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**PACIFIC HERRING NATAL HABITATS, PRINCE WILLIAM SOUND  
EXXON VALDEZ RESTORATION PROJECT 97166 FINAL REPORT**



by

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*Exxon Valdez* Oil Spill  
Restoration Project Final Report

Herring Natal Habitats  
Restoration Project 97166  
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## Herring Natal Habitats

### Restoration Project 97166 Final Report

**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 pallasii*) in Prince William Sound, Alaska. 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. Herring biomass estimated from spawn deposition surveys was 25,852 tonnes in 1994, 31,245 tonnes in 1995, 35,021 tonnes in 1996, and 21,839 tonnes in 1997. Biomass estimates obtained from spawn deposition and acoustic surveys were not significantly different in 1997.

**Key Words:** Exxon Valdez Oil Spill, herring, *Clupea pallasii*, spawn deposition surveys, spawning biomass, egg loss, herring recruitment, Prince William Sound, stock assessment.

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## Introduction

This project estimated the biomass of spawning adult Pacific herring *Clupea pallasii* 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 (Brown 1995). 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 (Brown 1995). 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 (Brown 1995). 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 field samples. In addition, measurements of oil in tissues from mussels 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 (Brown 1995).

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  $\pm 25\%$  of the true value 95% of the time, and describe the age, sex and size composition of the spawning population.
  - 1a. Quantify egg loss rates from spawning areas between egg deposition and hatching.
  - 1b. Incorporate variable egg loss rates into spawn deposition biomass estimates.
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

$$B = TB' \quad 1$$

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

$$Var(B) = T^2 Var(B') + (B')^2 Var(T) - Var(T)Var(B') \quad 2$$

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  $\pm 25\%$  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<sup>2</sup> 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 quadrat 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

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

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

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

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

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

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

The mean quadrat egg count in transect i was estimated from

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

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

The variance of T was estimated from

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

where

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

variance among transects,

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

variance among quadrates,

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

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

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

proportion of possible transects sampled, and

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

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

Diver estimates of the number of eggs in each quadrat 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 quadrat. All egg-containing vegetation within the quadrat 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. Calibration 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 1/4 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

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

where  $dc$  was the diver count,  $lc$  was the lab count, and  $\beta_{jk}$  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

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

where  $adc_{ij}$  was the adjusted diver count for quadrat  $j$  in transect  $I$  and  $dc_{ij}$  was the original diver count for quadrat  $j$  in transect  $i$ . The variance for the adjusted diver counts was

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

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

$$B' = \frac{\bar{W}S}{F(\bar{W}_f)} 10^3 \quad 16$$

where  $\bar{W}$  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,  $F(\bar{W}_f)$  is the estimated fecundity at the average weight of adult female herring in each summary area, and  $10^3$  is a conversion factor.

Estimates of average weight, sex ratio and fecundity were not independent because they were all estimated from the same samples. Therefore, the variance of B' was approximately

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

It was not possible to estimate the terms  $Cov(\bar{W}, S)$  and  $Cov[S, F(\bar{W}_f)]$ , because S was estimated from pooled or single AWL samples (depending on availability of fish). The term

$Cov[\bar{W}, F(\bar{W}_f)]$  was not included in the estimate of  $Var(B')$ , because previous analyses indicated it was very small.

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  $\pm 25\%$  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 ( $F(\bar{W}_f)$ ). 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

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

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

$$Var[F(\bar{W}_f)] = s^2 \left[ \frac{1}{n} + \frac{1}{q} + \frac{(\bar{W}_f - \bar{WF})^2}{\sum (W_i - \bar{WF})^2} \right] \quad 19$$

where  $s^2$  is the residual mean square from the fecundity-weight linear regression,  $\bar{W}_f$  is the mean female body weight in the spawning population,  $\bar{WF}$  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)

*Objective 1a:*

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.

*Objective 1b:*

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 quadrat in the intertidal zone. Egg loss rate was then calculated for each intertidal quadrat using equations 20 and 21 calculated from the 1994 and 1995 egg loss data

$$z = 0.0809 + 0.0004 * AE \quad 20$$

$$z = 0.0524 + 0.0006 * AE \quad 21$$

where  $z$  is the daily egg loss rate and  $AE$  is the cumulative air exposure between peak day of spawn and dive surveys. 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

$$y_{ij} = adc_{ij} e^{zt} \quad 22$$

where  $y_{ij}$  is the number of eggs in quadrat  $j$  and transect  $i$  adjusted for diver bias and egg loss (Eqn. 6),  $adc_{ij}$  is the number of eggs in quadrat  $j$  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. Quantitative 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 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:

$$\gamma = \frac{\bar{\sigma}}{\bar{W}} = a \bar{l}^b \quad 23$$

where  $\sigma$  is the mean acoustic backscattering coefficient,  $W$  is the mean weight (kg),  $l$  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  $10 \log (\sigma/w)$ , where  $10 \log (\sigma/w)$  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 ( $\sigma$ ). 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

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

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 ( $\beta_{jk}$ ) is given by

$$\beta_{jk} = [(C \bar{g} / \Psi \langle \sigma \rangle)] E_{jk} \quad 25$$

where  $C$  is a calibration factor,  $\bar{g}$  is the mean TVG correction factor,  $\Psi$  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 ( $\beta_{ih}$ , kg m<sup>-2</sup>) is given by

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

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 ( $\beta_h$ , kg m<sup>-2</sup>) is estimated from

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

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  $\beta_h$  is given by

$$\text{Var}(\bar{\beta}_h) = \sum_i W_{ih}^2 \frac{S_h^2}{n_h} + 2 \sum_{i < j} \sum_j W_{ih} W_{jh} \text{Cov}(B_{hi}, B_{hj}) \quad 28$$

where

$$S_h^2 = \sum \frac{(\beta_{ih} - \bar{\beta}_h)^2}{(n_h - 1)} \quad 29$$

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 ( $\beta$ , kg) is then given by

$$\beta = \sum_h \bar{\beta}_h \cdot A_h \quad 30$$

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

$$Var(\beta) = \sum_h A_h^2 Var(\bar{\beta}_h) \quad 31$$

### *Objective 3:*

Studentized t-tests were conducted to tests 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 a difference between the 1995 spawn deposition biomass estimate obtained using an air-exposure egg loss model and the 1995 acoustic biomass estimate, because Thorne et al. (1996) did not estimate the variance of the acoustic biomass estimate.

