many years is missing or the previous year's data have been substituted. For simplification and increase in statistical power, all ages were combined into a single matrix of weight-at-age data for subsequent analyses.

3.3. Methods

Since the Togiak herring recruitment estimates correspond to age 4 and the other populations correspond to age 3, the recruitment data were identified with the year-class. An exploratory analysis of the data was performed to determine the statistical properties of the data. Based on this analysis it was necessary to transform some of the data for use in later analyses.

Temporal and spatial relationships of Pacific herring populations were determined through correlation and multivariate analyses. Correlation analysis was used to measure the association between two random variables. Typically this is measured by the standard Pearson sample correlation coefficient. Alternate correlation coefficients include two rank-based measures; Kendall's τ and Spearman's ρ (Dowdy and Wearden, 1991; Hollander and Wolfe, 1973; Zar, 1984). Generally, the rank-based alternatives are preferable in determining significance levels, since they are not as sensitive to outliers and non-normality as the standard Pearson estimate. A "robust" correlation measure was computed by trimming 10% of the outlying data and re-computing the correlation statistics (Rousseeuw and Leroy, 1987).

Some interrelationships among herring populations could be inferred from pairwise correlation analysis, as in Zheng (1996), but a more comprehensive approach is the use of multivariate clustering methods with scaled variables. These methods are used with no groups defined *a priori* and are considered as unsupervised pattern recognition techniques (Ripley, 1996). For this study, multivariate clustering analyses were used to determine interrelationships of herring populations based on their recruitment and weight-at-age time series.

Multidimensional scaling (MDS), also known as principal coordinate analysis, is a classical multivariate method commonly used for dimension reduction of multivariate data (Venables and Ripley, 1997; Ripley, 1996; Johnson and Wichern, 1992). Both metric and non-metric forms of MDS exist. Metric MDS relies on a distance measure, usually one of the cases of the Minkowski distance measure (Johnson and Wichern, 1992). Metric MDS analysis is a general dimension reduction technique which uses any distance or (dis)similarity measure. A special case of MDS analysis with a Euclidean distance measure is principal component analysis. Non-metric MDS relies on a monotonic transformation of the distance measures and is considered to be more robust than metric MDS analysis (Venables and Ripley, 1997; Ripley, 1996).

Interpretation of the results from a MDS analysis is accomplished by graphical examination of the first few dimensions for patterns and groupings. Variables which are related will be located in close proximity to each other. For this study, the first two dimensions from both metric and non-metric MDS with Manhattan, Euclidean, and maximum distance measures will be used to determine herring population associations. The amount of variance explained by the dimension reduction in MDS can be measured using the eigenvalues obtained from singular value decomposition of the distance matrix (Johnson and Wichern, 1992). This will be used to determine the best MDS analysis from the varied choices of distance measures.

The robustness of the MDS analyses can further be explored by performing a jacknife procedure, where each year is removed and the MDS analysis repeated. The relative influence of each year may be investigated from the change in position of each point compared to the original analysis. Years with a large relative influence may be marked as suspect outliers and removed from the analysis.

Multidimensional scaling analysis requires some subjective interpretation of the resulting scatter plots. In an attempt to reduce the subjectivity of clustering analyses such as MDS analysis, partitioning methods have been developed which divide variables into a pre-assigned number of groups (Venables and Ripley, 1997; Ripley, 1996). A classical example of a partitioning method is the *k*-means algorithm (Ripley 1996). Modern robust partitioning algorithms have been developed based on *k*-medians, also known as *k*-medoids, and fuzzy logic (Kaufman and Rousseeuw, 1990). Both *k*-medians and fuzzy *k*-medians will be applied to the Pacific herring data.

A randomization test was used to test the significance of groupings found in the partitioning analyses. The randomization test involves randomly permuting the recruitment data for each herring population. This randomized data is then used to re-compute the partitioning analysis. The results are compared to the original analysis and the number of times the randomly permuted data groups match the groups found in the original analysis is used to determine the level of significance (Edgington, 1995).

Lastly, a divisive hierarchical clustering method was applied to the Pacific herring data. The divisive clustering algorithm functions by successively splitting the variables into clusters and seems to perform best when only a few clusters are expected in the outcome (Ripley, 1996). Pacific herring populations are believed to form large-scale associations, making divisive clustering an appropriate technique.

3.4. Results

Throughout this report, the following population abbreviations will be used:
[insert TABLE 3.2 here]

3.4.1. Recruitment Data

Logarithmic transformations of Pacific herring fishery recruitment and biomass data appear to be normally distributed, as indicated by a Kolmogorov-Smirnov test of composite normality. One exception is the Kodiak/Kamishak Bay recruitment time series that contains one possible outlier, low recruitment in 1972, but this is inconsequential to the overall analysis. Since several of the analyses to be used in this study assume some level of normality, log transformed data were used.

The typical pattern of Pacific herring recruitment time series could be described as persisting at some moderate level with an occasional large year-class event occurring every 4-6 years. A graphical analysis of the residuals from the mean of the log transformed recruitment time series for each herring population indicates that there is some synchronicity in strong year-class events (Figure 3.2). The 4-year cycle described by Zebdi and Collie (1995) clearly shows up for PWS, SIT, and SEAK for positive year-class deviations in 1976, 1980, 1984, and 1988. Other years with synchronous positive year-class deviations among some areas include 1951-52, 1959-60, 1977, 1981, 1985, and 1993 (Figure 3.2). Years with synchronous weak year-classes for most areas include 1954, 1962-66, 1972-75, 1982-1983, 1986-87, and 1990-92. In some years (e.g. 1976, 1984, 1988) strong year-classes occur in the north and weak year-classes occur in the south, followed by a strong year-class in the south the next year (Figure 3.2).

Pairwise correlation estimates indicate many highly significant correlations among the herring recruitment time series (Figure 3.3). The populations in Figure 3.3 are roughly arranged in order of their geographic latitude. The trend in the correlation matrices indicates that populations close to each other are more likely to be significantly, positively correlated with each other, as compared to populations located farther apart, which in some cases appear to be negatively correlated. Analysis of the 10% trimmed time series revealed similar correlation patterns as those found in Figure 3.3.

Some groupings can be discerned from Figure 3.3, but it is difficult to clearly identify them. The British Columbia populations are correlated with each other. The KOD, PWS, SIT, SEY, and SEAK populations appear to be highly correlated, while TOG appears unrelated to most other populations (Figure 3.3). Most of the British Columbia population associations appeared to be significant in the trimmed analysis, and KOD, PWS, SIT, and SEAK seem to be related as well. Overall, it is difficult to distinguish the population associations based on the correlation matrices alone and this is best handled in a multivariate analysis setting.

The first two dimensions from the MDS analysis indicated associations similar to those suggested by the mean deviations and correlation analyses. The metric and non-metric MDS analyses indicated very similar groupings and associations for the herring populations for several different distance measures. The Manhattan distance measure resulted in the best fit, as measured by the amount of variance explained, in both the metric and non-metric MDS analyses.

Based on the MDS analyses, the PWS, SIT, SEAK, and KOD populations appear tightly clustered together and generally separated from the remaining populations. The four lower latitude British Columbian populations (QCI, CC, VCI, SOG) appear to form a distinct grouping as shown in Figure 3.4. Another probable group appears to be formed by the SEY, CRG, and KAH populations (Figure 3.4). The PR population appears to be an isolate, but is consistently positioned between the British Columbia group and the SEY, CRG, and KAH group (Figure 3.4). The positioning of the Bering Sea populations (NOR, TOG) appeared to vary with each different distance measure and each type of MDS analysis. The TOG population consistently appeared to be far removed from the remaining populations, while the NOR population appeared randomly positioned, implicating these populations as possible outliers in the analysis.

Since the Bering Sea populations are suspect outliers and because they are geographically isolated from the remaining Northeast Pacific herring populations, the MDS analysis was repeated with the Bering Sea populations removed. Again, the percent of variance explained for the different distance measures indicated that the Manhattan distance measure was best. The metric MDS analysis of the Northeast Pacific populations indicated identical groupings to those found with the inclusion of the Bering Sea populations, no matter which distance measure was used. The percent of variance explained (61.5%) and the stress measurements indicated these are slightly better descriptions of the data compared to those which included the Bering Sea populations. Therefore, all further analyses exclude Bering Sea data.

The jacknife analysis of the NE Pacific herring populations for each year of data indicates the period from 1971 to 1977 was more influential than other years (Figure 3.5). The period 1925 to 1947 seems to have little effect on the MDS analysis. This is a direct result of missing data for many of the herring populations during that time period.

The silhouette plot (Figure 3.6) is used to describe the results from partitioning analyses. These plots separate similar variables into the number of partitions specified. The strength of membership within each group is identified by the width measurement and indicated in the plots by a horizontal bar. The best choice for the number of partitions can usually be determined by the partitioning which results in the highest average width measurement. A negative width measurement indicates poor association.

The *k*-medians and fuzzy *k*-medians were used to compute silhouette plots for partitions, *k*, of 3 to 6 groups. Since the MDS analysis indicated the Bering Sea populations are not associated with any of the other herring populations, the partitioning analysis was performed without the Bering Sea data. Euclidean, Manhattan, and maximum distance measures all revealed identical results, confirming the robustness of these techniques. In fuzzy partitioning, specifying the number of groups does not always yield that number of groups in the results, due to the nature of fuzzy logic, which assigns a probability of membership to each group and allows for ambiguity in group assignment (Kaufman and Rousseeuw, 1990). The best choice for the number of partitions, based on the average width, was $k = 4$ groups for the fuzzy *k*-medians partitioning method; which resulted in 3 groups appearing in the silhouette plot (Figure 3.6). The grouping structure in Figure 3.6 is very similar to the groupings suggested in the MDS analyses, the difference being the association of the PR population with SEY, CRG, and KAH. A randomization test of significance was performed for the fuzzy partitioning analysis with $k = 4$ groups selected. For 10,000 random permutations, not one time did the partitioning structure match that found in the above analysis, suggesting that the associations found were not due to chance.

The divisive hierarchical analysis, like the partitioning analyses, was robust to different distance measures. The result is plotted as a dendrogram and it confirms the pattern of the population associations indicated above (Figure 3.7). The first two branches in the dendrogram result in groupings which agree with the MDS and partitioning analyses in Figures 3.4 and 3.6, respectively.

The dendrogram in Figure 3.7 allows some insight into the relationships of the populations within each of the groupings. In the group containing KOD, PWS, SIT and SEAK, it seems that KOD is more closely related to PWS than it is to SIT and SEAK, which appear closely associated. In the SEY, KAH, CRG, PR group it appears the SEY and KAH populations form a closely associated pair as well as the CRG and PR populations (Figure 3.7). The lower latitude British Columbia populations form a relational pattern which corresponds to their latitudinal positioning.

The jacknife analysis of the MDS results for the NE Pacific herring populations suggested some years may be more influential compared to others (Figure 3.5). In order to test if the multivariate analyses are being influenced by the 1971-77 time periods and earlier data, the MDS analysis and divisive hierarchical analysis were repeated for the most recent years, 1978-93. This period was chosen because of the hypothesized regime shift in the mid-1970's. Figures 3.8 and 3.9 indicate some change in the relationships of the herring populations in recent years. The KOD population does not appear to be as closely related to the PWS, SIT, SEAK group (Figure 3.8). Also, the lower latitude British Columbia populations do not appear as closely related to each other compared to Figure 3.4, but remain separated from the remaining populations. These observations are confirmed in the dendrogram shown in Figure 3.9. In this tree the KOD population appears on a separate branch, but the remaining structure is very similar to the dendrogram shown in Figure 3.7.

3.4.2. Weight-at-age Data

Since the magnitude of herring weight-at-age information is fairly similar for each population, the unscaled data were used for the multivariate analysis. The MDS analysis of the unscaled weight-at-age data with all ages combined shows two apparent groups and three isolates (Figure 3.10). In this figure, nearly 90% of the variance is explained by the first two dimensions of the MDS analysis. As in the recruitment analyses, the Bering Sea populations appear to be different from the Northeast Pacific herring populations. Within the Northeast Pacific, the KOD population appears to be different from the remaining populations, which seem to be separated into the closely associated PWS, SIT, SEAK, CRG, SEY group and the British Columbia, KAH group (Figure 3.10).

A divisive hierarchical analysis indicated similar groupings as those revealed by the MDS analysis. In Figure 3.11 the Bering Sea herring populations are separated from the Northeast Pacific at the first branching. The Northeast Pacific herring populations appear to be branched into the KOD population, the British Columbia populations, and the Southeast Alaska populations plus PWS (Figure 3.11).

3.5. Discussion

The graphical analysis in Figure 3.2 clearly indicates that when strong year-classes occur, they occur for several populations, suggesting a large-scale phenomenon. The occurrence of a strong 1988 year-class seems to be a phenomenon shared by populations from Norton Sound to Prince Rupert, suggesting a very large-scale control. Similarly, many of the northern Pacific Ocean populations in 1984 had positive recruitment. However, other strong year-classes erupt on a smaller scale, such as the 1976 year-class, which was strong for PWS, SIT, and SEAK only. The pattern of these year-class eruptions indicates some separation into Alaskan events and British Columbia events, but there are several cases of overlap between the two as well. This seems to indicate that herring populations are responding sporadically to large-scale controls which themselves are irregular in geographic range.

It is apparent from the analyses of this study that Pacific herring population fluctuations, as measured by recruitment, are synchronous among certain groups. The best descriptions of the groupings of herring populations are those indicated by the MDS plot in Figure 3.4 and within the Northeast Pacific, the hierarchical dendrogram in Figure 3.7. The Pacific herring populations in this study appear to be separated into the Bering Sea and the Northeast Pacific populations. Within the Northeast Pacific there appears to be three or four groups. The PWS, SIT, and SEAK populations are closely related and may be related to the KOD population depending on the time frame used in the analysis. The remaining herring populations seem to fall into two groups, the SEY, KAH, CRG, PR group and the lower latitude British Columbia group. The question is: Do these groupings make sense?

The groupings of Pacific herring populations suggested by multivariate analyses appear to follow the geographic location of the herring populations but not exactly (Figure 3.1). The lower latitude British Columbia populations all seem to be related to each other and are geographically close. The PR population in British Columbia appears to be related to the SEY, CRG, and KAH populations in Alaska, yet separate from the KOD, PWS, SIT, SEAK group, with which it shares some latitudinal overlap (Figure 3.1). The difference between the lower latitude British Columbia populations and neighboring populations may be explained by the Alaska current, which separates British Columbia waters from Southeast Alaskan waters (Zebdi and Collie 1995, Zheng 1996).

The KOD, PWS, SIT, and SEAK group are not geographically close, but are all located on outside waters. There may be a difference in Alaskan herring populations based on whether their spawning grounds are inside protected islands or more exposed to the Gulf of Alaska. Zheng (1996) suggested this same hypothesis, based on his correlation analysis. The inside herring populations in the Gulf of Alaska include SEY, KAH, CRG, and PR which were grouped together in the multivariate analyses. The outside populations would include KOD, PWS, SIT, and SEAK. The analysis of the most recent recruitment data, year-classes 1978-1993, suggests the KOD population may be changing its relationship to the PWS, SIT, SEAK group. However, the other groupings appear to hold together in this analysis, indicating that these group descriptions are robust (Figures 3.8 and 3.9).

The weight-at-age analysis suggests similar groupings as from the recruitment analysis. This multivariate analysis of the Pacific herring weight-at-age data was performed using the unscaled data. Therefore, the magnitude of the data, in this case the size of herring, will affect the relationships. In the MDS plots the first dimension corresponds to the size of herring (Figure 3.10). These plots indicate the Bering Sea populations are different from the Northeast Pacific stocks, a direct result of the large size difference between Bering Sea herring and Northeast Pacific herring. The KOD herring are fairly large in size and are therefore differentiated from the other Northeast Pacific populations. The rest of the Northeast Pacific herring are relatively similar in size and appear to separated into a northern and southern group. Membership of these groups is not agreed upon in the MDS and hierarchical analyses (Figures 3.10 and 3.11). The MDS analysis indicates the KAH population is more closely associated with the British Columbia populations, while the hierarchical analysis places this population with the Alaskan populations.

Both the weight-at-age and recruitment data analyses seem to indicate that there is a close relationship within the NE Pacific Ocean herring populations. These analyses agree in that there is a difference between the lower latitude British Columbia populations and the northerly Southeast Alaska herring populations. It is not clear exactly where the dividing line occurs between the northerly and southerly NE Pacific Ocean herring populations, but it seems to be in the general vicinity of the KAH and PR populations (Figure 3.1). Zheng (1996) suggested very little difference between PR and the remaining British Columbia herring populations. Within each of these groups there appears to be close relationships as indicated by shared strong year-classes and correlation analyses (Figures 3.2 and 3.3).

As mentioned in the introduction, one of the motivating factors for this study was to determine if the PWS herring population stood out as different from surrounding herring populations. The close relationship of PWS to SIT recruitment data and other populations' weight-at-age data suggests no abnormal pattern can be detected with the PWS population. The analysis of the 1978-93 recruitment data indicates the PWS-SIT relationship is robust and persists in the most recent years. Figure 3.10 indicates a close relationship between PWS and several Southeastern Alaska herring populations. The Exxon Valdez oil spill occurred in 1989, and there might not yet be enough data since the spill to detect changes in the recruitment or weight-at-age data since that time, particularly if oil spill effects were concentrated on the early life history stages.

Perhaps a closer look at the correlation between PWS and SIT in recent years might reveal deviations from the relationship which correspond to the 1989 oil spill. Figure 3.12 shows a scatter plot of the relationship between these populations with the year-classes labeled. The plot suggests that the years from 1989-93 are well within the normal pattern of the relationship. If there is any deviation from this relationship, it occurred in 1991 in which the PWS recruitment was lower than the SIT recruitment. However, 1991 appears to have been a weak year-class for all Pacific herring populations in the Bering Sea and NE Pacific Ocean (Figure 3.2). The last three year-classes for PWS might suggest a deviation from the relationship with SIT, but there is not enough data to truly indicate changes in the PWS population recruitment time series which are not within the normal range for herring population fluctuations.