#### *Objective 4:*

Studies are being conducted at the University of Alaska Fairbanks to evaluate environmental factors affecting the recruitment of herring in PWS, British Columbia, Sitka Sound, the eastern Bering Sea, and Norton Sound. E. H. Williams is expected to complete a Ph.D. dissertation describing the results of this work in December 1998.

## **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.

#### *Objective 1a:*

Cumulative time of air exposure as a function of the depth of deposited eggs was found to be the predominate 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.

#### *Objective 1b:*

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 in 1995 was approximately 5,393 tonnes more than the 1994 biomass 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 in 1996 was approximately 3,776 tonnes more than the 1995 biomass, 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 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.

#### *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/kg. 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/kg. 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:*

Spawn deposition biomass estimates obtained using an air-exposure egg loss model were significantly different from all biomass estimates obtained using other methods in 1994, 1995 and 1996 (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:*

Studies are being conducted at the University of Alaska Fairbanks to evaluate environmental factors affecting the recruitment of herring in PWS, British Columbia, Sitka Sound, the eastern Bering Sea, and Norton Sound. E. H. Williams is expected to complete a Ph.D. dissertation describing the results of this work in December 1998.

## 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 late 1980's and those obtained from other methods suggest that this may be a problem (Morstad et al. 1997). In addition, spawning is probably not observed during periods of poor weather when aerial surveys are not practical. But, aerial surveyors attempt to minimize the occurrence of unobserved spawning through frequent surveys.

Loss of eggs between spawn deposition and dive surveys and adjustments for diver-specific bias in visual egg counts also appear 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).

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 quadrat 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. 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 predominate 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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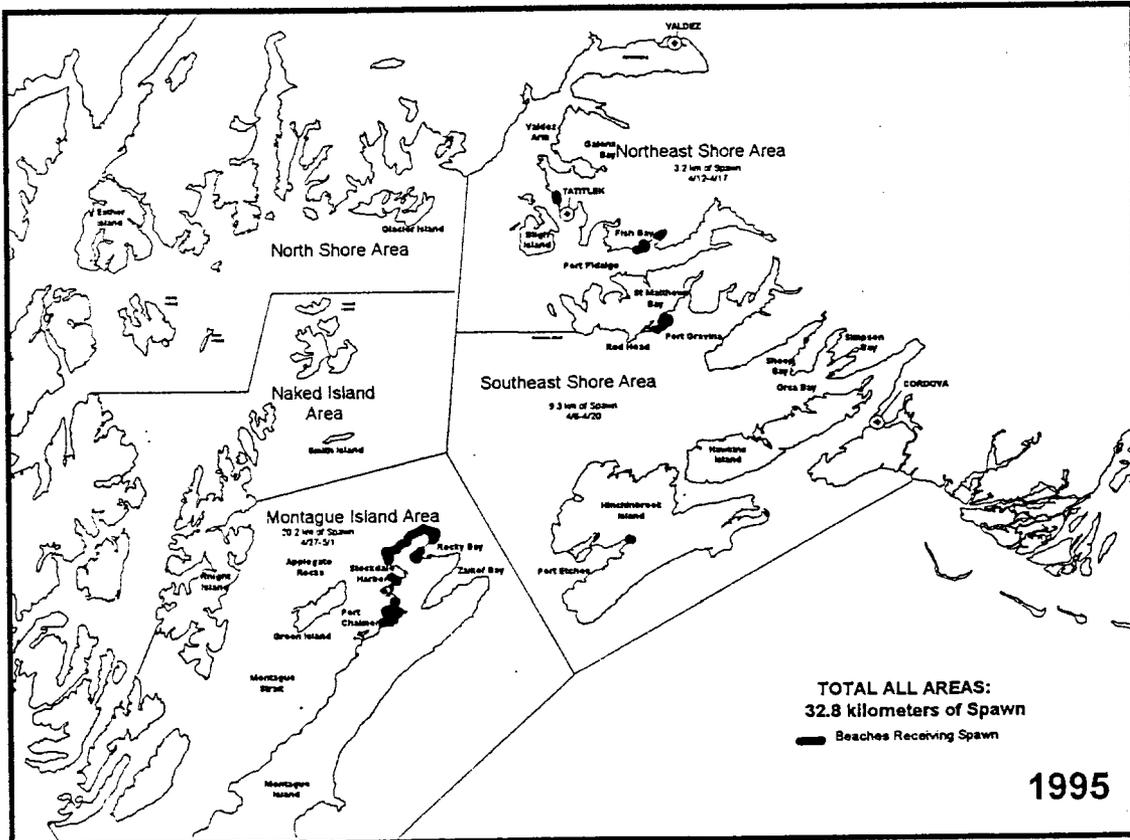
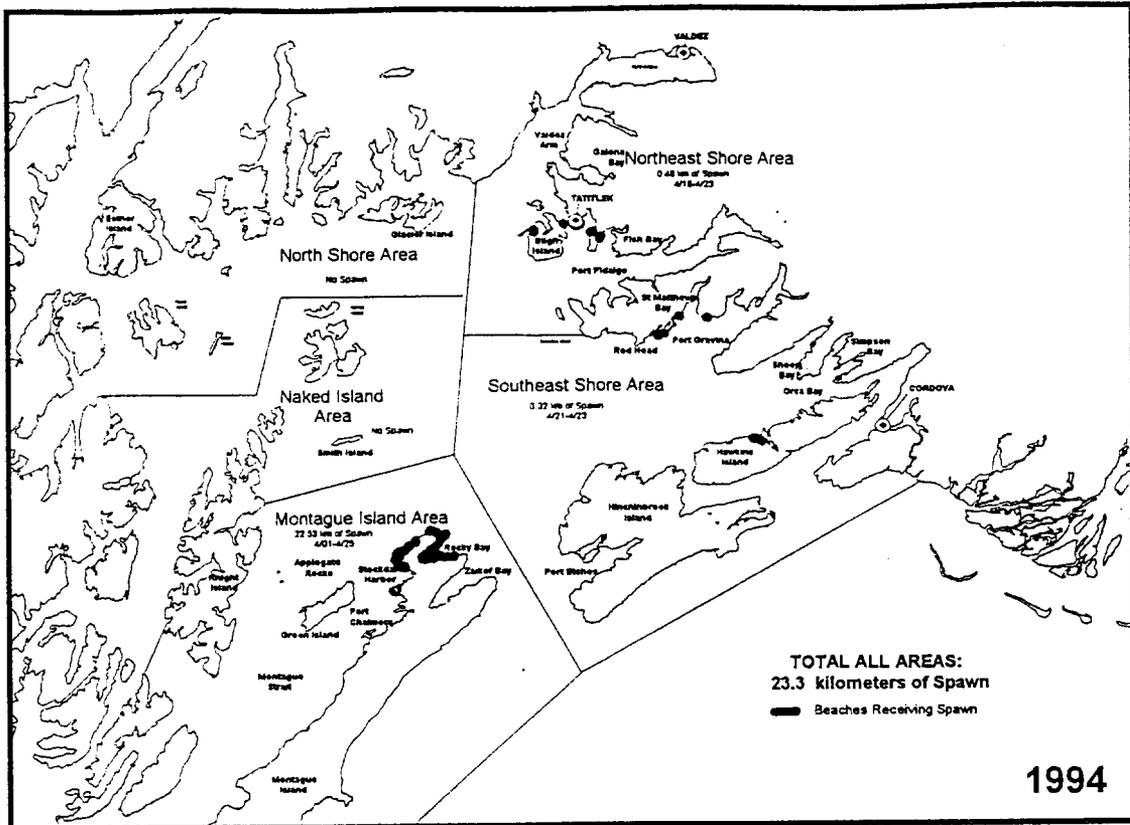