The weight-at-age analysis indicates PWS herring do not differ from other Alaskan herring populations. A closer look at the mean standardized residuals for ages 3-7 reveals that PWS herring did experience a decrease in weight-at-age, particularly for the 1987 year-class. However, the decreased weight-at-age for PWS in 1987 appears to be part of an overall decrease in weight-at-age for most of the Eastern Pacific herring populations during that same time period (Figure 3.13). This decrease in weight-at-age appears to be followed by a sharp increase, possibly the result of a density dependent response. Overall, it does not appear that PWS herring weight-at-age patterns are any different from other Pacific herring populations.

The correlation and multivariate analyses of Pacific herring data in this study indicate there are close relationships among herring populations. These relationships suggest herring may form distinct associations, possibly as the result of large scale oceanographic influences. We are conducting further research on the association of herring populations to oceanographic features. This additional research may reveal the mechanisms which are responsible for the apparent associations found in this study, thereby allowing for better management and possibly prediction of herring population levels.

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TABLE 3.1. Pacific herring recruitment estimates from age-structured models in millions of fish.

Year Class	Norton Sound	Togiak	Kodiak/ Kamishak	PWS	Seymour Canal	Sitka	Southeast	Craig	Kah-Shakes	Prince Rupert	Queen Charlotte	Central Coast	Vancouver Island	Strait of Georgia
1917							*.6*							
1918							*45.2*							
1919							*18.5*							
1920							*39.8*							
1921							*55.2*							
1922							*171.3*							
1923							*238.2*							
1924							*164.0*							
1925			*83.0*	*122.4*			*2080.1*							
1926			*234.7*	*301.3*			907.9							
1927			*124.3*	*209.5*			295.5							
1928			*97.8*	*247.1*			856.0							
1929			*115.5*	*189.0*			265.6							
1930			*1368.8*	*1337.8*			2124.8							
1931			*140.8*	*115.7*			171.5							
1932			*75.4*	*103.5*			160.5							
1933			85.6	*82.8*			218.6							
1934			366.2	908.2			581.1							
1935			1084.6	782.2			166.8							
1936			103.9	145.2			45.2							
1937			88.1	194.1			24.3							
1938			627.6	219.5			76.8							
1939			1050.0	31.1			283.3							
1940			658.3	131.2			191.8							
1941			381.7	220.0			535.7							
1942			237.0	125.5			224.9							
1943			532.3	461.6			869.2							
1944			101.1	103.5			152.6							
1945			69.9	112.5			149.4							
1946			363.8	64.2			305.2							
1947			18.3	155.3			150.6							
1948			5.9	20.2			79.9			610.3	186.1	304.5	214.4	869.3
1949			8.4	17.7			102.5			319.5	198.7	116.6	172.7	1029
1950			67.0	202.1			211.2			327.4	275.8	152.8	249.4	1172.3
1951			29.2	22.1			92.5			770.5	1346.2	955	426.3	2112
1952			588.9	427.6			1717.9			224.1	164.7	102.2	240.6	1286.3
1953			14.3	9.4			112.9			603.5	215.4	117.9	322	732.8
1954			4.7	21.9			72.7			188.8	67.7	230.5	419	666.2
1955			10.2	38.2			73.1			338.8	93.1	375.2	515.8	580.6
1956			30.0				602.5			696.2	149.9	450.1	689.9	1528
1957							1009.7			227.3	75.4	107.2	453.4	1001.8
1958							94.0			1197.1	239.9	213.2	221.4	523.7
1959							70.0			604.8	290.5	603.1	518.8	1207.4
1960							87.3			349.7	552	305.1	275.8	1142.4
1961							23.0			929.4	113.4	284.6	381.9	1041
1962							16.4			128.9	303.2	105.1	101.8	530.9
1963							117.9			19.2	20	136.8	92.6	237.6
1964						*442.1*	442.1			52.9	15	119.2	165.8	225.1
1965						*54.2*	54.2			53.7	19.7	24.3	4.3	68.3
1966						*27.5*	27.5			91.8	42.9	27.1	63.2	99
1967						*13.8*	197.3	*183.5*		487.9	119.5	134.8	333.6	319.2
1968						94.9	132.0	*37.1*		360.3	270.9	115.4	687.2	367.9
1969		*4.2*			*126.8*	147.9	161.0	*13.1*	*429.1*	164.8	234	143	516.7	288.6
1970		*12.9*		353.9	*48.1*	*26.7*	69.2	*42.6*	*100.4*	323.8	641.5	244	631.8	453.6
1971		*0.9*		130.3	*44.1*	134.0	151.6	17.6	*126.3*	307.1	516	160.5	676.9	700.5
1972	*4.7*	*80.6*	*0.6*	116.7	*6.0*	*22.3*	33.2	10.9	*32.1*	135.7	458.5	213.4	1131.1	945.2
1973	*5.4*	238.5	*7.1*	110.3	6	92.0	98.2	6.2	5.8	79.2	119.8	103	471.6	652.8
1974	*15.7*	265.8	*42.2*	81.8	8.9	*40.1*	44.6	4.5	46.2	151.6	156.2	51.3	287.9	1116.9
1975	*4.0*	18.5	200.5	146.4	7.2	173.7	176.2	2.5	28.5	76.7	175.4	58	458.1	883.3
1976	*32.4*	86.3	214.8	889.6	13.1	921.9	932.5	10.6	41.3	74.2	98.6	39.6	131.8	478.2
1977	*160.8*	1475.0	355.5	172.3	99.8	208.7	618.8	410.1	385.7	736.4	1938.5	404.5	288.6	660
1978	76.3	1444.1	201.2	98.5	29.8	28.1	83.5	55.4	86	165.8	140.7	78.4	206.1	502.5
1979	128.0	605.3	207.9	107.1	21.4	116.1	270.1	154.0	88.6	204.3	57.3	84.5	108.3	401.1
1980	54.9	180.8	134.3	369.5	61.2	821.0	883.1	62.1	80.7	228.1	62	37.4	74.7	316.9
1981	99.6	344.8	167.6	292	109.4	305.0	426.3	121.3	147.9	670.3	418.9	31.7	143.2	279.6
1982	109.5	83.7	36.0	86.6	67.1	62.4	89.6	27.2	54	133.8	186.2	122.8	307.2	451.4
1983	39.7	280.5	186.4	94.8	51.1	245.4	289.5	44.1	42.7	130.8	42.9	51.5	298.4	689
1984	44.6	217.9	303.8	1267.1	42.5	1550.0	2611.7	1061.7	110	509.1	88.9	98.1	121	391.9
1985	7.0	33.0	67.1	138.7	23.9	170.7	654.3	483.6	55.9	440.8	631.3	588.8	724.7	1219.3
1986	26.7	42.9	45.7	41.7	32.3	11.1	160.8	149.7	42.8	276.3	242.9	41.9	125.9	368.2
1987	4.6	476.3	93.3	61.9	19.8	49.9	112.1	62.2	33.4	150.9	84.3	37.3	158.6	882.6
1988	118.4	287.0	379.3	1229.9	82.9	1573.6	1818.1	244.5	173.5	717.8	54	123.9	93	422.4

TABLE 3.2. Population abbreviations for Pacific herring populations in this report.

NOR	Norton Sound	CRG	Craig
TOG	Togiak	KAH	Kah-Shakes
KOD	Kodiak/Kamishak Bay	PR	Prince Rupert
PWS	Prince William Sound	QCI	Queen Charlotte Islands
SEY	Seymour Canal	CC	Central Coast
SIT	Sitka	VCI	W. Vancouver Island
SEAK	Southeast	SOG	Strait of Georgia

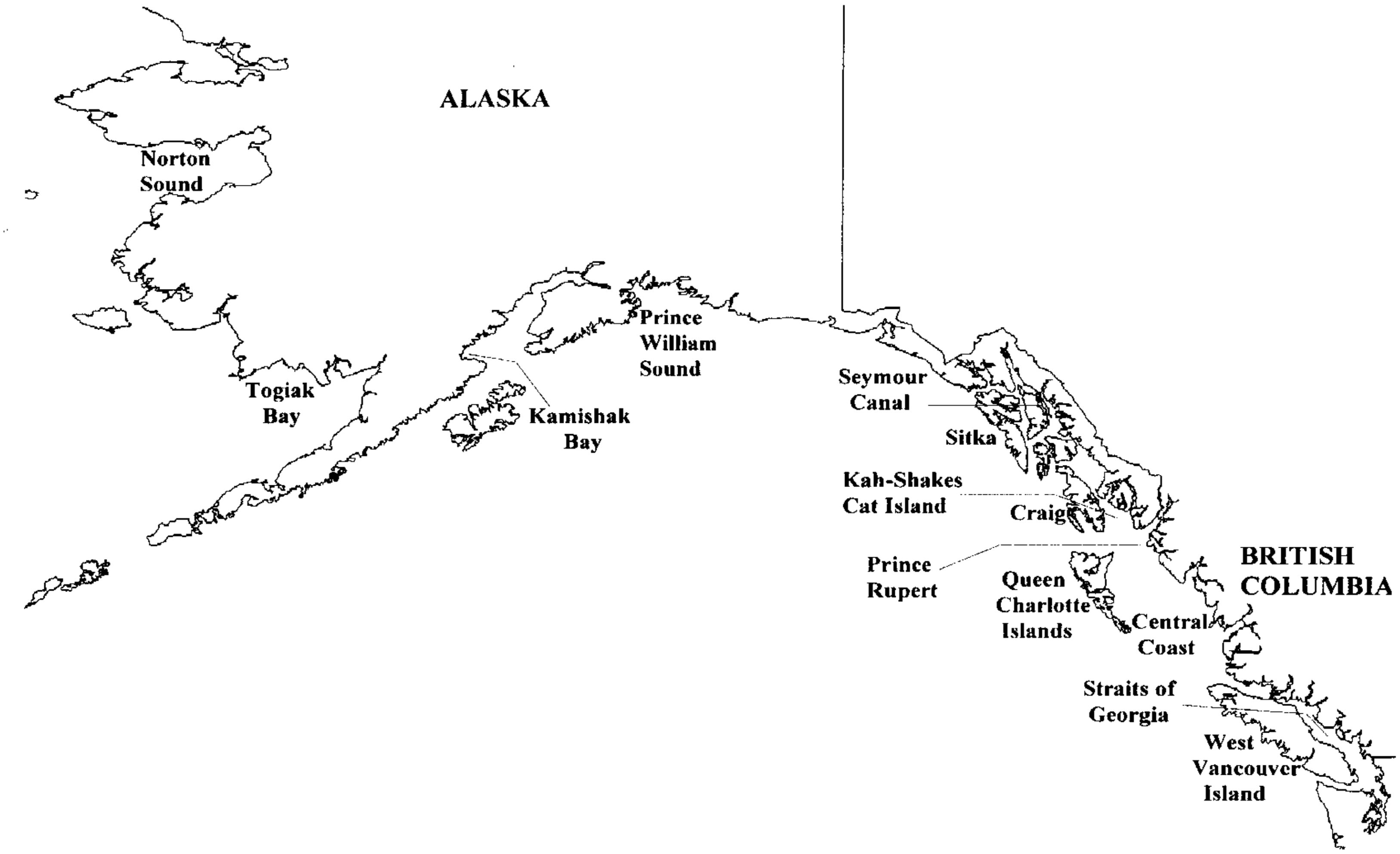

FIGURE 3.1. Map of Alaska and British Columbia coasts showing the location of major Pacific herring, *Clupea pallasi*, populations.

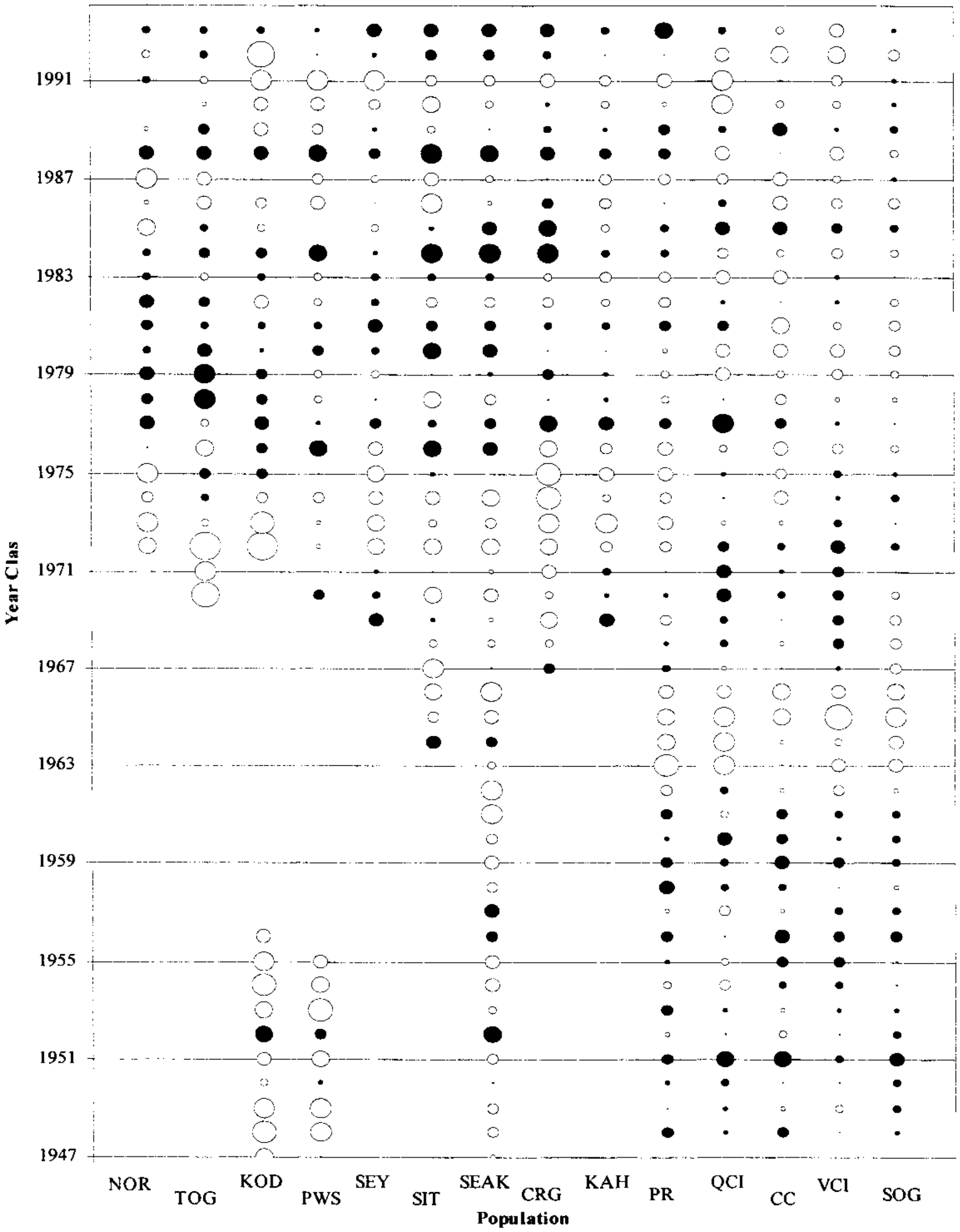

FIGURE 3.2. Bubble plot of log transformed Pacific herring recruitment deviations from the mean (black is positive, clear is negative). The area of the circle is relative to the magnitude of the deviation.

	NOR	TOG	KOD	PWS	SEY	SIT	SEA	CRG	KAH	PR	QCI	CC	VCI	SOG
Norton Sound		0.020	0.026	0.414	0.002	0.284	0.204	0.045	0.008	0.085	0.592	0.446	0.067	0.022
Togiak	0.367		0.075	0.958	0.655	0.321	0.442	0.107	0.710	0.637	0.118	0.130	0.021	0.710
Kodiak/Kamishak	0.342	0.281		0.000	0.048	0.015	0.000	0.096	0.017	0.671	0.932	0.215	0.040	0.316
Prince William Sound	0.126	0.008	0.470		0.039	0.000	0.000	0.298	0.017	0.795	0.604	0.256	0.256	0.105
Seymour Canal	0.468	0.065	0.303	0.301		0.036	0.016	0.030	0.000	0.001	0.183	0.870	0.272	0.012
Sitka	0.165	0.145	0.372	0.612	0.300		0.000	0.260	0.097	0.454	0.630	0.803	0.125	0.521
Southeast	0.195	0.112	0.407	0.435	0.343	0.690		0.001	0.040	0.195	0.570	0.222	0.188	0.670
Craig	0.307	0.236	0.255	0.152	0.310	0.154	0.464		0.005	0.000	0.917	0.692	0.026	0.327
Kah-Shakes	0.524	0.054	0.368	0.348	0.657	0.237	0.293	0.400		0.000	0.093	0.176	0.513	0.050
Prince Rupert	0.264	0.069	0.054	0.032	0.470	0.097	0.132	0.590	0.613		0.001	0.000	0.153	0.020
Queen Charlotte Isl.	-0.082	-0.228	0.011	0.065	0.190	-0.062	-0.058	0.014	0.240	0.338		0.001	0.000	0.005
Central Coast	0.117	-0.221	-0.157	-0.141	0.023	-0.032	-0.125	0.054	0.193	0.357	0.344		0.000	0.000
Vancouver Island	-0.281	-0.337	-0.260	-0.141	-0.157	-0.198	-0.134	-0.305	-0.093	0.146	0.357	0.442		0.001
Strait of Georgia	-0.351	-0.054	-0.127	-0.202	-0.357	-0.083	-0.043	-0.134	-0.280	0.237	0.286	0.362	0.326	

FIGURE 3.3. Correlation estimates (lower triangle) and p-values (upper triangle) for log transformed Pacific herring recruitment estimates using Kendall's Tau correlation measure. Darker shade indicates p-values <.01 and lighter shade indicates p-values <.05.

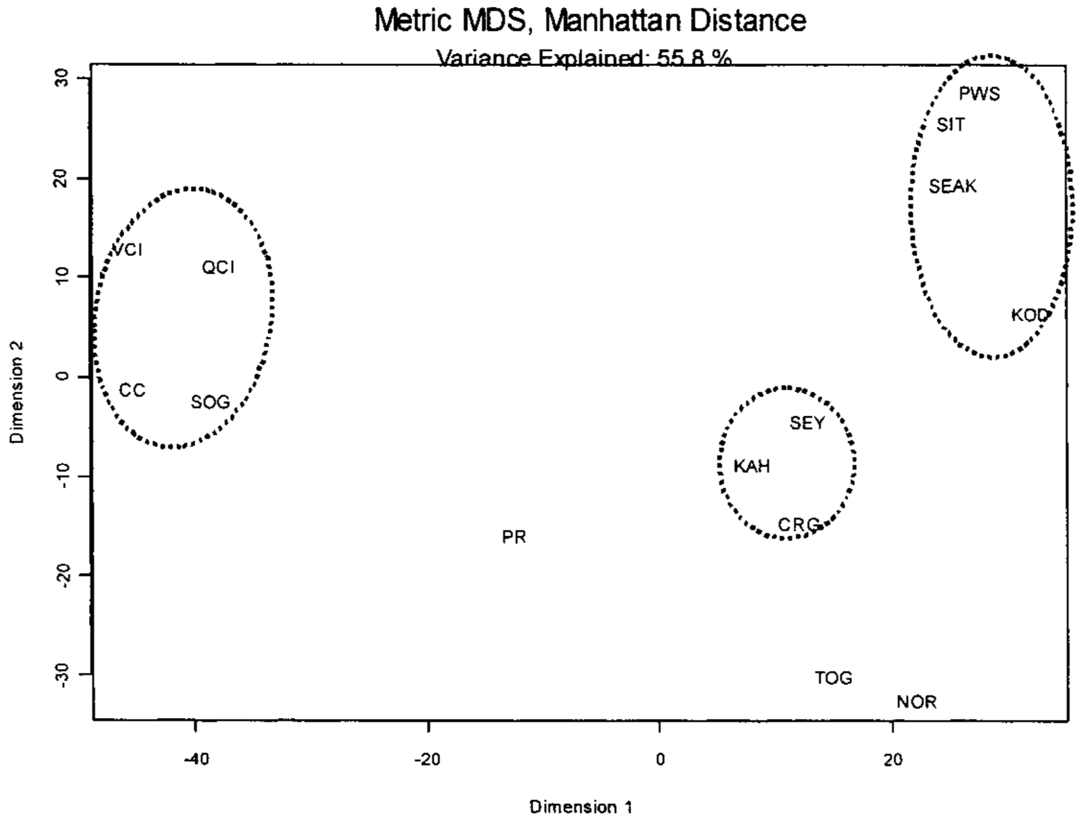

FIGURE 3.4. Scatter plot of first two dimensions from a metric multidimensional scaling analysis of Bering Sea and Northeast Pacific herring recruitment estimates.

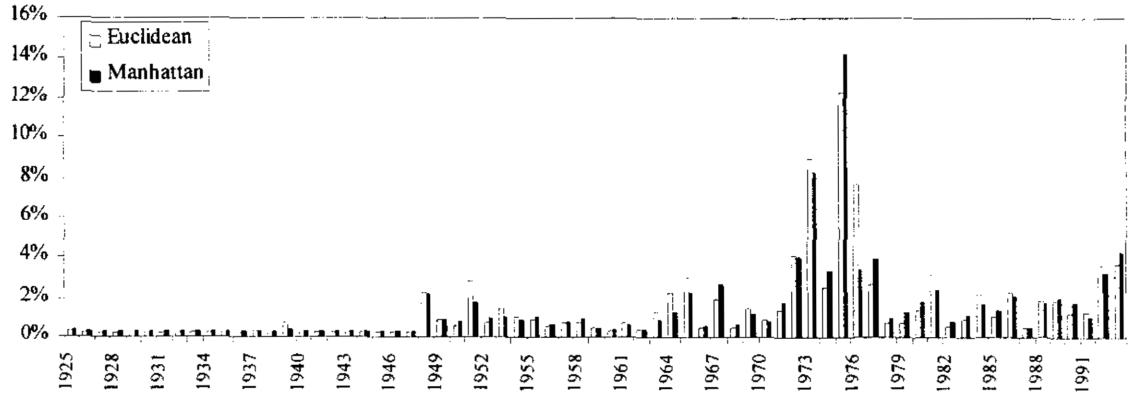

FIGURE 3.5. Percent influence of each year of Northeast Pacific herring recruitment data from a jacknife analysis of the first two dimensions from multidimensional scaling.

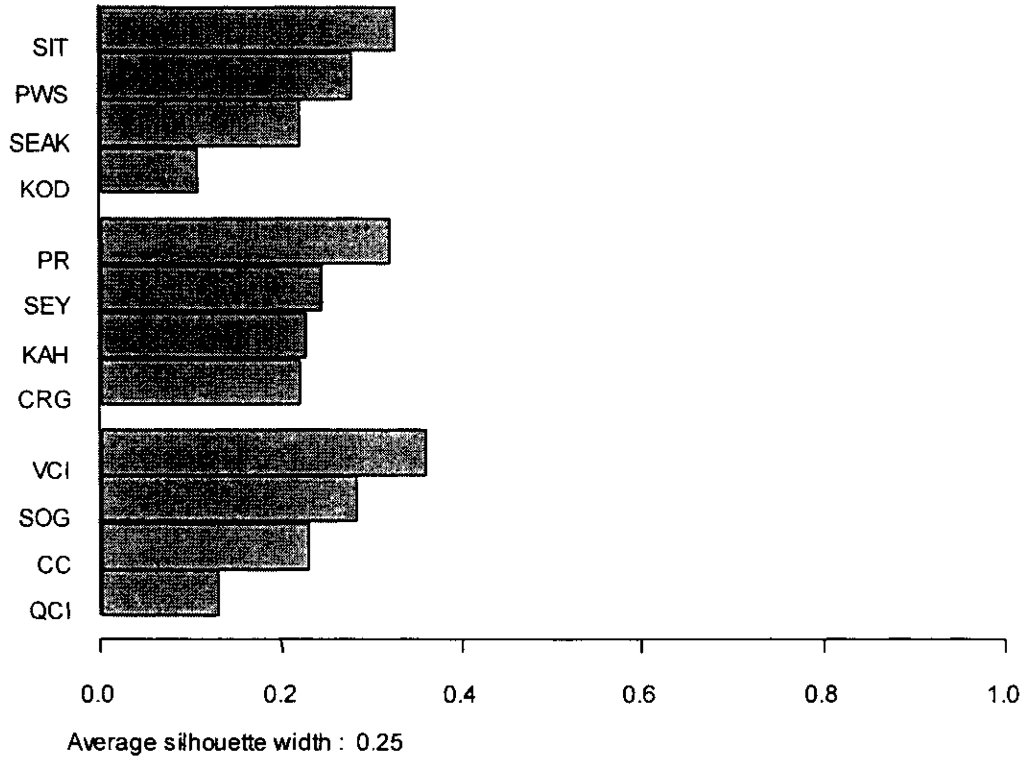

FIGURE 3.6. Silhouette plot of results from fuzzy k-medians partitioning analysis with $k = 4$ partitions for Northeast Pacific herring recruitment estimates.

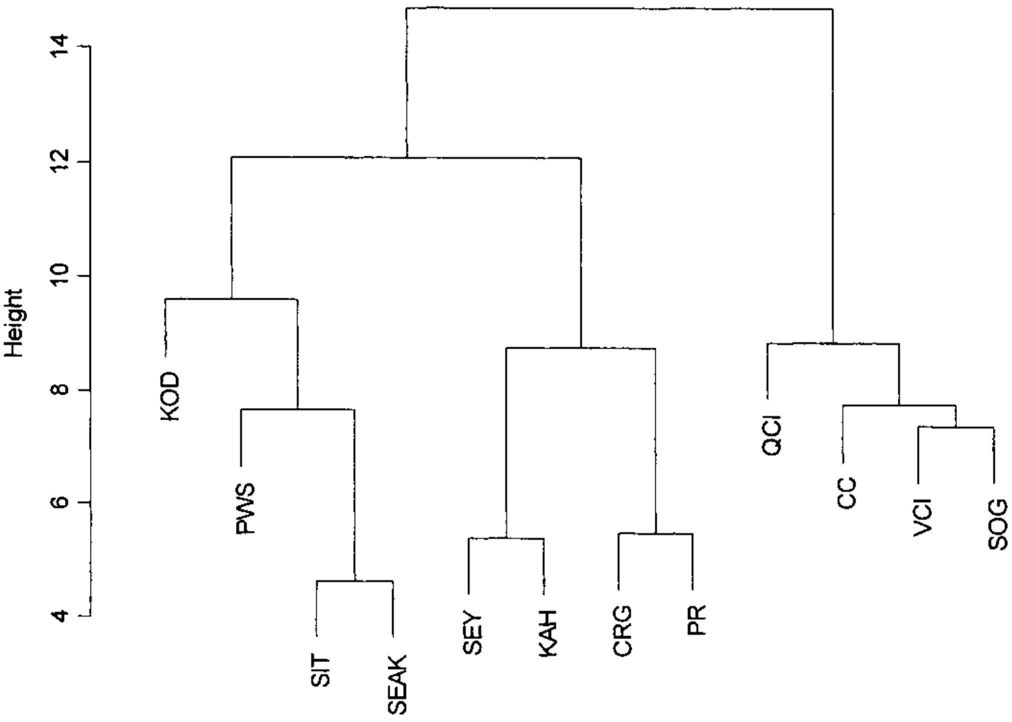

FIGURE 3.7. Dendrogram from divisive hierarchical analysis of Northeast Pacific herring recruitment estimates.

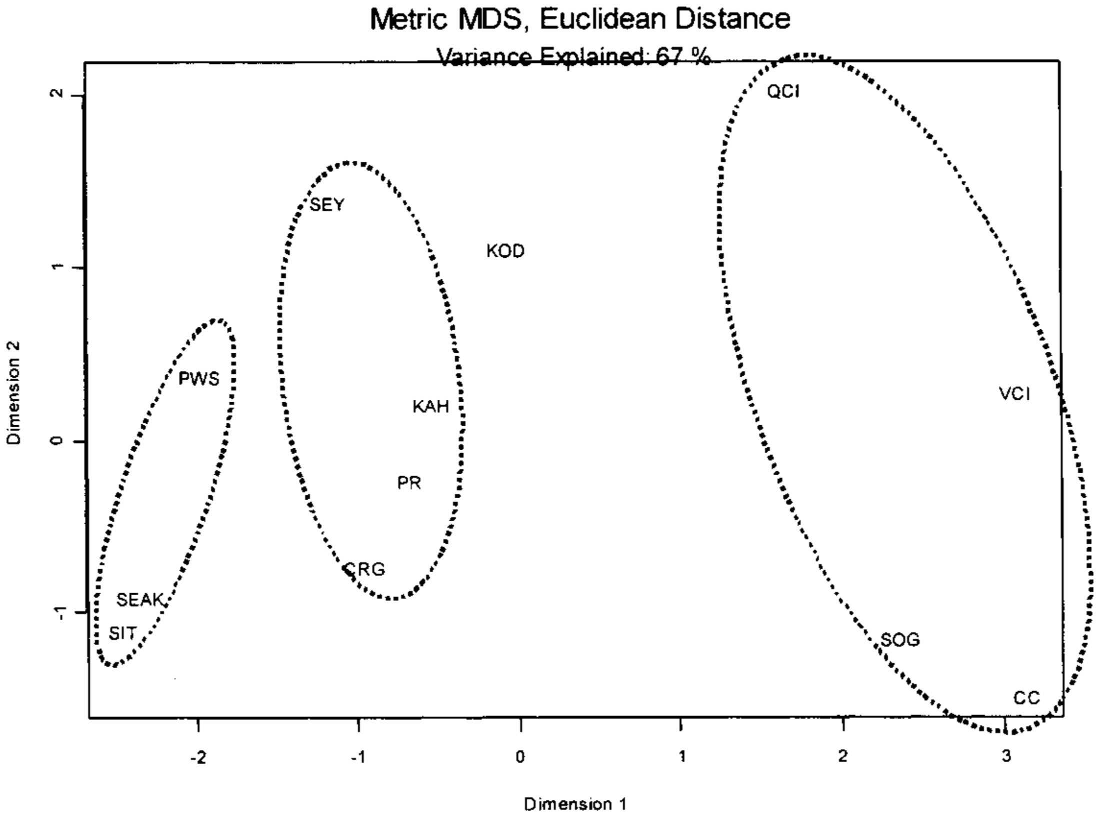

FIGURE 3.8. Scatter plot of first two dimensions from a metric multidimensional scaling analysis of Northeast Pacific herring recruitment estimates corresponding to the 1978-93 year-classes.

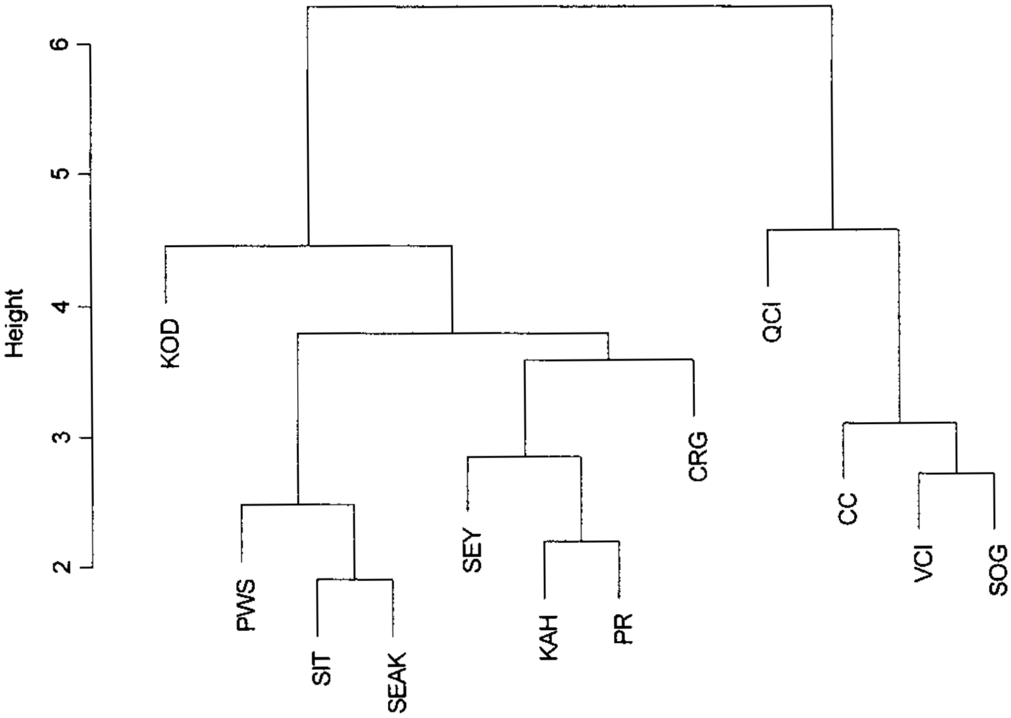

FIGURE 3.9. Dendrogram from divisive hierarchical analysis of Northeast Pacific herring recruitment estimates corresponding to the 1978-93 year-classes.

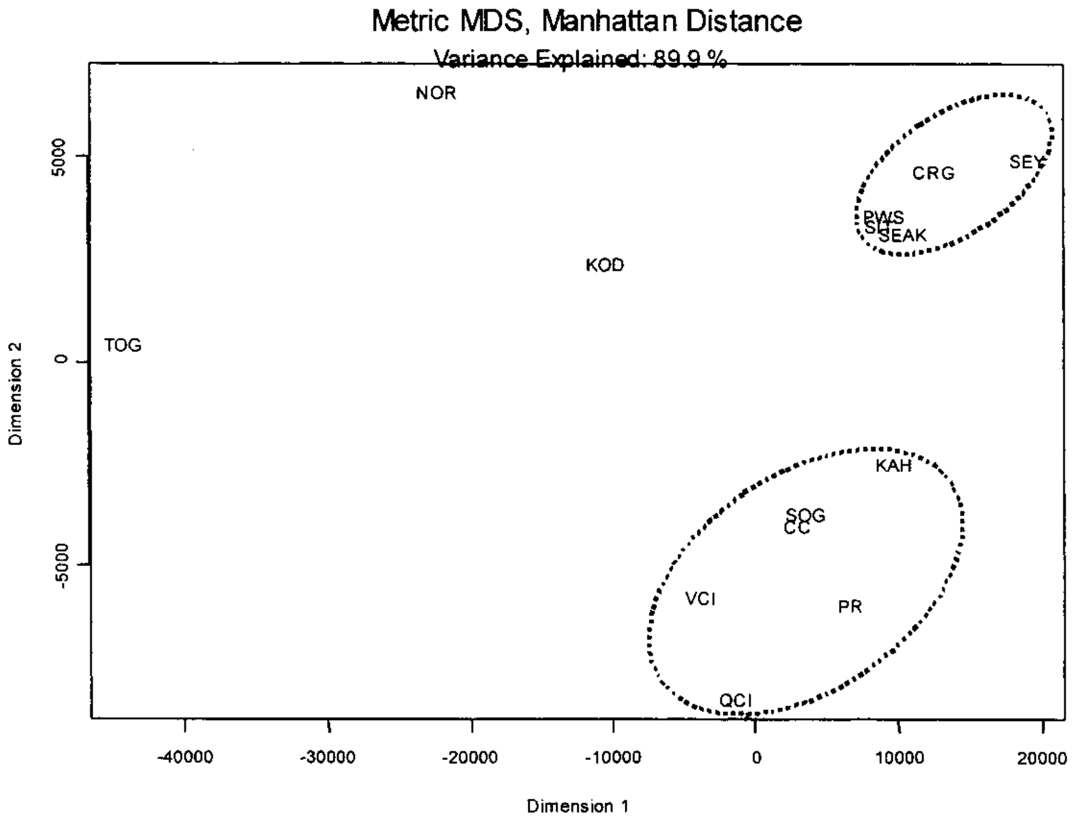

FIGURE 3.10. Scatter plot of first two dimensions from a metric multidimensional scaling analysis of Pacific herring weight-at-age data for ages 3-8 from the Bering Sea and Northeast Pacific.