Figure 1. Location of spawning herring and kilometers of shoreline observed during aerial surveys, Prince William Sound, Alaska, 1994 to 1997.

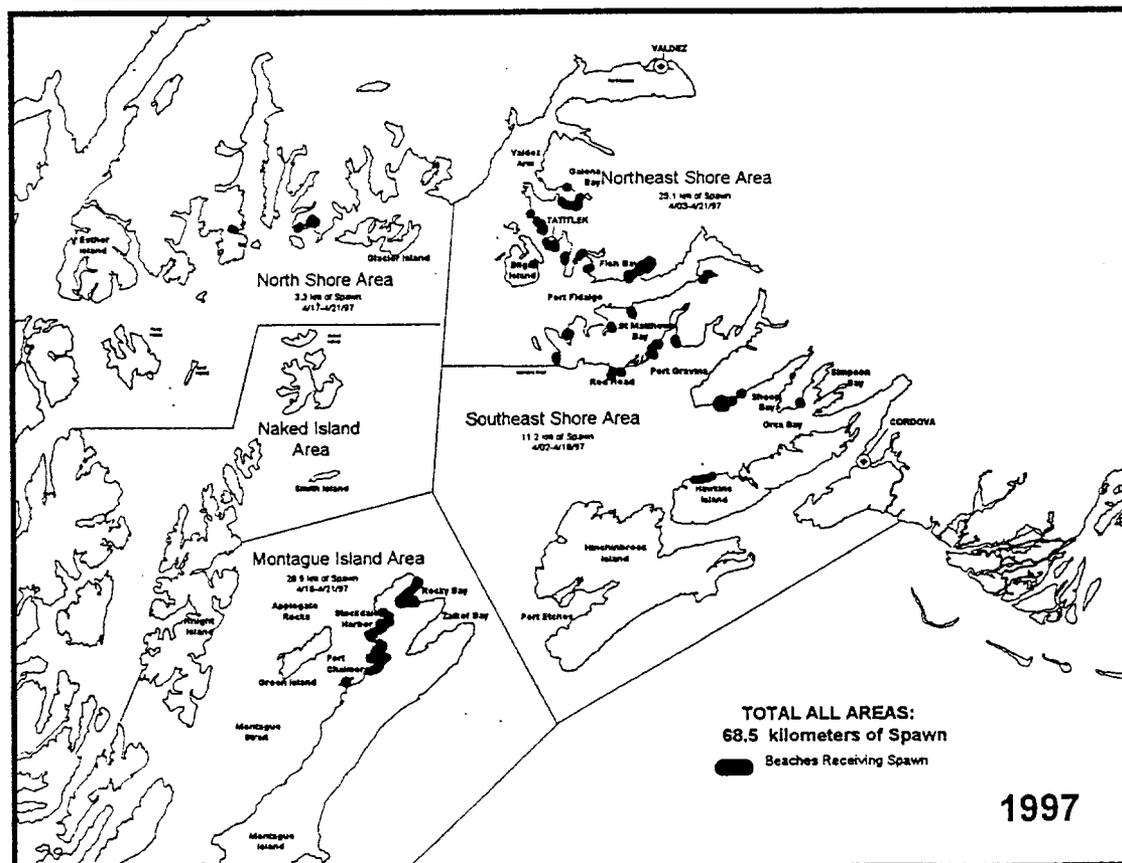
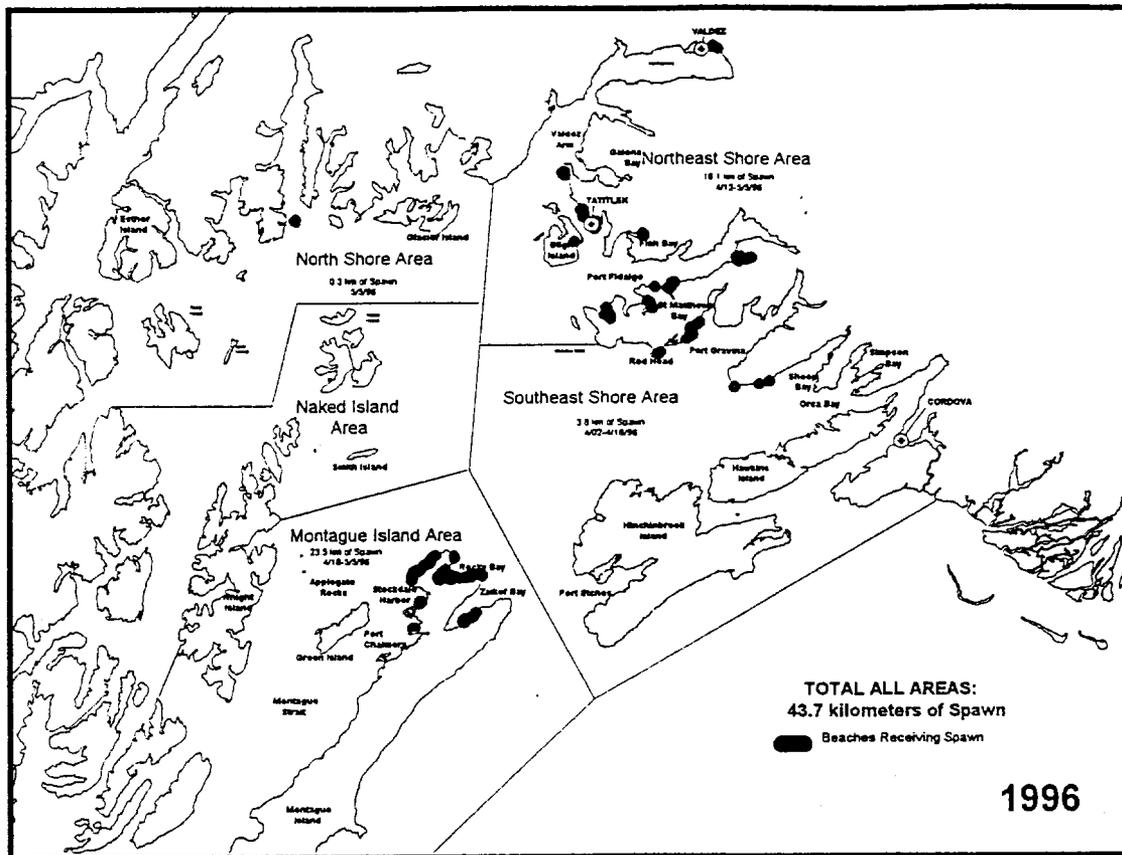


Figure 1. (continued).

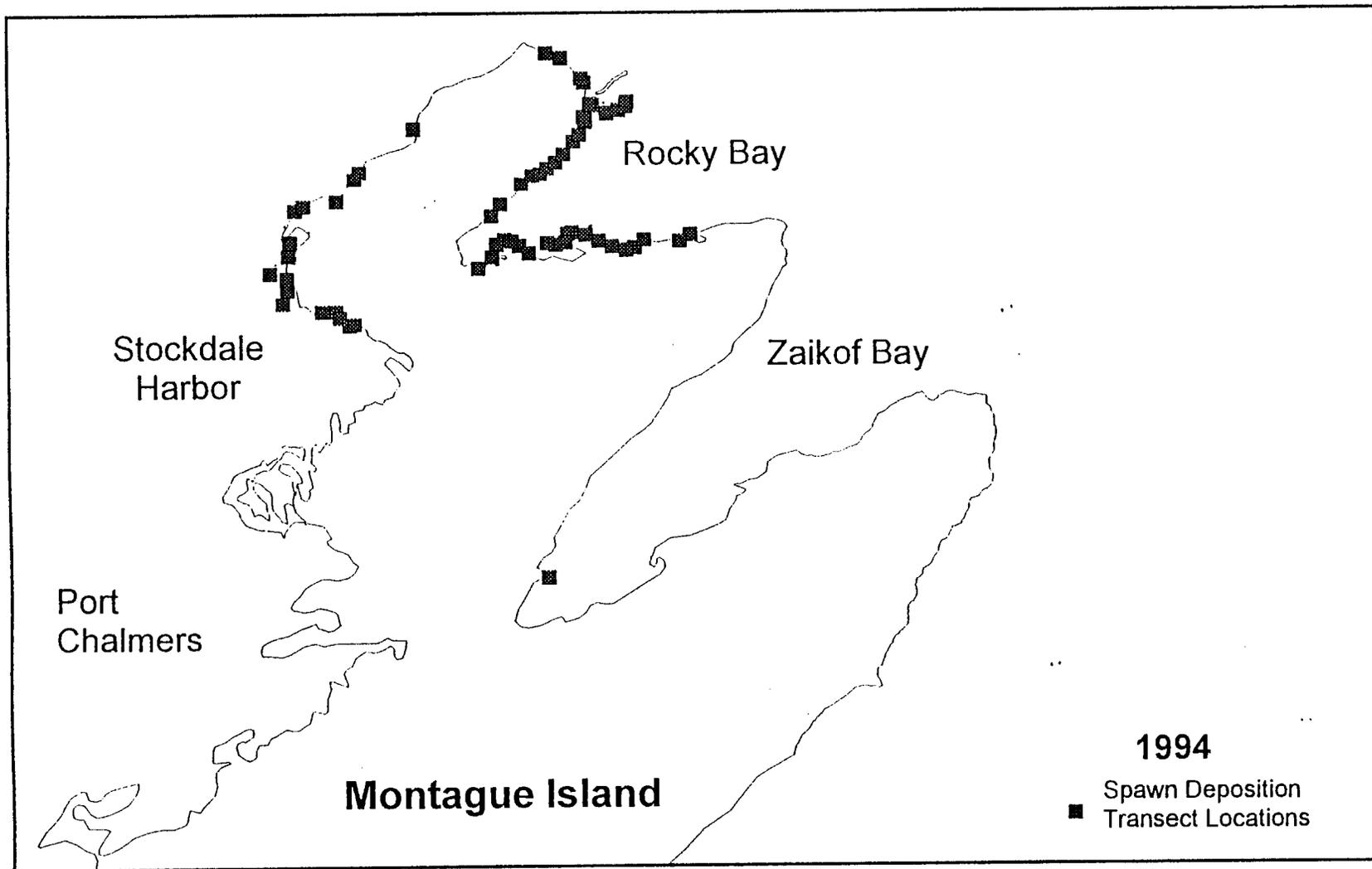


Figure 2. Spawn deposition transect locations in the Montague Island summary area, Prince William Sound, Alaska, 1994 to 1997.