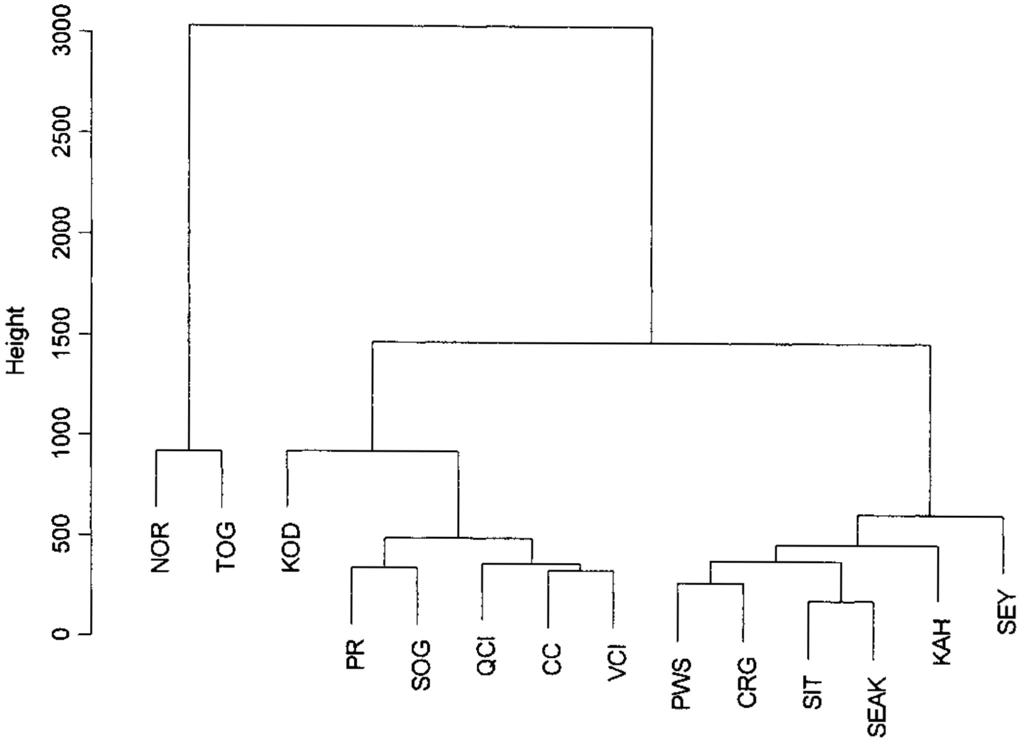

FIGURE 3.11. Dendrogram from divisive hierarchical analysis of Pacific herring weight-at-age data for ages 3-8 from the Bering Sea and Northeast Pacific.

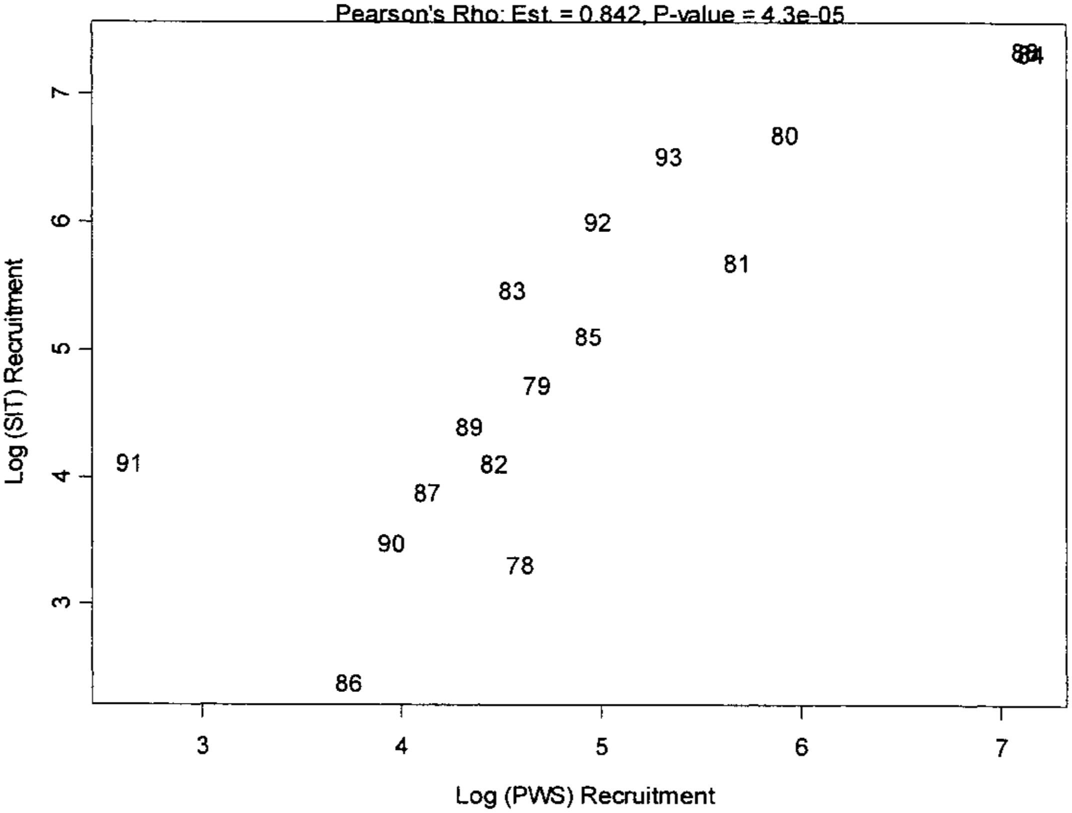

FIGURE 3.12. Scatter plot and correlation estimate of PWS and SIT herring recruitment estimates for the 1978-93 year-classes.

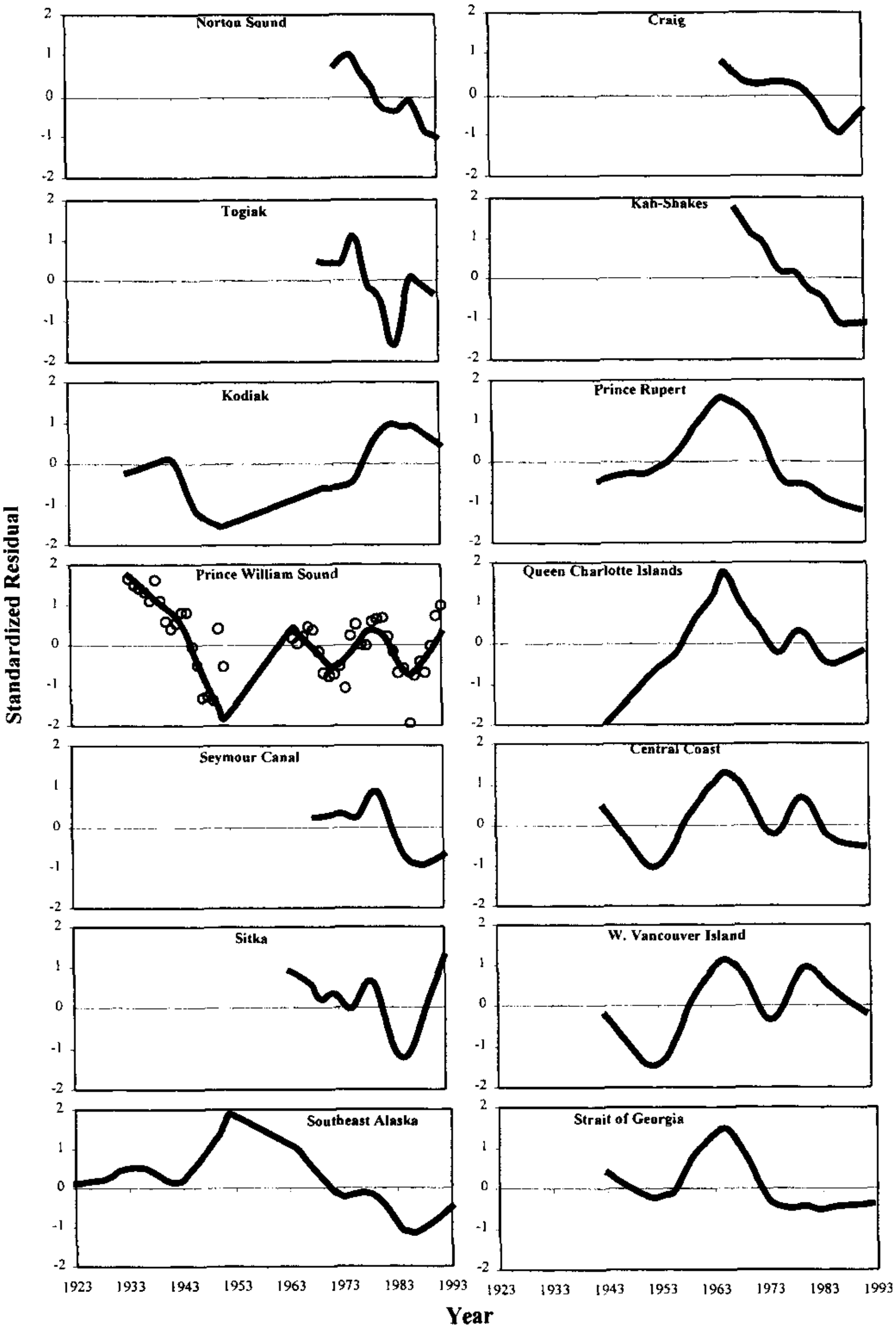

FIGURE 3.13. Lowess smoothed plots of mean standardized residuals of Pacific herring weight-at age data for ages 3-7. Data has been lagged to correspond to year-classes.

Chapter 4. Pacific herring, *Clupea pallasi*, recruitment: relations to environmental variables and forecasting models.

4.1. Abstract

Previous studies have shown that Pacific herring populations in the Bering Sea and Northeast Pacific Ocean can be grouped into associations based on similar recruitment time series. The scale of these associations is suggestive of large-scale influence on recruitment fluctuations from the environment. Recruitment time series from 14 populations were analyzed to determine links to various environmental variables and to develop recruitment forecasting models using a Ricker type environmentally dependent spawner-recruit model. The environmental variables used for this investigation included monthly time series of the following: southern oscillation index, North Pacific pressure index, sea surface temperatures, air temperatures, coastal upwelling indices, Bering Sea wind, Bering Sea ice cover, and Bering Sea bottom temperatures. Exploratory correlation analysis was used for focusing the time period to examine for each environmental variable. Candidate models for forecasting herring recruitment were selected by the Akaike Information Criterion, jacknife prediction error, and recent prediction error. Results indicated that forecasting models using air and sea surface temperature data lagged to the year of spawning generally produced the best forecasting models. Use of multiple environmental variable forecasting models did not appear much better than single environmental variable forecasting models.

4.2. Introduction

Pacific herring, *Clupea pallasi*, is a wide-ranging species with a long history of exploitation. This member of the clupeoids is commonly found along the eastern coast of the Bering Sea and Northeast Pacific Ocean (Figure 1). Herring populations and/or management units are typically defined by spawning aggregations formed by spring time returning fish from wintering grounds (Hay 1985). Generally the age of first spawning for Pacific herring in the Bering Sea and Northeast Pacific Ocean is at age 3. The abundance of age 3 Pacific herring is the measure usually used for Pacific herring recruitment estimates.

An understanding of the recruitment dynamics of Pacific herring is essential to determining optimal harvesting strategies (Quinn et al. 1990). Density-dependent spawner-recruit relationships for many Pacific herring populations seem inadequate for explaining the changes in year class strength. For many herring stocks the method for forecasting Pacific herring recruitment is to simply use the historical median recruitment (F. Funk, Alaska Department of Fish and Game; Schweigert and Noakes 1991). However, the clupeoids are notorious for their large population fluctuations, which seem to be the result of cycles possibly driven by density-independent processes (Cushing 1982). Development of forecasting models including spawning biomass and the environment should be an improvement.

Density-independent influences of Pacific herring recruitment have been studied in a few British Columbia and Alaska populations for the purposes of improving recruitment forecasting. Several British Columbia herring recruitment time series have been found to be influenced by local environmental conditions including: sea surface temperature, sea surface salinity, river discharge, Ekman transport, and sea level (Stocker et al. 1985; Stocker and Noakes 1988; Schweigert and Noakes 1991; Beamish et al. 1994; Schweigert 1995). Only a couple of the Alaska herring populations have been analyzed for associations between recruitment and the environment (Wespestad 1991; Zebdi and Collie 1995). Bering Sea herring recruitment appears to be correlated with wind driven transport and sea surface temperatures (Wespestad 1991). Sitka Sound herring population fluctuations were found to be correlated with sea surface temperature and an index of upwelling (Zebdi and Collie 1995). Some of the recruitment forecasting models developed for Pacific herring have not lasted the test of time or occasionally contradict each other with respect to the nature of the relationship (Schweigert 1995). One factor generally agreed upon in these studies of Pacific herring recruitment is the relationship of recruitment to temperature.

Many of the studies linking Pacific herring recruitment to the environment tend to focus on coastal variables corresponding to sites close to herring spawning grounds. This effectively makes the assumption that the environmental influence on recruitment occurs during the spawning and early life history stages of herring, which is the most commonly held belief for fisheries in general (Hjort 1914; Cushing 1975, 1990; Iles and Sinclair 1982; Wooster and Bailey 1989). Recent studies have pointed toward similarities in recruitment patterns for Pacific herring, leading to the possibility that herring may be responding to more large scale influences (Schweigert 1995; Zebdi and Collie 1995).

A study of several fish stock recruitment patterns, including Pacific herring, indicated that recruitment success may be synchronous across large areas of the Northeast Pacific Ocean (Hollowed et al. 1987; Hollowed and Wooster 1995). A more detailed multivariate analysis of the recruitment patterns of Pacific herring in the Bering Sea and Northeast Pacific Ocean confirms the existence of large-scale associations of herring populations with highly correlated recruitment time series (Chapter 3, Williams and Quinn *in preparation*, Zebdi and Collie 1995, Zheng 1996). The geographic range of the herring population associations is suggestive of large-scale environmental influences (Chapter 3, Williams and Quinn *in preparation*).

Pacific herring associations appear to follow the location of oceanographic domains suggested by Ware and McFarlane (1989) (Chapter 3, Williams and Quinn *in preparation*). The oceanographic domains are delineated by the location of ocean currents and differences in sea surface temperatures (Ware and McFarlane 1989). It appears that the major Pacific herring populations in the Northeast Pacific Ocean and the Bering Sea can be grouped into the associations shown in Table 4.1 (Chapter 3, Williams and Quinn *in preparation*).

The purpose of this paper is to analyze recruitment time series for 14 herring populations from the Bering Sea and Northeast Pacific Ocean to determine important correlations with large-scale and local environmental variables (Figure 4.1). Environmentally dependent Ricker type, spawner-recruit models were used to model and forecast Pacific herring recruitment. In order to avoid potential spurious correlations, an exploratory correlation analysis of recruitment time series was applied in order to indicate overall patterns in the relationships between the environment and Pacific herring. Patterns in the correlation analysis were used to focus the time period of the environmental data to be used in the spawner-recruit modeling (Walters and Collie 1988). The selective process used for determining environmental variables should result in more "robust" forecasting models of Pacific herring recruitment.

4.2.1. Data

Time series of Pacific herring recruitment and spawning biomass were assembled from the Bering Sea, Gulf of Alaska, and eastern Pacific Ocean. The available herring data span seven decades and two fishery types. Reduction fishery data for catch-age composition and weight-at-age exist for stocks in Kodiak, Prince William Sound, and Southeast Alaska for years 1920-1966 (Reid 1971). Around 1970 the modern sac-roe fisheries started and continue to this day. Recruitment and spawning biomass estimates for selected stocks are available from age-structured analyses performed by the Alaska Department of Fish and Game, the Division of Fisheries and Oceans, British Columbia, and the authors (Funk et al. 1992; Schweigert and Stocker 1988, Williams and Quinn 1998).

To obtain recruitment and spawning biomass estimates for the reduction fisheries, the age composition data was analyzed using cohort analysis (Chapter 3, Williams and Quinn *in preparation*, Quinn and Deriso *in press*). Resulting population abundance estimates were converted to biomass using annual weight-age data. Terminal fishing mortality was estimated using catch curve analysis to estimate total mortality, which allowed for the estimation of fishing mortality using the estimate of natural mortality from the modern sac-roe fishery.

Inclusion of the reduction fishery data extends the time series backward in time. Based on the distribution of catches in the reduction fishery it was assumed that the Kodiak reduction fishery data could be combined with the Kamishak Bay sac-roe fishery data, and that Southeast Alaska could be extended using a summation of Sitka and Craig data (Reid 1971). Recruitment estimates used in this study from the age-structured analyses are for age 3 fish for all the stocks, except for Togiak, which are for age 4 fish. Estimates of survival in these age-structured models were used to back-calculate older age compositions in the first year, in order to extend the time series of recruitment estimates by a few more years.

The typical pattern of Pacific herring recruitment time series is highly variable with large year class events occurring at occasionally regular intervals of between 3-9 years. The large year class events can dominate the recruitment time series with the ratio of the largest year class to the weakest being as high as 429 (Zheng 1996). The dominance of large year classes in herring recruitment time series suggests environmental influences are more likely to occur on an annual scale. This is contradictory to recent studies which indicate biological variables exhibit more correlation with physical variables at the decadal scale (Francis et al. 1998, Hare and Francis 1995, Francis and Hare 1994). However, these analyses have primarily focused on salmon and groundfish populations and rarely, if ever, are Pacific herring implicated in the hypothesized "regime shift" of the North Pacific.