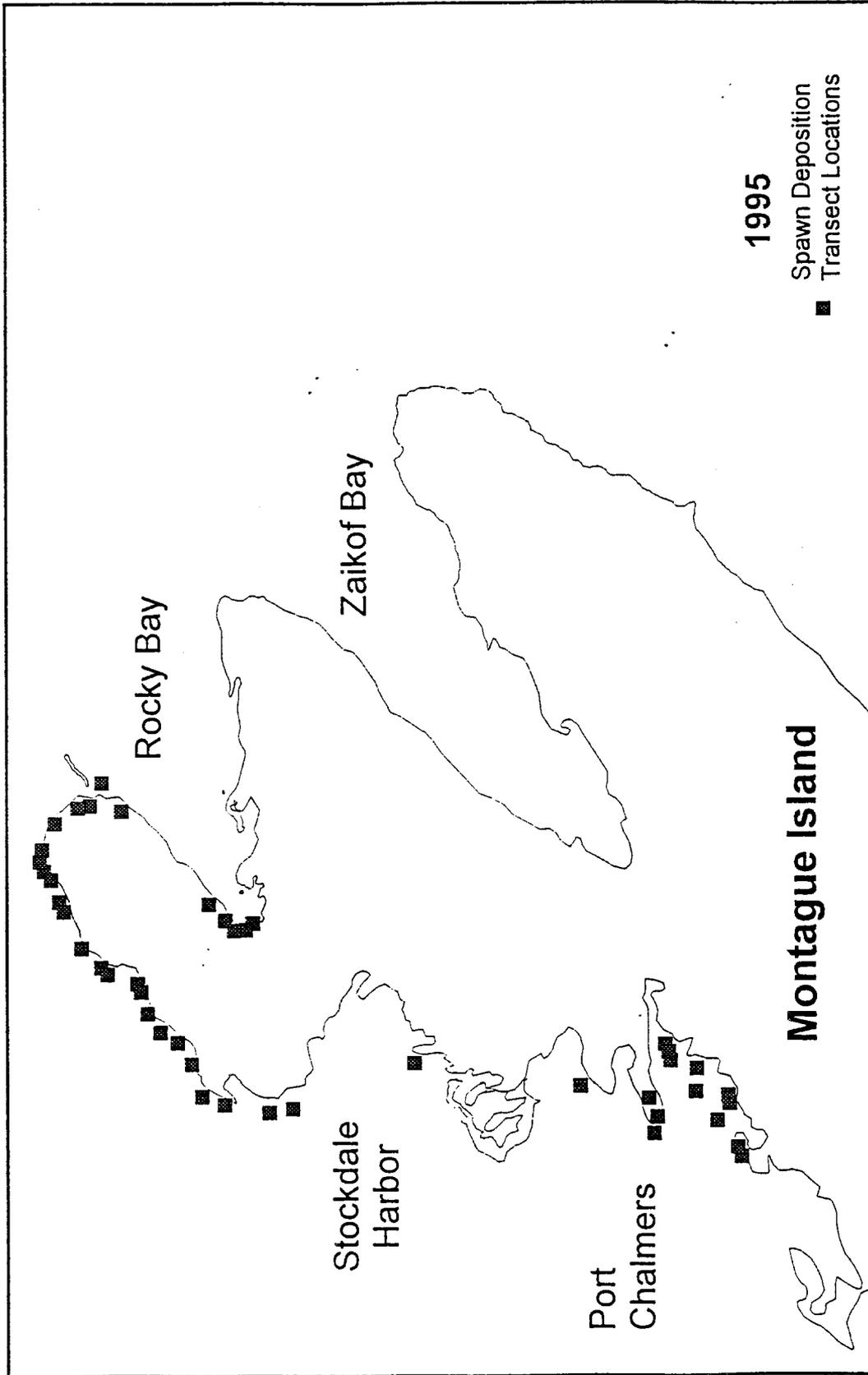


Figure 2. (continued).

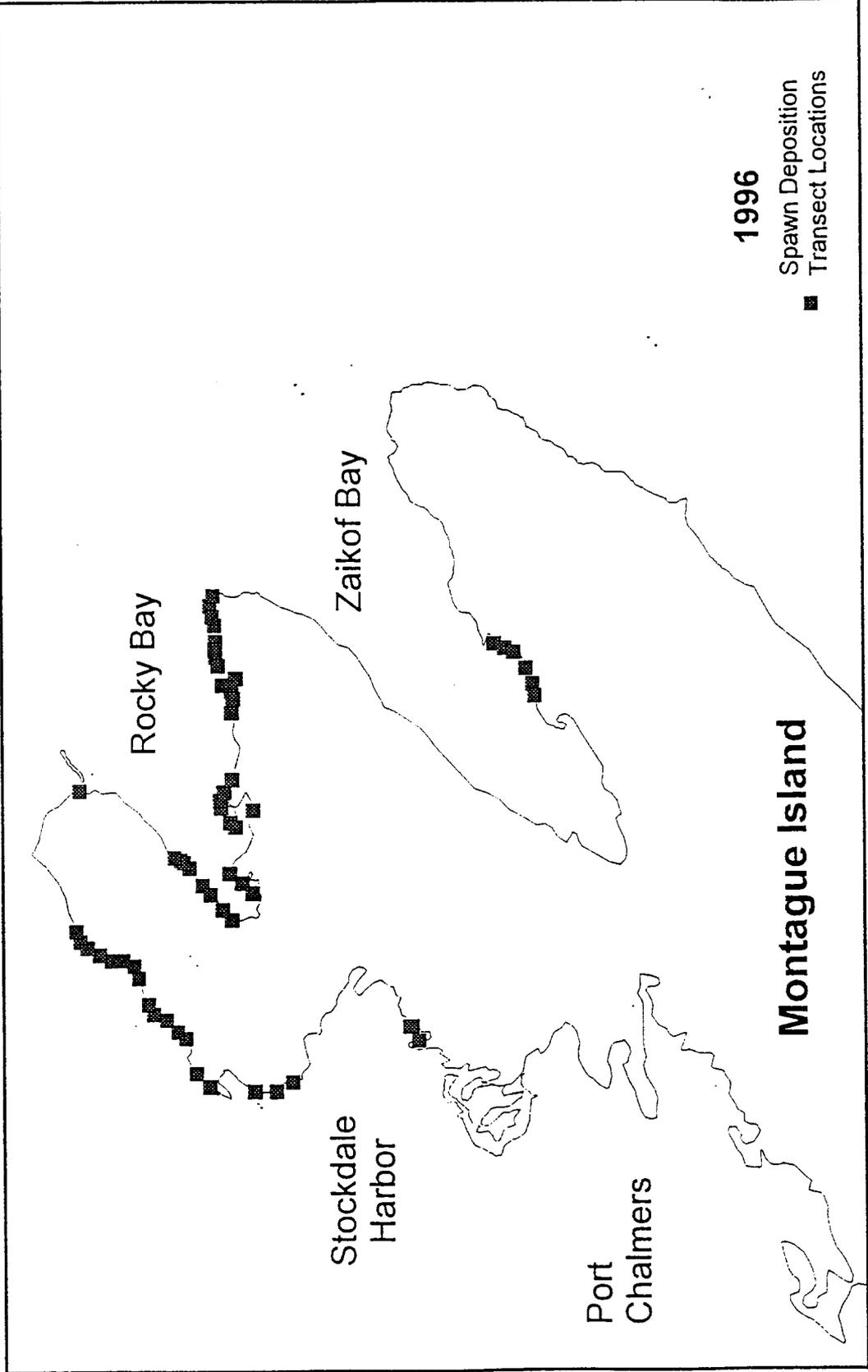


Figure 2. (continued).

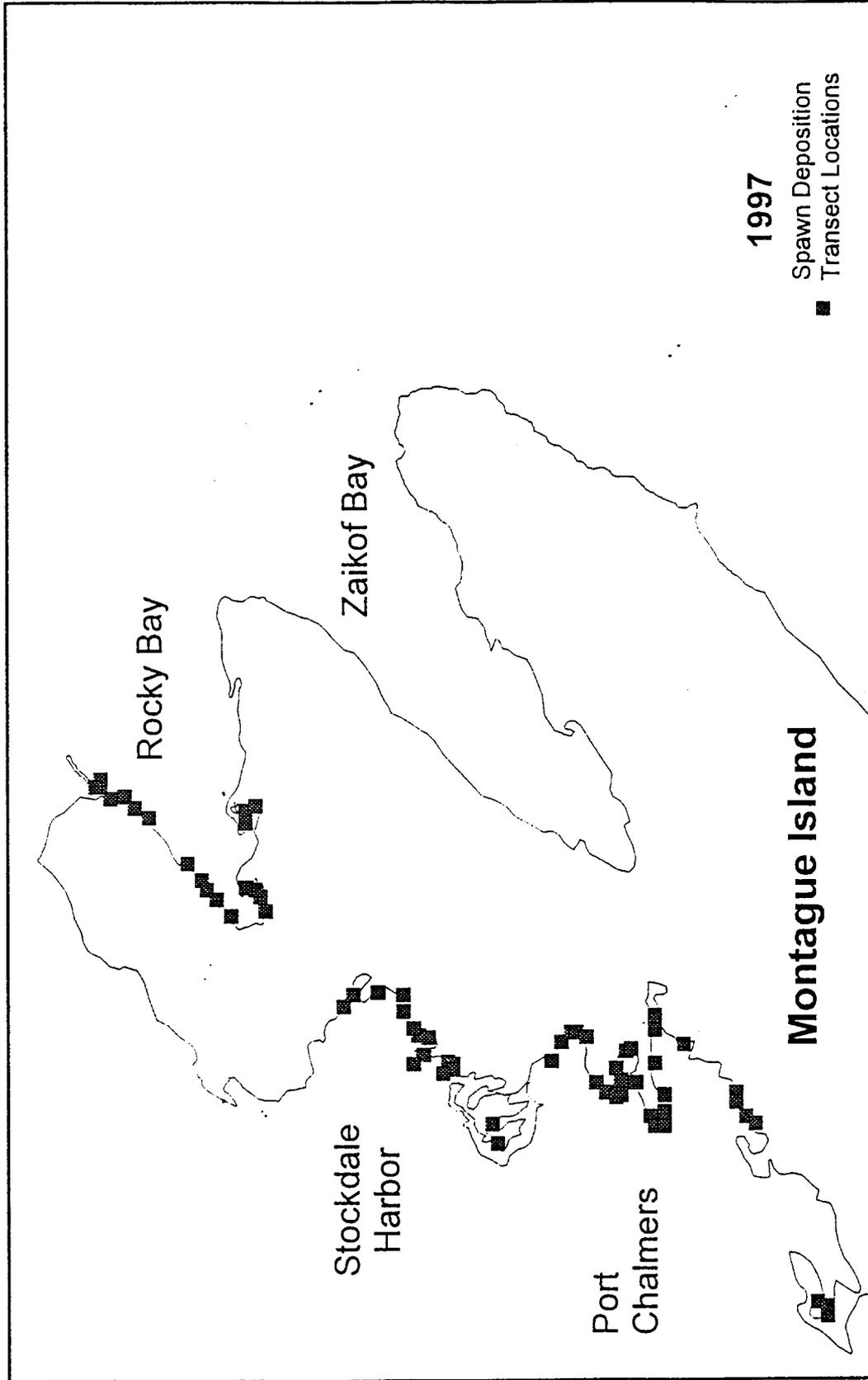


Figure 2. (continued).