Monthly environmental time series for air temperature, sea surface temperature, North Pacific atmospheric pressure (a measure of the Aleutian low pressure system), southern oscillation (negative values are associated with El-Niño - Southern Oscillation events), and coastal upwelling were collected for analysis with the Pacific herring recruitment time series. Additional data specific to the Bering Sea included monthly ice cover, monthly wind anomalies, and annual bottom temperatures (Niebauer 1988; Niebauer and Day 1989, Quinn and Niebauer 1995). A recent interdecadal climate index for the North Pacific has been developed based on eigen-analysis of sea surface temperatures (Mantua et al. 1997). Since this index has been shown to be closely associated with both the North Pacific pressure and southern oscillation indices, and the sea surface temperatures used for its calculation are the same ones in this study, it will not be used in this analysis.

Air temperatures were obtained from the Global Historical Climate Network database for various coastal cities corresponding to the location of herring spawning sites. Sea surface temperatures were collected from the Comprehensive Ocean-Atmosphere Data Set (COADS) (Woodruff et al. 1987). The COADS data consists of a 2° latitude by 2° longitude grid of averaged ship observations of sea surface temperatures. The North Pacific atmospheric pressure index, southern oscillation index, Bering Sea ice cover, and Bering Sea wind data were obtained from H. J. Niebauer (Niebauer 1988, Niebauer and Day 1989, Quinn and Niebauer 1995). The Bering Sea bottom temperatures are from an annual survey performed aboard the *RV Oshoro Maru* (Ohtani and Azumaya 1995). The coastal upwelling data series was obtained from the Pacific Fisheries Environmental Group (Internet Address: http://upwell.pfeg.noaa.gov/products/upwell.html).

The interrelationship of environmental and oceanographic variables in the Bering Sea and Northeast Pacific Ocean is complex and intertwined. On a global scale it appears that the southern oscillation index is related to the whole North Pacific environment due to the link of El-Niño events to the Aleutian low pressure system (Niebauer 1988). Variability in the Aleutian low appears to drive as much as 30-40% of the variability in the Bering Sea. Negative signals in the southern oscillation index (El-Niño event) are associated with an intensification of the Aleutian low pressure system (as measured by the North Pacific pressure index), which in turn draws warm, moist air northward along the northeast Pacific coast. The North Pacific pressure index tends to lag behind the southern oscillation index by 2 months (Niebauer 1988; Niebauer and Day 1989).

Most of the North Pacific environment can be linked to the southern oscillation index and the North Pacific pressure index. Air temperatures, wind and ice cover appear to lag behind the southern oscillation index and North Pacific pressure index by 5-6 and 0-6 months, respectively. Sea surface temperatures appear to lag behind air temperatures by 0-3 months (Niebauer 1988; Zebdi and Collie 1995). This is a highly generalized view of the North Pacific environment on a large scale and probably not indicative of smaller scale associations, which are certainly more variable.

4.3. Methods

Relationships of Pacific herring recruitment and the environment were determined through correlation analyses. Correlation is typically measured by the standard Pearson sample correlation coefficient. Alternate correlation coefficients include two rank-based measures; Kendall's τ and Spearman's ρ (Dowdy and Wearden 1991; Hollander and Wolfe 1973; Zar 1984). Generally, the rank-based alternatives are preferable in determining significance levels, since they are not as sensitive to outliers and non-normality as the standard Pearson estimate.

The presence of autocorrelation in the time series of data can affect the inferences of a correlation analysis (Brockwell and Davis 1995; Pyper and Peterman 1998). Spurious correlations between two time series can occur, particularly when lagging the time series. The standard method of preventing spurious correlation in the presence of autocorrelation is to "prewhiten" the time series by fitting an autoregressive model and using the model residuals for the correlation analysis (Box and Jenkins 1976). Significant autocorrelation in just one of the two time series will not greatly affect the correlation analysis; however significant autocorrelations in both time series can result in spurious correlations (Haugh 1976).

Prewhitening is not necessarily the proper procedure when faced with autocorrelated time series in a correlation analysis. Removal of the autocorrelation in a time series prior to correlation analysis may increase Type II error rates (Pyper and Peterman 1998). Significant correlation coefficients arising from two autocorrelated time series can be the result of the time series properties of the two series. Prewhitening will remove the time series properties from the two time series, leaving white noise. However, the excised time series properties may be the very feature important to the relationship between the two time series. Furthermore, the theory behind prewhitening is based on large sample sizes (n = 50-200) (Brockwell and Davis 1995; Haugh 1976). Most of the herring population data in this study is less than 50 years in length (Table 4.1). For these reasons, prewhitening was not used in this study.

For this study, correlation analysis was performed in an exploratory setting, using an exploratory measure of correlation. Since correlation analysis assumes some level of normality and herring recruitment data appear to be lognormally distributed, the time series were ln-transformed (Williams and Quinn *in preparation*). The exploratory correlation measure consists of the ln transformation of the inverse of the computed p-value from Kendall's τ correlation measure. A ln transformation was required based on the highly skewed distribution of inverse p-values. The sign of the exploratory measure was changed to correspond to the direction of the relationship. For robustness, the exploratory correlation measure was repeated with 10% of the outlying data trimmed (Rousseeuw and Leroy 1987). The final measure to be used in the exploratory analysis was computed by taking the average of the full and trimmed exploratory correlation measures, as shown here

$$\frac{\pm \mathrm{Ln}\left(\dfrac{1}{p.value_{raw}}+1\right) \pm \mathrm{Ln}\left(\dfrac{1}{p.value_{10\%trim}}+1\right)}{2}.$$

Based on this "conservative" correlation measure an average p-value of 0.05 for the raw and trimmed data, indicating a potentially significant correlation, will result in an exploratory correlation measure of +/- 3.

The exploratory correlation analysis was applied similarly to the cross-correlation function used in time series analysis, in which time series are lagged at sequential time intervals to determine relationships. In this analysis only lags which allow for the environmental variable to be a possible predictor of recruitment were explored. The extent of the lags will be limited to one year prior to spawning. This corresponds to four year lags for all the herring populations except Togiak Bay which was extended to cover five year lags because of the increased age of recruitment. Subsets of the air and sea surface temperature data sets were selected based on the nearest locations to the spawning grounds of the particular herring population. For the air temperature and sea surface temperature data, two city locations and five grids were selected, respectively.

Since Pacific herring populations appear to be closely associated based on their recruitment time series, the pool of potential time periods for predictions was reduced to those which appear to follow a pattern of similarity shared by other populations. Patterns were determined by averaging and summarizing environmental correlations by lags and by months. The populations were grouped according to the associations suggested in previous studies and shown in Table 4.1 (Chapter 3, Williams and Quinn *in preparation*; Zebdi and Collie 1995).

The monthly environmental time series were standardized into anomalies before use in forecasting models. The use of anomalies rather than raw data is preferred for environmentally dependent spawner-recruit modeling, since the coefficient may be more easily interpreted (Hilborn and Walters 1992). For simplification, these anomalies were averaged into yearly thirds for use in the forecasting models. Yearly thirds were chosen in order to correspond roughly to the pre-spawning, hatching/larval, and juvenile phases of Pacific herring life history.

The Pacific herring recruitment, spawning biomass, and environmental variables were fit using the linearized form of the Ricker environmental spawner-recruit model:

$$(1) \qquad \ln(R / S) = a - \beta S + \gamma_1 E_1 + \ldots + \gamma_i E_i,$$

where R is the number of recruits, S is the spawning biomass, E_i is the ith environmental variable, and $\{a, \beta, \gamma_1, ..., \gamma_i\}$ are the coefficients (Quinn and Deriso, 1999). Initially, only a single environmental variable was fit. The environmental variables from the best 5 sea surface temperature, 2 air temperature, southern oscillation index, North Pacific pressure index, and upwelling sets of single variable models were then used for subsequent analysis in multiple environmental predictor models. Model fitting was accomplished with the linear model fitting algorithm in the S-Plus statistical software package.

Model fit was judged by the use of the Akaike Information Criterion (AIC), jacknife prediction error, and recent prediction error. The AIC is essentially a corrected residual squared error with a penalty weight based on the number of parameters used in the model (Akaike 1974; Venables and Ripley 1997). The jacknife prediction error was computed by systematically leaving one year of data out of the analysis, fitting the model to the reduced data set, and then calculating the mean of squared differences between each excluded point and its model prediction for each year (Efron and Tibshirani 1993). The recent prediction error followed the same basic procedure as the jacknife prediction error method, except that just the last three years were removed, predicted, and the error computed. The jacknife and recent prediction errors were used for selecting single environmental variable models, while the AIC was used for selecting multiple environmental variable models using the *stepAIC* algorithm in S-Plus (Venables and Ripley 1997). The jacknife and recent prediction errors are preferred measures of model fit for selection of forecasting models. However, no multiple regression algorithm has been developed which uses the jacknife or recent prediction error for model selection. For this reason the AIC was used for selecting the best multiple predictor model.

For many of the environmental time series there are variable amounts of missing data in the past resulting in models of various sample sizes. Although the AIC and jacknife prediction error measures have corrections for sample size, there is still some dependence on the total number of points. Since all the environmental data sets include the three most recent years, the recent prediction error is a more comparable measure between competing models of varying sample size for the same herring populations.

The potential pool of Pacific herring recruitment forecast models was reduced by a series of comparisons of environmental models to the non-environmental Ricker spawner-recruit model for each population. The first step was to remove all models that did not show a decrease in the recent prediction error with the addition of environmental parameters. Next, models with the same sample size as the non-environmental spawner-recruit model were analyzed based on the jacknife prediction error. If there was no decrease in the jacknife prediction error, then the model was removed from the pool of potential forecast models.

The final selection of a single environmental spawner-recruit model for each environmental variable was based on the lowest jacknife prediction error. A stepwise fitting procedure was performed to determine the best multiple predictor model, as mentioned above. The final pool of forecasting models consists of a set of single environmental variable models for each environmental variable and a single multiple variable forecasting model for each of the Pacific herring populations.

4.4. Results

4.4.1. Exploratory Correlation Analysis

Exploratory correlation measures were summed across months and averaged within groups according to those in Table 4.1. The exploratory correlation analysis of Pacific herring recruitment in Norton Sound and Togiak Bay with Bering Sea wind and bottom temperatures revealed very low correlation levels, so the results are not shown.

The Norton Sound and Togiak Bay populations were separated from the Bering Sea group due to the differing ages of recruitment (Figure 4.2).

The overall pattern of correlations for Pacific herring recruitment time series with air and sea surface temperatures is strikingly similar within groups. This pattern indicates the British Columbia group tends toward having negative correlations with temperature, while the remaining groups show positive correlations with temperature. For the temperature data it appears that a lag of three years is stronger than the remaining lags in almost every case except the outer Gulf of Alaska group with sea surface temperatures. The pattern of lag correlations is similar for both of the Bering Sea stocks despite the difference in age of recruitment (Figure 4.2).

The relationship of Pacific herring recruitment and the southern oscillation index resulted in an opposite relationship compared to the temperature pattern. The British Columbia populations show a positive correlation, while the remaining populations tend to be mostly negative. The most important lag for the southern oscillation data appears to be four years, except in the outer Gulf of Alaska group (Figure 4.2). The North Pacific pressure index reveals no patterns or strong correlations at any of the lags, with the possible exception of a three year lag in the British Columbia group. The low magnitude of the correlation measures for the North Pacific pressure index indicates that the higher magnitude seen with other variables is not simply due to random chance (Figure 4.2).

The upwelling data show a tendency toward negative correlations for all of the populations and a possible pattern emerging with a lag of four years. However, the pattern of an opposite relationship between the British Columbia group and the remaining populations does not appear with the upwelling data. There were no corresponding upwelling data for the Bering Sea stocks and exploratory measures are instead shown for Bering Sea ice data. Bering Sea ice cover appears to be correlated with both Norton Sound and Togiak Bay at a lag of two years. A higher level of correlation between the Togiak Bay population and the Bering Sea ice cover occurs at a lag of five years (Figure 4.2).

In an attempt to further elucidate patterns of correlations between Pacific herring recruitment and environmental variables, the exploratory correlation measure was examined by months. For air and sea surface temperature data, the average for the two and five selected stations, respectively, was used to examine the correlations by month. For robustness and graphing convenience, a lowess smoothed line ($f = 0.15$) was fit to the reverse ordered monthly correlation measure data. Based on the similarity in lag correlations (Figure 4.2), the Norton Sound and Togiak Bay populations were combined into a Bering Sea group for the monthly analysis (Figure 4.3).

The lowess smoothed lines in monthly analysis of Figure 4.3 confirm some of the patterns seen in the analysis of annual lags. Sea surface and air temperature data both show consistently opposite relationships between the British Columbia populations and the remaining herring populations (Figure 4.3). The peaks of the smoothed lines seem to be synchronous in these panels and are indications of time periods which may be useful for herring recruitment forecasting. The highest peaks in correlation for the temperature time series appear to be in the time period corresponding to a three year lag. During the fourth year lag, the temperature correlations appear to diminish, but in the first third (last portion of backward time scale) they appear to increase slightly (Figure 4.3).

A similar pattern as in the temperature time series can be seen in the North Pacific pressure index correlations. For the British Columbia group the peak correlation appears during the time period corresponding to a three year lag and there is a slight increase in the first third of the lag -4 time period (Figure 4.3). The Bering Sea, outer Gulf of Alaska, and inner Gulf of Alaska herring groups do not indicate a strong peak in the lag -3 time period, but do show increasing negative correlations in the first third of the lag -4 time period.

The southern oscillation index correlation analysis indicates a consistently positive relationship with the British Columbia populations, which is consistent with the temperature correlations (i.e. negative southern oscillation events are associated with increased temperatures in the North Pacific). Furthermore, the time period of the peak correlation appears to be during the lag -4 time period, which lags the peak temperature correlations appropriately (Niebauer 1988; Niebauer and Day 1989). The Bering Sea, outer Gulf of Alaska, and inner Gulf of Alaska groups indicate a weaker, yet consistent correlation pattern in the lag -4 time period of the southern oscillation index time series. The apparent trough in the outer Gulf of Alaska group during the lag -2 time period is does not fit into the overall pattern for Pacific herring recruitment correlations, but may represent a more local scale phenomenon (Figure 4.3).

The upwelling index indicates no strong correlations with the Pacific herring recruitment. The first and second thirds of the lag -4 time period indicate a possible pattern in the correlations, but this does not fit the paradigm of an opposite relationship between the British Columbia group and the remaining populations (Figure 4.3). Given the low magnitude of the exploratory correlation measure relative to analyses of other variables, it appears that upwelling may not be useful for herring recruitment forecasting.

The life history stages at which the peak correlations occur are important in determining if the observed pattern is appropriate. The temperature and North Pacific pressure correlations indicate that the lag -3 and the first third of the lag -4 time periods are most important (Figure 4.3). Biologically, the lag -3 time period corresponds to the times just before spawning, during spawning and during early larval development. This period is consistent with the dominating paradigm in fisheries science of the early life history critical stage hypothesis. The lag -4 time period corresponds to one year prior to spawning and is not readily reconcilable.

Based on the patterns of the exploratory correlation analysis, a subset of time periods to be explored for use in recruitment forecasting models was developed (Table 4.2). The time period for all of lag -3 and the first third of lag -4 was chosen for the air temperature, sea surface temperature, and North Pacific pressure index time series (Table 4.2). For the southern oscillation and upwelling indices, the lag -4 time period was chosen for exploration of potential herring recruitment forecasting models.

4.4.2. Recruitment Forecast Models

The Ricker spawner-recruit models without environmental data were fit for comparison with models including environmental data (Table 4.3). All of these models have a negative β parameter indicating the presence of overcompensation. Furthermore, the magnitude of the parameters is similar within groups of herring populations. The lowest a and highest β parameters are found in the outer Gulf of Alaska groups, while the highest a and lowest β values tend to occur in the inner Gulf of Alaska group (Table 4.3).

The screening process used for the environmental spawner-recruit models eliminated many potential candidate variables, particularly those not resulting in an improvement in the recent prediction error. The environmental model fits were judged based on the change in the AIC, jacknife prediction, and recent prediction errors relative to the non-environmental spawner-recruit models (Table 4.3). In Tables 4.4-4.7 the change in model performance was computed as the difference for the AIC and percent change for the prediction error estimates. Inferences about the nature and strength of the influence of the environmental parameters can be judged by the sign and magnitude of the γ parameter in the model (Hilborn and Walters 1992).

The Bering Sea herring populations are limited by a small sample size relative to the other populations. The best fit models for each environmental variable are shown in Table 4.4. The best fit for the Norton Sound population with sea surface temperature data occurred in lag -4 and the γ parameter indicated a positive relationship. An improved fit was also obtained with the Bering Sea ice cover and North Pacific pressure index, indicating a negative relationship. The sea surface temperature fit appears to be the best for Norton Sound based on the jacknife prediction error. The Togiak Bay recruitment model resulted in a positive relationship with Bering Sea ice cover in the first third of the year of the lag -5 year and air temperature data from King Salmon, Alaska during the early part of the lag -3 year. The ice cover fit with Togiak Bay herring seems to be the best single variable environmental spawner-recruit model with respect to the jacknife prediction error (Table 4.4).

The outer Gulf of Alaska group of herring populations resulted in very similar forecasting models for each of the environmental variables (Table 4.5). For all four populations in this group positive correlation models resulted with sea surface temperature data and three of the four indicated that the first part of lag -3 resulted in the best fit. The southern oscillation index resulted in improved forecasting models in three of the four populations, indicating a negative relationship to this variable (Table 4.5). Air temperature data resulted in improved recruitment models for Prince William Sound and Southeast Alaska. Large improvements in the prediction error were apparent with Southeast Alaska and air temperature.

The inner Gulf of Alaska group resulted in the most environmentally dependent spawner-recruit models showing improvement in the fits relative to the non-environmental spawner-recruit models. Nearly every population in this group gained improved forecasting power with the addition of each environmental variable (Table 4.6, Figure 4.4). Although the corresponding lag for each environmental variable with the best fit was not always agreed upon for each population, there was some overlap between populations which shared relations with the same environmental variable. Craig and Kah-Shakes shared positive correlations with the Little Port Walter, Alaska air temperature data and Kah-shakes shared a sea surface temperature variable with the Seymour Canal population. The Kah-Shakes group indicated a positive relationship with the North Pacific pressure index, while the other members of the group indicated a negative relationship. Upwelling data revealed a consistent negative relationship with all the members of the inner Gulf of Alaska herring group (Table 4.6).

The British Columbia group of forecasting models were all improved with the sea surface temperature and southern oscillation index data. In every case, the sea surface temperature data revealed a positive relationship and the southern oscillation data resulted in a negative relationship (Table 4.7). Aside from all the populations sharing a relationship with the southern oscillation index, the Queen Charlotte Islands and Central Coast populations shared a relationship with the sea surface temperature data at 131°W Longitude and 53°N Latitude. Nearly all the British Columbia populations showed improvements in all three error measurements for almost every environmental variable.

The multiple regression models for Pacific herring recruitment forecasting did not always result in improved prediction power (Table 4.8). Herring populations not shown in Table 4.8 resulted in single environmental parameter regression models equivalent to one of the models mentioned above as selected by the applied stepwise multiple regression procedure. The multiple regression models for Prince William Sound and Craig were worse in forecasting power than the non-environmental spawner-recruit models. The Queen Charlotte Islands multiple regression model did result in an improvement as measured by the jacknife prediction error, but not by the recent prediction error. The remaining multiple regression models all showed improvement compared to the best single environmental variable forecasting model (Table 4.8).

4.5. Discussion

The exploratory correlation analysis resulted in patterns in which the lags in Table 4.2 were the most significant. The important question is, do these lags correspond to the known information about Pacific herring, the environment and their interrelationships? The predominating view of the North Pacific environment is that it is dominated by the position and intensity of the Aleutian low pressure system as measured by the North Pacific pressure index. Studies have shown that the North Pacific pressure index is related to the southern oscillation index by a lag of approximately 2 months (Niebauer 1988; Niebauer and Day 1989). The North Pacific pressure index is correlated with air and sea surface temperatures, but the lag at which this occurs ranges from 0-6 months (Niebauer 1988; Niebauer and Day 1989). However, there is some conclusive evidence that the southern oscillation index lags behind air and sea surface temperatures by about 5-9 months. So, there is slightly conflicting published results indicating where the North Pacific pressure index fits into the relationship of the southern oscillation index and temperatures.

The correlation analysis revealed the peak correlation times for air and sea surface temperatures occurred at lag -3, while the peak correlation for the southern oscillation index appeared to be at lag -4. If herring are responding to some large-scale environmental forcing, being primarily driven by the southern oscillation, then this is consistent with known relationships. In our study we used the same lag times for the North Pacific pressure index as we did for the temperature data (Table 4.2). In a sense we are assuming that the North Pacific pressure index is closely correlated with the temperature data. This implicates the southern oscillation index as lagging behind the North Pacific pressure index by 6-12 months, which does not completely agree with previous correlation studies (Niebauer 1988; Niebauer and Day 1989).

We reconcile this disagreement in peak correlation lag times for the southern oscillation and North Pacific pressure indices by indicating that in our analysis the links between herring recruitment and the North Pacific pressure index are weaker than the links with the southern oscillation index. The North Pacific pressure index may not be an accurate representation of the intermediary link between the southern oscillation and temperatures in the North Pacific. The southern oscillation index correlations resulted in a consistent pattern that matched the patterns seen in the temperature data (Figures 4.2 and 4.3).

The exploratory correlation analysis did result in an overall pattern of relationships of herring and the environment. It appears that herring are related to both local and global scale environmental variables. A fairly consistent pattern emerged in which British Columbia herring showed opposite relationships as compared to the remaining Northeast Pacific herring populations. This lends credibility to previous studies indicating the grouping structure used in this analysis is a real phenomenon

(Chapter 3, Williams and Quinn *in preparation*; Zebdi and Collie 1995; Zheng 1996). Further, the lags at which these relationships occurred was fairly consistent across all the herring populations, indicating similar responses to the environment (Figures 4.2 and 4.3). The dominant pattern of environmental forecasting variables indicated that temperatures during the first third of lag -3 and the southern oscillation index during the first third of lag -4 generally resulted in the best forecasting models (Tables 4.4-4.7). Additional analysis of these lag correlations with annual environmental variables averaged across months indicated the use of shorter time scales, such as months or yearly thirds, are more revealing (Appendix, Figures A1-A3). Generally, the North Pacific pressure and upwelling indices did not result in the best models and appeared inconsistent in their usefulness for forecasting Pacific herring recruitment.

The multiple environmental variable models did not always result in improvements in the prediction errors, relative to the non-environmental spawner-recruit models (Table 4.8). This is a direct result of the use of the AIC in the multiple environmental variable model selection algorithm instead of the jacknife or recent prediction errors which were used for selecting single environmental variable models. The AIC does not always agree with the prediction error as seen in Figure 4.5. The discrepancies are a direct result of the differences between model selection based on modified residual sums of squares (AIC and BIC) and prediction errors (jacknife, recent, and bootstrapping). Since the primary purpose for the models presented in this research is forecasting, the jacknife and recent prediction errors are better measures of model goodness-of-fit.

The mechanism by which the environment is influencing herring recruitment fluctuations may be acting in a direct or indirect means. The strength of the correlations suggests that temperature is more influential than the rest of the environmental parameters. The only way in which air temperature comes in direct contact with herring is during low tides after the adhesive eggs have been attached to rocks and plants in the intertidal zone. Previous studies have shown that egg loss due to air exposure can be high, but it is not clear if this can ultimately determine future levels of recruitment (Jones 1972; Rooper 1996; Rooper et al., *in prep.*).

Water temperatures could have direct effects on egg condition, egg mortality, larval mortality, and timing of spawning (Blaxter 1992; Hay 1985; Taylor 1971). Egg and larval mortality appear to be unlikely since most of the sea surface temperature correlations appear to be stronger with sampling sites located offshore, away from coastal areas. Typically the coastal water temperatures are highly variable and localized due to terrestrial influences. However, given the annual migration patterns of adult Pacific herring, it is possible for offshore water temperatures to affect the condition of eggs in spawning adults. This hypothesis was suggested by Zebdi and Collie (1995) in their analysis of Sitka Sound herring.

How water temperature effects maturation of herring eggs and ultimately recruitment in adults is important to understanding the plausibility of such a hypothesis. It appears unlikely that fecundity of adult herring is affected by temperature changes, since there does not appear to be any evidence of this from the fishery (which harvests eggs directly) or spawn deposition surveys. It is possible that hatching success and/or subsequent larval survival may be affected by reduced egg condition (McGurk et al. 1993).

Another plausible hypothesis for the mechanism by which herring recruitment is affected by water temperatures during the time of gonad maturation is through indirect effects. It is likely that the correlation of herring recruitment with air and sea surface temperatures is simply a proxy for some other more direct influence. The fact that the direction of the correlations with temperature change from more northerly herring populations to more southerly populations is suggestive of an indirect affect. Unfortunately temperature could be seen as a proxy for nearly any mechanism from predator abundance to food availability.

The most likely scenario is that sea surface temperatures in the first third of the year (the peak time for herring correlations) affect the relative timing of Pacific herring spawning to subsequent physical ocean conditions. Ocean conditions such as the onset, strength, and/or duration of both the spring bloom and coastal currents may affect herring survival, depending on the relative timing of spawning. The dominate paradigm in fisheries leans toward the larval stage of herring life history as being the most important for determining year class strength (Hjort 1914, Cushing 1975, Iles and Sinclair 1982).

Previous studies have indicated that offsets in timing of herring spawning and set-up of ocean conditions can affect Pacific herring survival (McGurk et al. 1993; McGurk 1989; McGurk 1984; Stevenson 1962). However, these studies disagree as to the ultimate source of mortality. Both food availability (Cushing's (1975) match-mismatch hypothesis) and retention mechanisms (Iles and Sinclair's (1982) member-vagrant hypothesis) have been implicated in previous studies of Pacific herring.

The drastic change in the nature of the correlations from Gulf of Alaska populations and British Columbia populations suggests that different mechanisms may be operating in each area. Stevenson (1962) and McGurk (1989) studied Pacific herring from British Columbia and suggested that advection may be the most important mechanism for herring larval survival. Another study by McGurk et al. (1993) examined Pacific herring in Southeast Alaska and suggested that egg condition and predation may be more important sources of mortality for Pacific herring. This study also suggested that advection was a minor source of larval loss/mortality. Perhaps British Columbia herring are more susceptible to advection forces, compared to Gulf of Alaska herring, which may be affected by other forces, such as predation and/or egg condition.

There appear to be some differences in coastal current conditions between Southeast Alaska and British Columbia. All of the coastal Northeast Pacific Ocean is affected by freshwater run-off, which is comparable to the discharge from the Mississippi River plume. The seasonal freshwater discharge from numerous small streams creates a cross-shelf salinity gradient which drives a poleward coastal baroclinic jet named the Alaska Coastal Current (ACC) (Freeland et al. 1984; Royer 1982; Schumacher et al.

1989). Off the coast of Vancouver Island, the coastal current is named the Vancouver Island Coastal Current (VICC), which appears to undergo seasonal changes in direction (Hickey et al. 1991; Freeland et al. 1984). The flow of the VICC becomes much more variable during the spring months, with a complete reversal in direction developing in the southerly areas by May. A little further to the north, around the Queen Charlotte Islands, there appears to be a southerly flowing coastal current, which switches to a northerly flow during the spring months (Freeland et al. 1984). Further north, it appears that the coastal current remains in the northerly direction year-round, with some seasonal weakening (Royer 1982).

Clearly, there are differences in the coastal currents between Southeast Alaska and British Columbia. The problem is discerning how temperature anomalies are affecting these coastal currents. The currents are clearly affected by seasonal changes in freshwater discharge, with the British Columbia currents experience a spring transition (Freeland et al. 1984). Monthly freshwater discharge appears to be at its minimum during the winter months, with a steady increase toward a season maximum in summer/fall. Perhaps warm temperature anomalies in spring result in increased freshwater discharge, thereby disrupting the spring transition in coastal currents in British Columbia. This implies that the spring transition in coastal currents is favorable to Pacific herring survival in British Columbia, thereby justifying the negative correlation of herring recruitment and temperature. In Southeast Alaska, the coastal current remains northward all season long, and perhaps strengthening of this current during the spring months is favorable to herring. Deviations from this relationship of Pacific herring recruitment and coastal currents could further be explained by wind anomalies that also affect the ACC and VICC (Freeland et al. 1984; Royer 1982; Schumacher et al. 1989).

Despite not knowing the exact mechanism governing year class fluctuations, we have demonstrated a clear indication that Pacific herring populations in the North Pacific are closely linked to the environment and that this can be utilized for the purposes of improving upon current methods of forecasting recruitment. The forecast models contained herein can be applied directly for herring forecasts, but should probably just serve as a template for annual computations of herring recruitment. The time scale of environmental data used for the forecasting models in this research was averaged over yearly thirds for convenience. Further model improvements may be attained by examination on a monthly scale, for which data is typically available.

Clearly, we have not presented evidence of the mechanism by which the environment acts to influence Pacific herring recruitment. In fact the additional variation explained by the forecasting models in this research is not nearly enough to cease any further research into causes of Pacific herring recruitment fluctuations (Figure 4.4). It is likely that the actual mechanism by which the environment acts on Pacific herring recruitment changes from time to time. The dominant pattern for Pacific herring recruitment time series indicates a high degree of variability, with strong year class events occurring every 3-10 years. The strong year classes can be as much as 429 times more than the weakest recruitment event of the same time series (Zheng 1996). Perhaps a closer examination of the strong year class events and local environmental conditions may indicate possible mechanisms that influence Pacific herring recruitment.

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TABLE 4.1. Pacific herring population associations from the Northeast Pacific Ocean as suggested by Williams and Quinn (1998).

Bering Sea **(BS)**	Outer Waters Gulf of Alaska **(OGOA)**	Inner Waters Gulf of Alaska **(IGOA)**	British Columbia **(BC)**
Norton Sound (NOR)	Kodiak/Kamishak Bay	Seymour Canal	Queen Charlotte Islands
Togiak Bay (TOG)	Prince William Sound	Craig	Central Coast
	Sitka Sound	Kah-Shakes	West Vancouver Island
	Southeast Alaska	Prince Rupert	Strait of Georgia

TABLE 4.2. Lagged time periods based on exploratory correlation analyses selected for use in forecasting models.

	Lag -1			**Lag -2**			**Lag -3**			**Lag -4**		
Yearly Third	**3**	**2**	**1**	**3**	**2**	**1**	**3**	**2**	**1**	**3**	**2**	**1**
Sea Surface Temperature							X	X	X			X
Air Temperature							X	X	X			X
Southern Oscillation										X	X	X
North Pacific Pressure							X	X	X			X
Upwelling										X	X	X

TABLE 4.3. Ricker type spawner-recruit model fits and prediction errors for Pacific herring populations in the Bering Sea and Northeast Pacific Ocean.

		Ricker Parameters			**Prediction Error**	
Pacific Herring Populations	**n**	***a***	***β***	**AIC**	**Jacknife**	**Recent**
Norton Sound	13	3.38	-0.0780	1.37	1493	699
Togiak Bay	16	2.65	-0.0076	3.83	212630	112979
Kodiak/Kamishak Bay	38	1.40	-0.0087	39.63	83660	8220
Prince William Sound	47	1.96	-0.0138	22.20	102174	14329
Sitka Sound	24	2.05	-0.0051	15.88	214027	78140
Southeast Alaska	65	2.55	-0.0158	35.20	299589	191947
Seymour Canal	18	4.73	-0.6928	-3.85	1463	4423
Craig	20	4.07	-0.1403	26.09	66315	10655
Kah-Shakes	18	3.51	-0.1421	-13.11	7526	2299
Prince Rupert	43	3.77	-0.0517	3.27	144772	835799
Queen Charlotte Islands	43	3.96	-0.0865	18.32	140895	22271
Central Coast	43	3.29	-0.0616	-3.86	43723	1332
West Vancouver Island	43	3.35	-0.0346	5.16	69450	48046
Strait of Georgia	43	3.73	-0.0225	-41.79	159054	51084

TABLE 4.4. Best Ricker type spawner-recruit model fits and prediction errors for a single environmental variable for Pacific herring populations in the Bering Sea group.

Environmental Variable	Yearly Third	Lag	n	Ricker Parameters			AIC	Prediction Error	
				a	*β*	*γ*		Jacknife	Recent
Norton Sound									
SST (165W 55N)	1	4	13	3.35	-0.077	0.276	1.31	-8.5%	-10.6%
Ice	1	3	13	4.16	-0.095	-0.635	0.44	-7.3%	33.4%
NPPI	3	3	13	3.47	-0.080	-0.225	1.19	-0.5%	-8.2%
Togiak Bay									
Ice	1	5	16	2.22	-0.00644	0.449	-2.28	-13.8%	-65.9%
AT (King Salmon	1	3	15	2.30	-0.00637	0.525	-3.22	1.1%	-4.5%

TABLE 4.5. Best Ricker type spawner-recruit model fits and prediction errors for a single environmental variable for Pacific herring populations in the outer Gulf of Alaska group.

Environmental Variable	Yearly Third	Lag	n	Ricker Parameters a	β	γ	AIC	Prediction Error Jacknife	Recent
Kodiak/Kamishak Bay									
SST (145W 57N)	2	3	17	2.09	-0.0228	0.457	-26.35	-86.4%	-11.0%
NPPI	1	3	26	2.31	-0.0423	-0.793	-16.51	-73.0%	-8.3%
Prince William Sound									
SOI	2	4	47	1.93	-0.0132	-0.327	-1.73	-2.0%	-4.6%
AT (Kodiak)	2	3	47	1.99	-0.0144	0.175	0.89	-1.3%	-12.0%
SST (143W 57N)	1	3	33	2.30	-0.0219	0.533	-10.47	4.2%	-49.5%
UPW	2	4	32	2.11	-0.0217	-0.196	-5.67	10.4%	-49.9%
NPPI	1	3	32	2.03	-0.0198	-0.211	-5.43	10.6%	-53.4%
Sitka Sound									
SOI	1	4	24	2.32	-0.0174	-0.384	0.37	-9.2%	-38.5%
SST (135W 55N)	1	3	24	1.80	0.0057	-0.310	0.65	-4.5%	-41.6%
Southeast Alaska									
AT (Sitka)	1	3	65	2.57	-0.0163	0.428	-5.82	-5.0%	-42.9%
SOI	2	4	65	2.53	-0.0153	-0.149	0.82	-0.8%	-8.4%
SST (133W 51N)	1	3	62	2.54	-0.0148	0.323	-1.72	-0.6%	-18.6%

TABLE 4.6. Best Ricker type spawner-recruit model fits and prediction errors for a single environmental variable for Pacific herring populations in the inner Gulf of Alaska group.

Environmental Variable	**Yearly Third**	**Lag**	**n**	**Ricker Parameters**			**AIC**	**Prediction Error**	
				a	β	γ		**Jacknife**	**Recent**
Seymour Canal									
AT (Annex Cr.)	1	3	14	4.92	-0.744	0.126	-22.19	-70.3%	-82.0%
SST (137W 57N)	1	3	18	4.62	-0.648	0.283	-3.57	-19.4%	-7.3%
NPPI	1	3	18	4.70	-0.681	-0.192	-0.20	-11.5%	-12.5%
SOI	2	4	18	4.68	-0.673	-0.244	-0.88	-8.2%	-8.5%
UPW	1	4	18	4.74	-0.697	-0.161	0.34	-5.2%	-1.7%
Craig									
SST (133W 51N)	1	4	20	4.23	-0.162	0.578	-0.26	-8.9%	-49.2%
NPPI	1	4	20	4.12	-0.147	-0.394	0.63	-6.9%	-47.2%
UPW	1	4	20	4.36	-0.180	-0.598	0.09	-4.8%	-25.2%
AT (L. Port Walter)	1	4	18	4.41	-0.208	0.922	-1.67	0.5%	-29.0%
Kah-Shakes									
SST (137W 57N)	1	3	18	3.65	-0.156	0.327	-3.78	-11.5%	-15.6%
NPPI	3	3	18	3.39	-0.129	0.113	0.02	-0.8%	-18.8%
UPW	2	4	18	3.31	-0.121	-0.251	-0.53	-0.4%	-0.4%
AT (L. Port Walter)	1	4	16	3.63	-0.150	0.013	4.81	14.2%	-28.9%
Prince Rupert									
AT (Prince Rupert)	2	3	40	3.91	-0.063	0.521	-9.73	-50.2%	-75.3%
SST (135W 55N)	2	3	43	3.84	-0.056	0.331	-3.23	-12.7%	-6.0%
SOI	1	4	43	3.77	-0.052	-0.256	-2.19	-7.6%	-20.4%
NPPI	1	4	43	3.79	-0.053	-0.187	-0.67	-2.3%	-5.5%
UPW	1	4	43	3.93	-0.062	-0.289	-1.36	-0.4%	-0.8%

TABLE 4.7. Best Ricker type spawner-recruit model fits and prediction errors for a single environmental variable for Pacific herring populations in the British Columbia group.