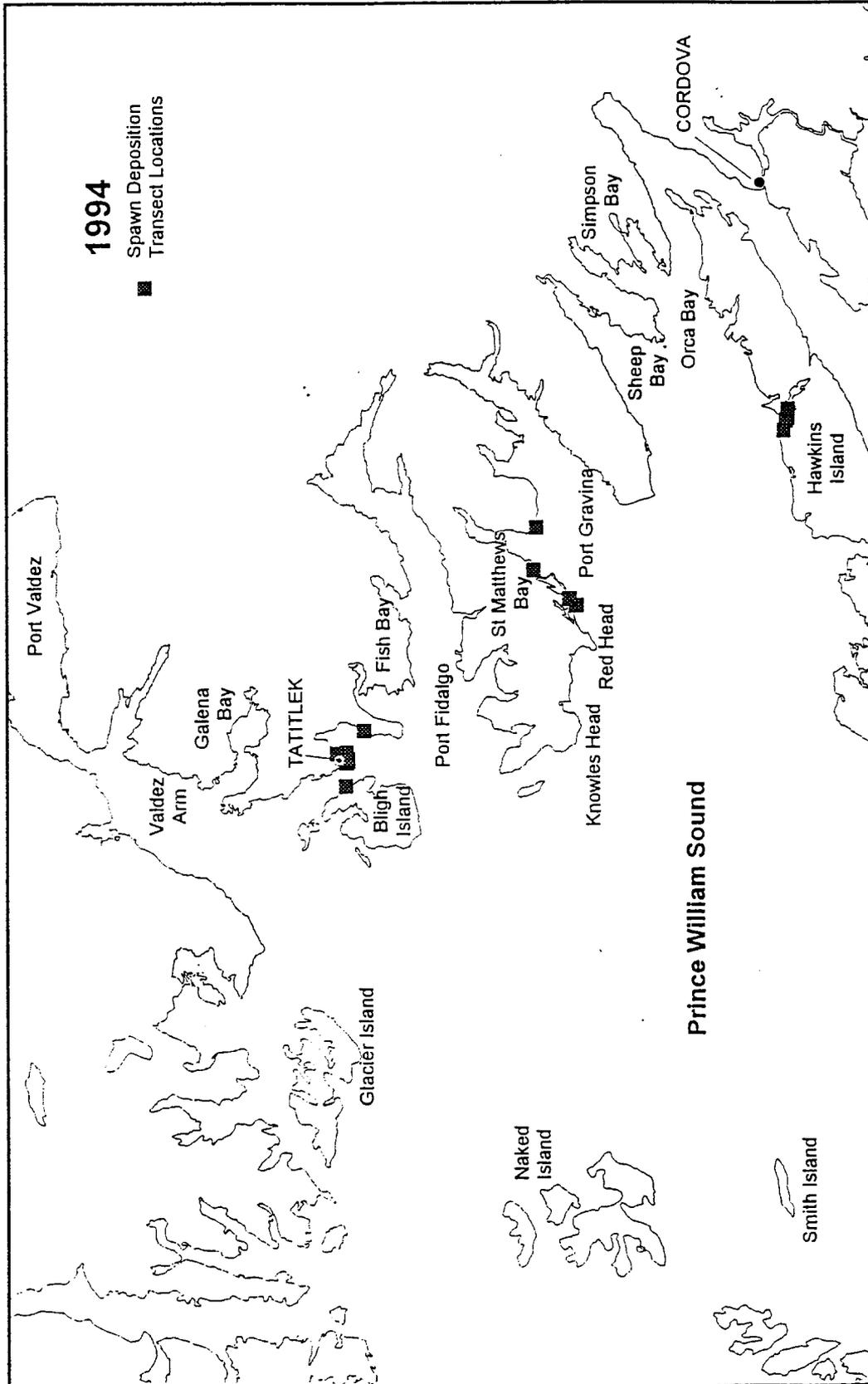


Figure 3. Spawn deposition transects in the Southeastern, Northeastern and Northern summary areas, Prince William Sound, Alaska, 1994 to 1997.