Environmental	**Yearly**			**Ricker Parameters**				**Prediction Error**	
Variable	**Third**	**Lag**	**n**	α	β	γ	**AIC**	**Jacknife**	**Recent**
Queen Charlotte Islands									
SST (131W 53N)	3	3	41	3.77	-0.079	-0.461	-9.87	-25.3%	-24.3%
UPW	2	4	43	4.06	-0.093	-0.470	-5.65	-10.2%	-6.7%
SOI	3	4	43	3.98	-0.087	0.274	-1.40	-2.7%	-30.4%
NPPI	3	3	43	4.00	-0.089	0.108	0.95	-1.2%	-9.6%
AT (St. James)	3	3	40	3.94	-0.080	-0.093	-3.11	4.8%	-20.0%
Central Coast									
SST (131W 53N)	1	3	41	3.01	-0.047	-0.468	-11.01	-39.4%	-81.3%
SOI	2	4	43	3.28	-0.061	0.151	0.78	-0.3%	-15.5%
West Vancouver Island									
SST (133W 51N)	1	3	43	3.39	-0.036	-0.430	-7.73	-23.6%	-42.1%
AT (Pachena)	1	3	40	3.37	-0.034	-0.360	-6.67	-21.7%	-83.9%
NPPI	1	3	43	3.36	-0.035	0.376	-7.27	-16.0%	-49.5%
SOI	1	4	43	3.43	-0.038	0.208	-1.56	-7.0%	-40.0%
UPW	3	4	43	3.25	-0.031	-0.165	-0.92	-1.8%	-27.3%
Strait of Georgia									
SST (129W 49N)	1	3	43	3.71	-0.022	-0.179	-2.47	-7.5%	-17.5%
SOI	2	4	43	3.75	-0.023	0.091	0.97	-1.4%	-1.8%

TABLE 4.8. Best Ricker type spawner-recruit model fits and prediction errors for multiple environmental variables for Pacific herring populations from the Bering Sea and Northeast Pacific Ocean.

Environmental Variable	Yearly Third	Lag	n	Ricker Parameters			AIC	Prediction Error	
				a	β	$\{\gamma_1 \cdots \gamma_i\}$		Jacknife	Recent
Kodiak/Kamishak Bay			17	2.75	-0.046		-36.32	-81.9%	-77.0%
UPW	1	4				-0.081			
SST (147W 57N)	1	3				0.517			
AT (Kodiak)	3	3				0.677			
Prince William Sound			23	2.86	-0.033		-24.64	20.1%	28.3%
UPW	2	4				-0.618			
SST (143W 57N)	2	3				-0.990			
SST (143W 57N)	1	4				-0.358			
SST (149W 57N)	2	3				1.056			
Seymour Canal			13	4.76	-0.681		-25.20	-78.6%	-88.5%
AT (Annex Cr.)	1	3				0.103			
AT (Annex Cr.)	3	3				0.177			
SST (137W 57N)	1	3				0.154			
SST (133W 51N)	1	3				0.072			
Craig			18	4.07	-0.146		-2.26	11.2%	281.5%
SST (135W 55N)	1	4				-1.493			
AT (L. Port Walter)	1	4				2.056			
Kah-Shakes			16	1.58	0.057		-9.33	-1.8%	-95.9%
SST (135W 57N)	3	3				0.243			
SST (137W 57N)	2	3				0.661			
UPW	2	4				-0.488			
AT (L.Port Walter)	1	4				0.482			
Prince Rupert			38	3.95	-0.068		-14.42	-60.9%	-85.8%
AT (Prince Rupert)	2	3				0.629			
SST (131W 55N)	2	3				0.286			
SOI	1	4				-0.324			
SST (131W 51N)	2	3				-0.328			
Queen Charlotte Islands			41	3.87	-0.085		-13.32	-87.5%	433.3%
SST (131W 53N)	3	3				-0.444			
UPW	2	4				-0.367			
W. Vancouver Island			41	3.39	-0.036		-11.06	-32.5%	-69.6%
SST (131W 53N)	1	3				-0.236			
SST (133W 51N)	1	4				-0.314			
NPPI	1	3				0.267			

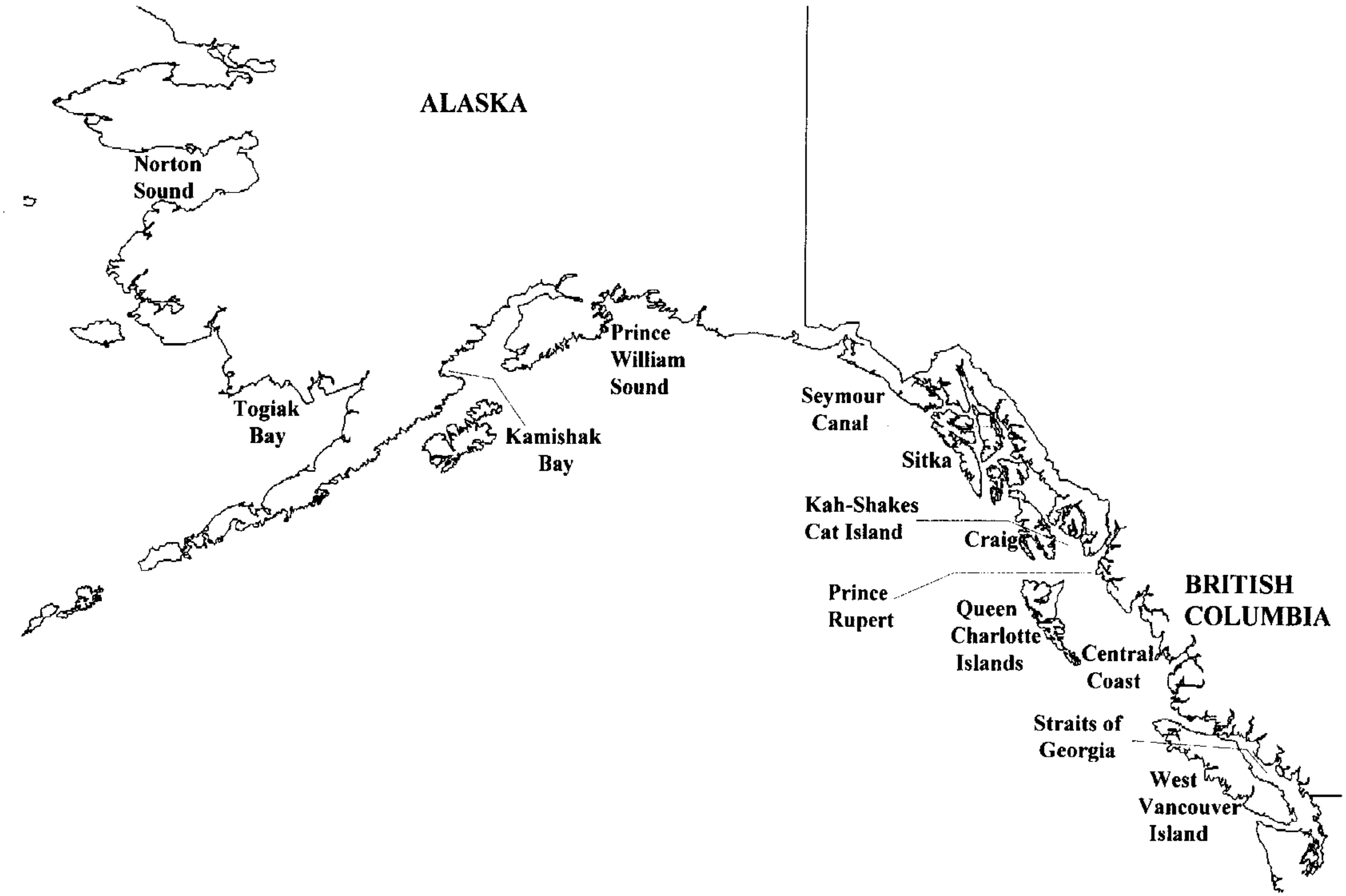

FIGURE 4.1. Map of Alaska and British Columbia coasts showing the location of major Pacific herring, Clupea pallasi, populations.

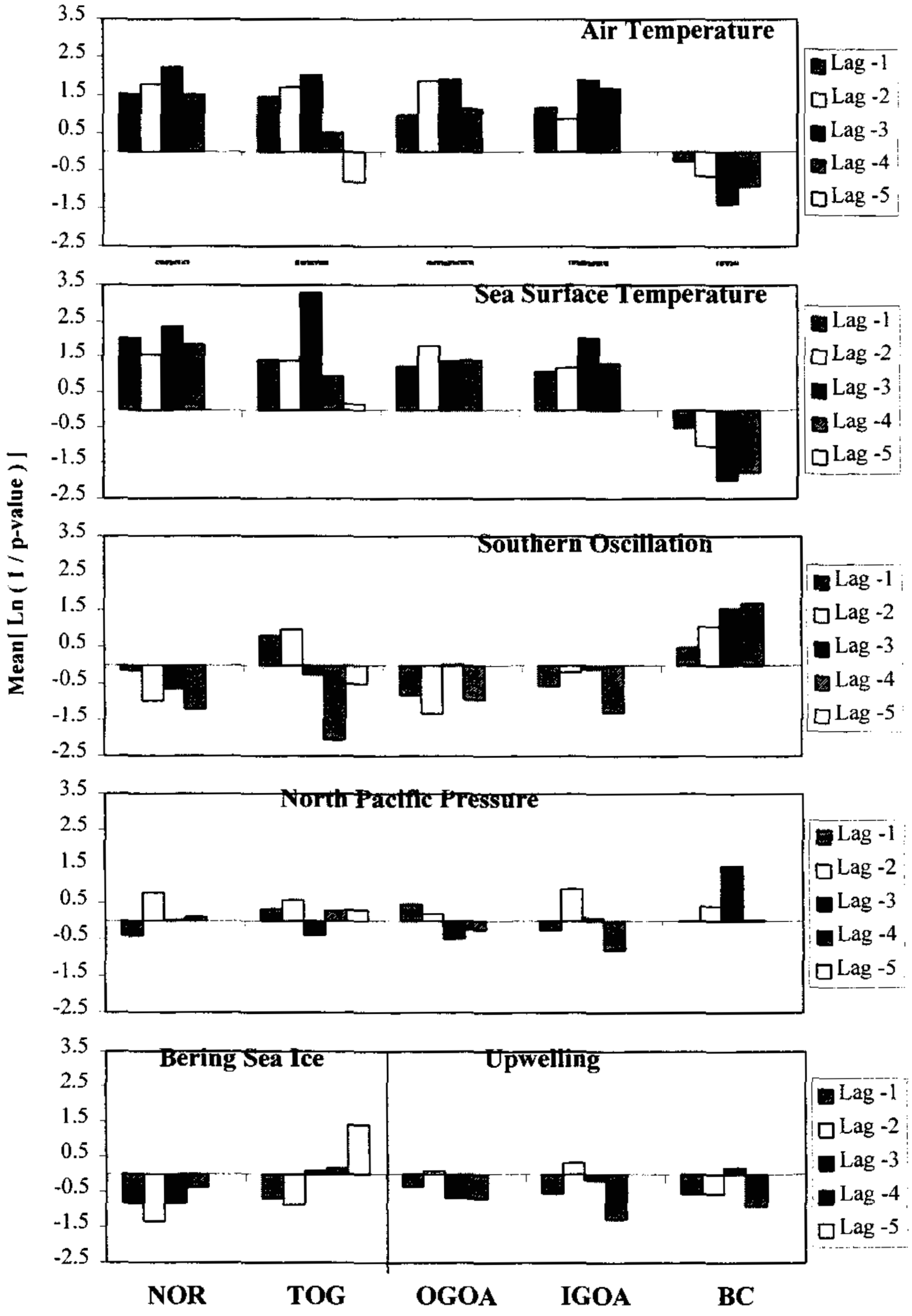

FIGURE 4.2. Mean exploratory correlation measures for various environmental variables lagged from 1 to 5 years for the Norton Sound (NOR) and Togiak Bay (TOG) herring populations and the outer Gulf of Alaska (OGOA), inner Gulf of Alaska (IGOA), and British Columbia (BC) herring population associations.

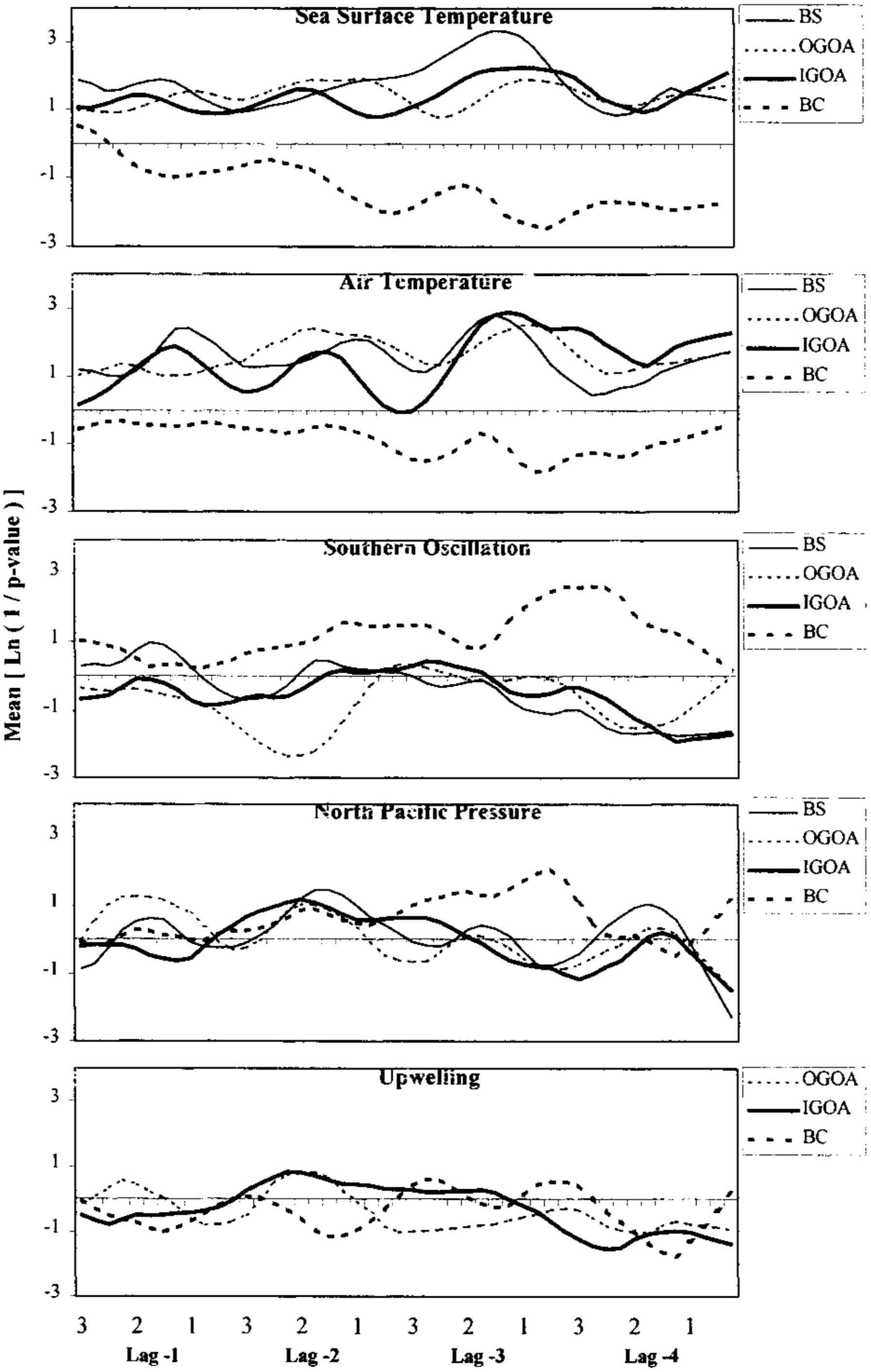

FIGURE 4.3. Lowess smoothed line fits (fraction smoothed = 0.15) for monthly (tick marks) exploratory correlation measures of environmental variables lagged from 1 to 5 years (labeled as thirds) for the Bering Sea (BS), outer Gulf of Alaska (OGOA), inner Gulf of Alaska (IGOA), and British Columbia (BC) herring population associations.

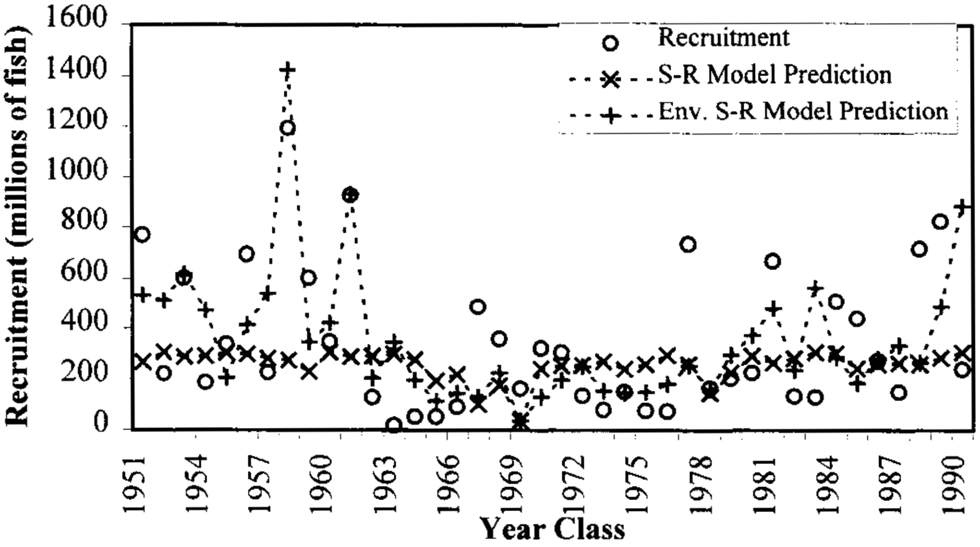

FIGURE 4.4. Recruitment values and predictions for Prince Rupert herring using a Ricker type spawner-recruit model with and without the addition of air temperature data from Prince Rupert.

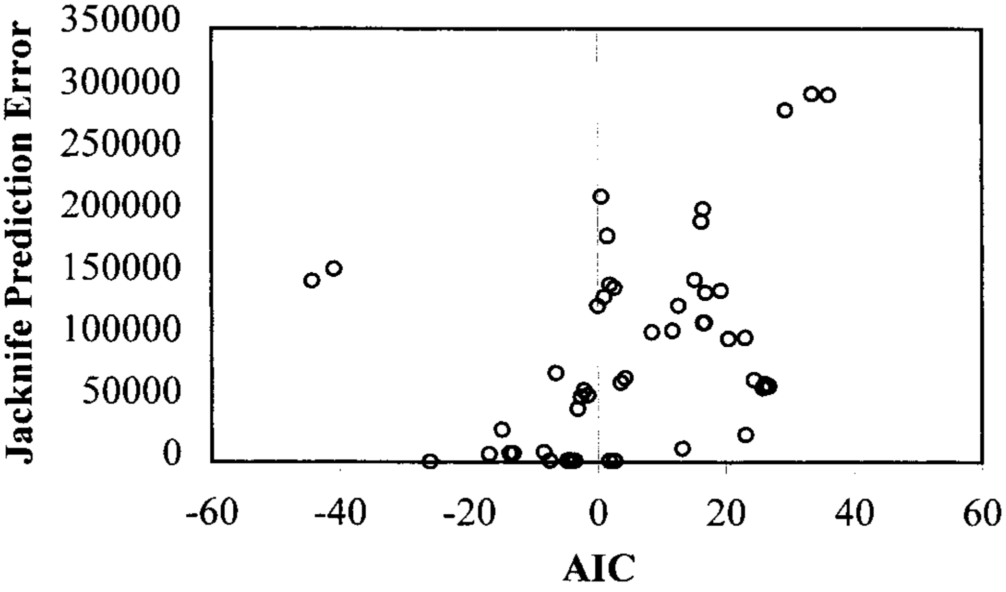

FIGURE 4.5. Relationship of the Akaike Information Criterion (AIC) and jacknife prediction error estimates from various Pacific herring forecasting models.

Conclusions

The field of fishery science exists because of the need to conserve renewable aquatic natural resources. Fishing is one of the more important activities which utilizes living aquatic resources. Recent history has demonstrated the capability of human fishing practices to deplete fish abundances in the oceanic environment, reinforcing the need for more effective management. The ideal fisheries management system would contain a survey of necessary information, statistical analysis of this information, and simulation of future estimates for various management actions. To this end the research presented herein provides an improved population model for Norton Sound herring (Chapter 1), a method for computing error levels of model estimates (Chapter 2), and a description of population interrelationships and recruitment forecast models for the major Pacific herring populations in the Bering Sea and Northeast Pacific Ocean (Chapter 3 and 4).

One of the more important features of any fisheries management system is the ability to accurately forecast population estimates and the effects of management scenarios on these estimates. Age-structured models such as the one presented in Chapter 1 can be used to forecast cohort abundances. The use of cross validation techniques such as the bootstrapping procedure presented in Chapter 2 are useful for computing error levels for model estimates. In this research the error calculations are presented as a separate process from population modeling. More advanced population models of Pacific herring could include error estimates as part of the fitting process (Ludwig and Walters 1989; Megrey 1989). Alternately, a population model could be framed in a Bayesian context, requiring independent prior information, but allowing for the calculation of probability distributions about parameter estimates (Kinas 1996; McAllister and Ianelli 1997; McAllister et al. 1994). Ultimately, the goal of population modeling is to provide forecasts of population parameters including error levels to the management process.

One of the more important forecasting parameters for fisheries management is the forecasting of recruitment or year class strength. Typically the forecasting of recruitment is a separate modeling process from the population assessment mentioned above (Quinn and Deriso *in press*). Depending on the maximum age of the species of concern, future recruitment may be a minor component of future biomass estimates and using an average of the most recent recruitment years may suffice. Pacific herring are relatively short lived and experience large fluctuations in their recruitment time series. Often times one year of recruitment will dominate the biomass of a particular herring population for several years. For this reason, accurate recruitment forecasts for Pacific herring can be important to the overall forecasting of herring data.

Recruitment in any fish population is ultimately dependent on the size of the spawning stock and for this reason spawner-recruit models have evolved. When these models are fit to spawner-recruit data, the fit often appears inadequate for accurate forecasting of recruitment. For this reason, research on the recruitment of fish populations, as in Chapter 3 and 4, is essential to producing improved recruitment forecasting models.

Pacific herring recruitment fluctuations have been implicated as being driven by both physical and biological forces. It is clear that all populations must experience biological limitations, typically in the form of a density-dependent relationship, usually with some type of compensation. Compensation occurs because there is an overload of individuals at some point in their life history. The overload may occur as early as the egg stage for herring, during which multiple layers of eggs will begin to suffocate underlying layers. Or, the compensation may occur in the larval phase during which competition for food or cannabilism may become a large source of mortality. In this research, density-dependence was modeled using the Ricker type spawner-recruit function. One assumption of this type and most other spawner-recruit models, is that compensation effects occur at a fairly constant population abundance level. It is possible that compensation is dependent on other factors such as, environmental conditions and food availability.

Pacific herring recruitment time series are highly variable with successful and unsuccessful recruitment years. Time series of herring indicate that large recruitment events are less frequent than smaller recruitment events. This may indicate that recruitment levels are normally suppressed and when a chain of favorable events occurs, then a large year class is produced. This could be viewed much like a Markov chain where there are discrete events in which, depending on the conditions during this time, will influence the conditions in the next time period. The overall probability of a successful year class could be viewed as a 'law of the minimum' scenario, in which any time period may inhibit a strong year class and only when conditions are right in every time period does a strong year class emerge.

The analysis in Chapter 3 indicated Pacific herring populations exhibit highly synchronous large year class events. This synchronicity suggests favorable large-scale environmental influences may be the driving force behind the recruitment fluctuations. However, the inconsistency in the population overlap at which the year class events occur in Pacific herring populations is suggestive of a high degree of variability in the spatial scale at which the large-scale environment force is acting. This implies that these herring populations might still behave independently, yet be driven by some shared large-scale influence. The associations suggested in Chapter 3 indicate populations seem to be responding similarly at a sub-global scale. There appear to be distinct boundaries to the geographic range for herring population similarities, yet there is evidence of shared influences on the global scale as well. This suggests that the scale at which the environment is acting on Pacific herring recruitment may be variable.

The exploratory correlation analysis performed in Chapter 4 indicated that the environment influences recruitment during the same life history stage. The dominating pattern of correlations suggested temperatures affected Pacific herring recruitment during the year of spawning, hatching, and larval development. A weaker correlation occurred between the southern oscillation index and the time period one year prior to the year in which temperature was correlated. The difference in the time of correlation for temperature and the southern oscillation is consistent with the idea that the southern oscillation effects the whole North Pacific, specifically temperatures at a lag of 5-9 months (Niebauer 1988; Niebauer and Day 1989). Still, the correlation of Pacific herring recruitment with temperatures did not explain all the variation in the spawner-recruit models. The increase in correlation from the southern oscillation to the temperature data suggests this is the direction towards the physical mechanism which ultimately determines Pacific herring recruitment. Furthermore, this suggests that the spatial scale at which the environment is acting on herring recruitment is at a comparable scale for temperature variability and at least smaller than that of the southern oscillation scale.

The time of the peak correlations suggests that survival during the early life history stages, in particular the larval stage, is affected by the physical environment. The classical views of recruitment fluctuations, such as Cushing's (1975) match-mismatch and Iles and Sinclair's (1982) member-vagrant hypotheses are both plausible explanations. The distinct change in the direction of the relationship between British Columbia stocks (minus Prince Rupert) and Southeast Alaska (including Prince Rupert) stocks is suggestive that temperature is serving as a proxy for some other physical or biological influence on herring recruitment. Previous studies, have suggested that coastal currents and advection processes play an important role in Pacific herring larval survival and there appaers to be distinct differences in the coastal currents between Britsh Columbia and Southeast Alaska (Freeland et al. 1984; McGurk 1989; Royer 1982; Stevenson 1962). However, the exact nature of the relationships of temperature to coastal currents and their subsequent relationship to Pacific herring recruitment remains vague and should serve as an area for further research.

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Appendix

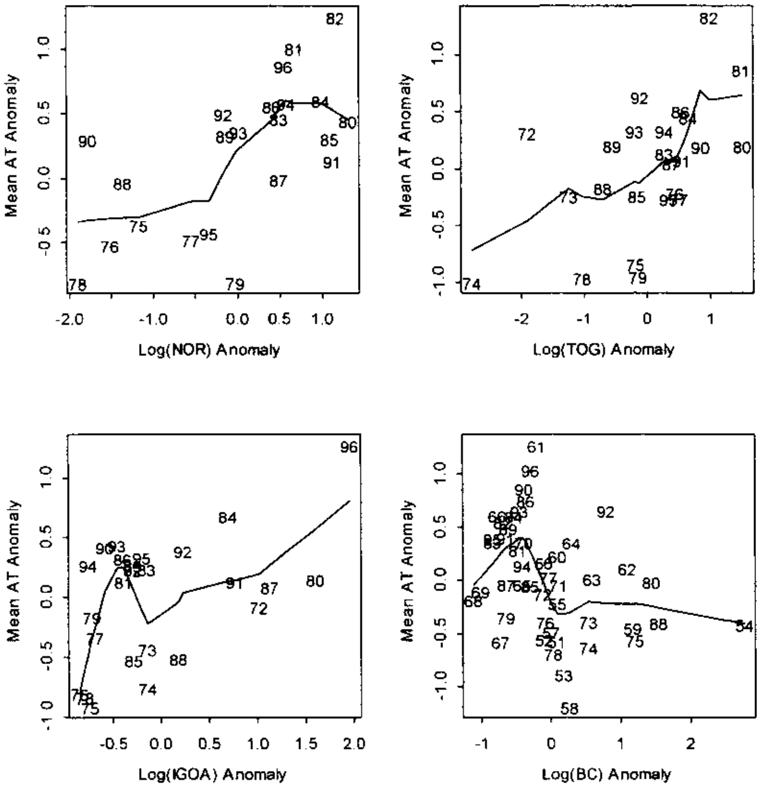

Figure A1. Relationship of mean annual air temperature anomalies (two stations at lag -3) and mean log transformed recruitment anomalies with lowess smoothed lines (f=0.15). Points labeled as year of recruitment anomaly.

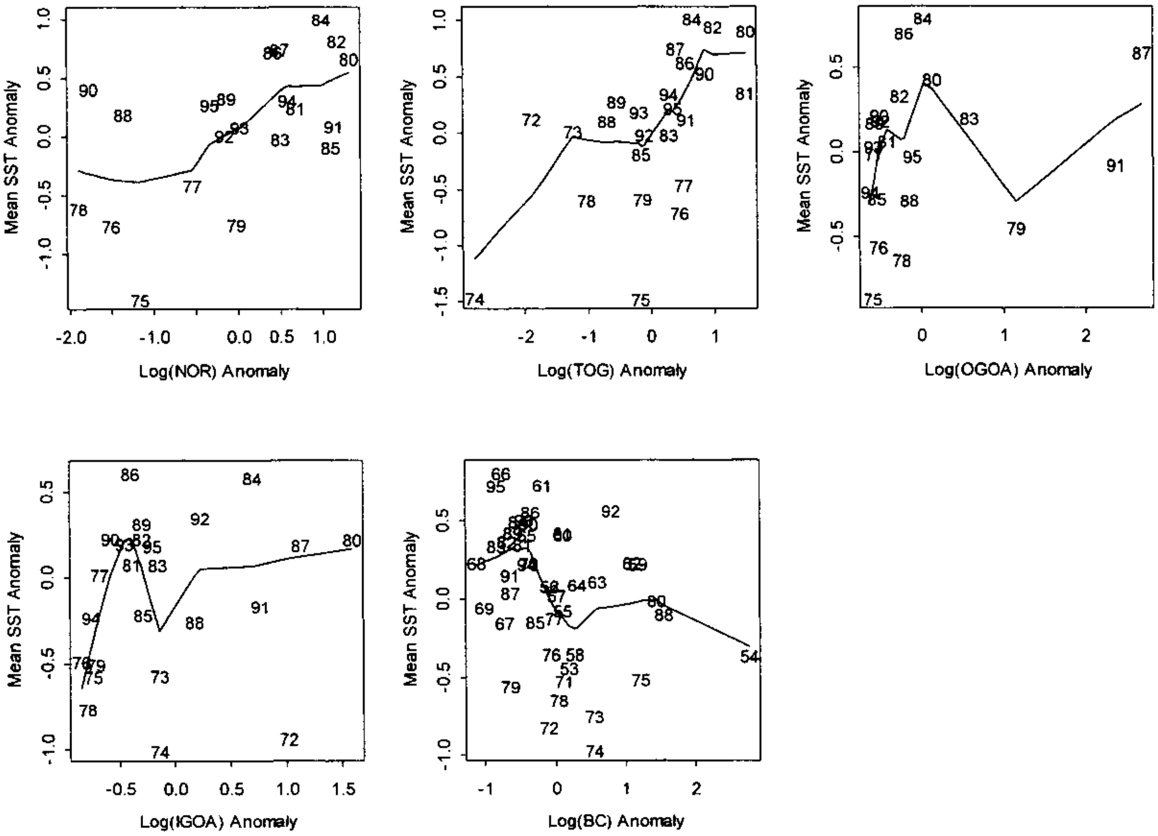

Figure A2. Relationship of mean annual sea surface temperature anomalies (five stations at lag -3) and mean log transformed recruitment anomalies with lowess smoothed lines (f=0.15). Points labeled as year of recruitment anomaly.

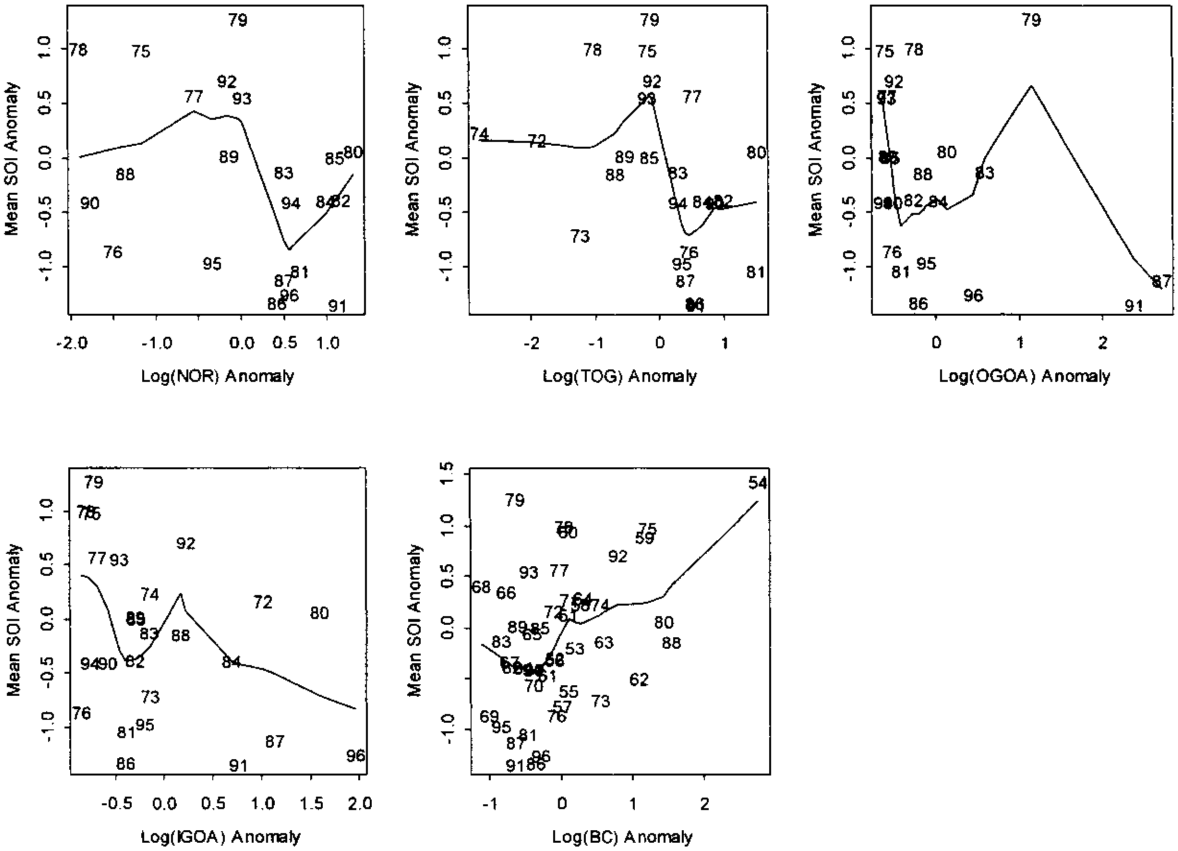

Figure A3. Relationship of southern oscillation anomalies (lag -4) and mean log transformed recruitment anomalies with lowess smoothed lines (f=0.15). Points labeled as year class of recruitment anomaly.