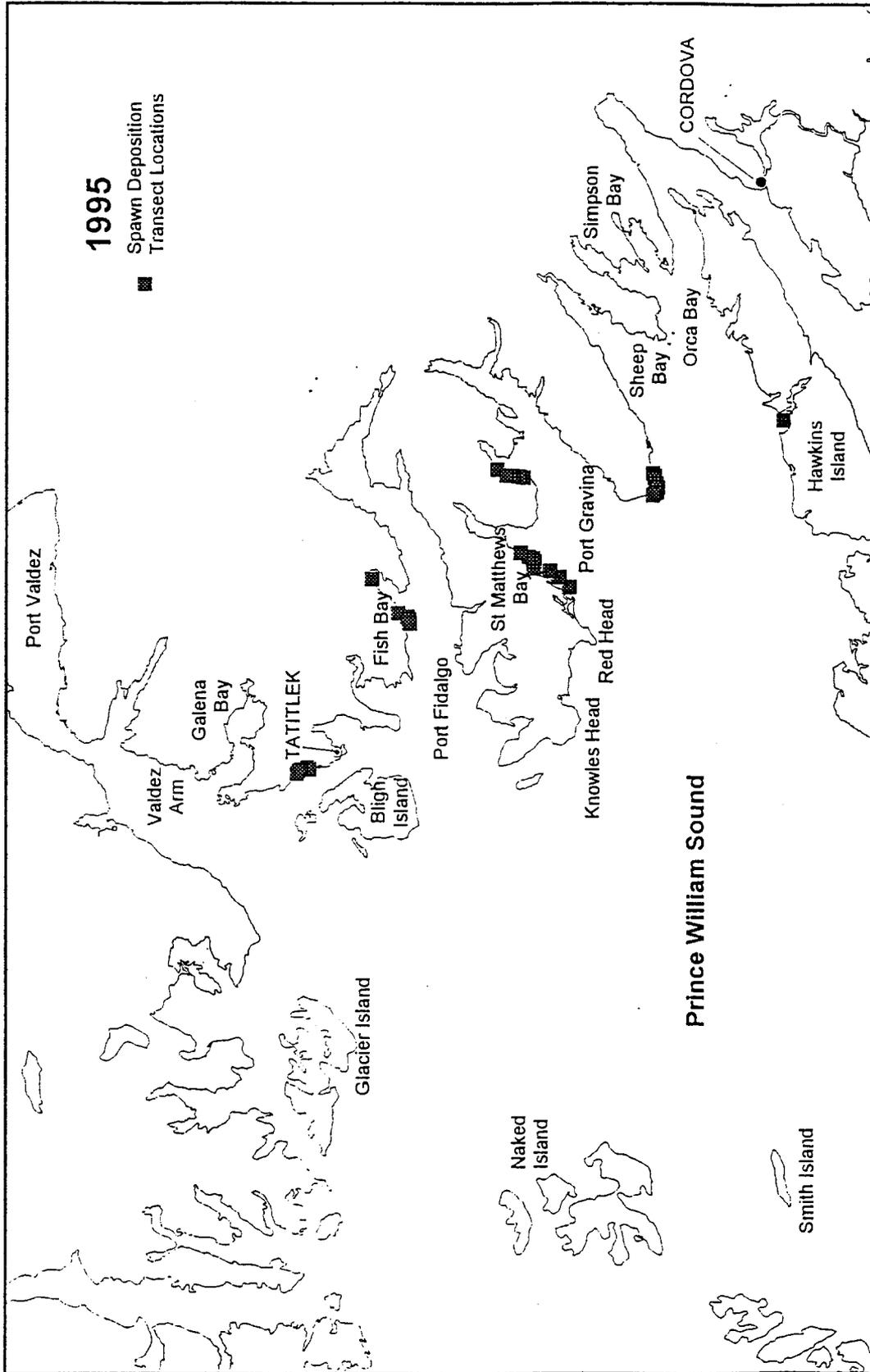


Figure 3. (continued).

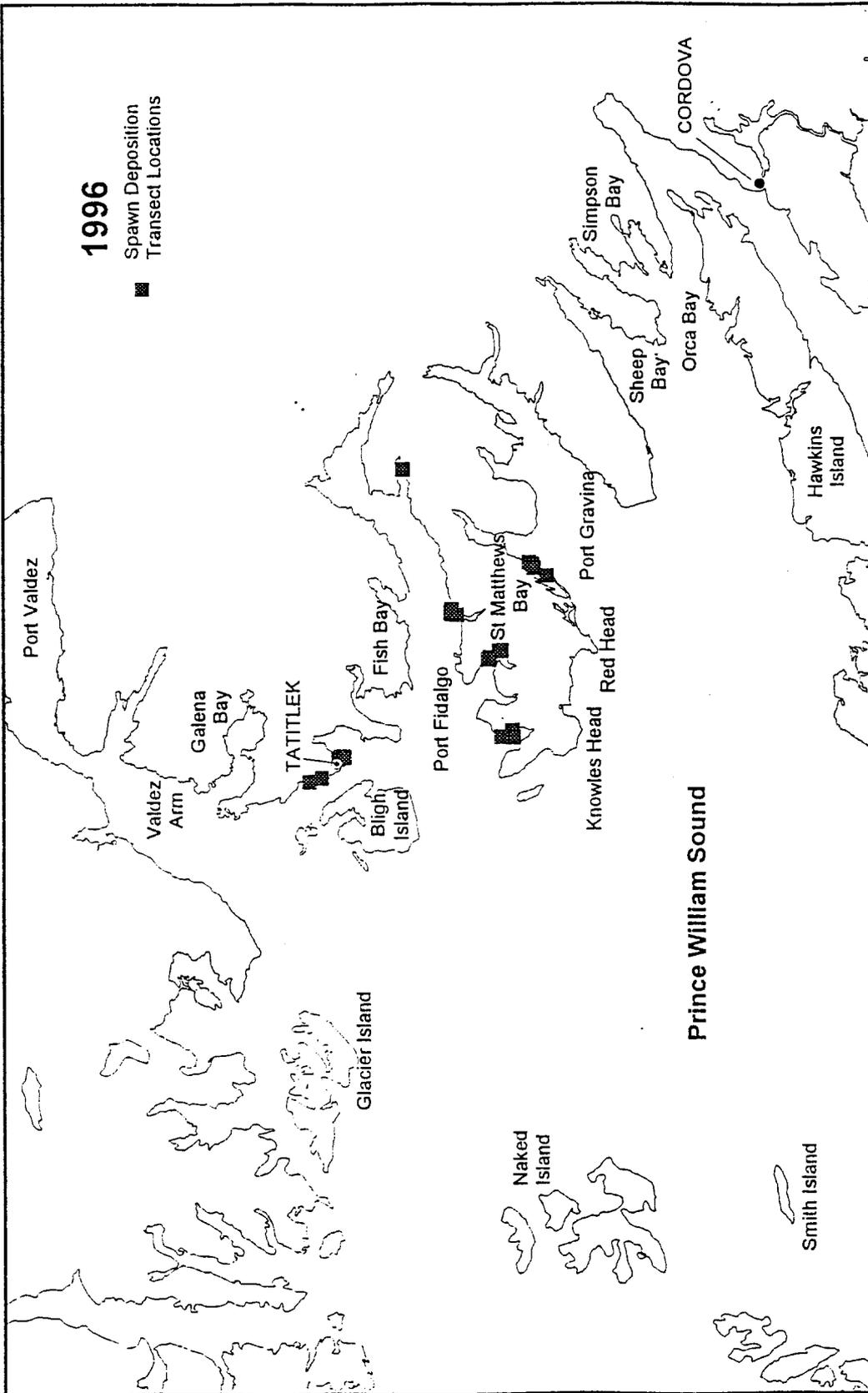


Figure 3. (continued).

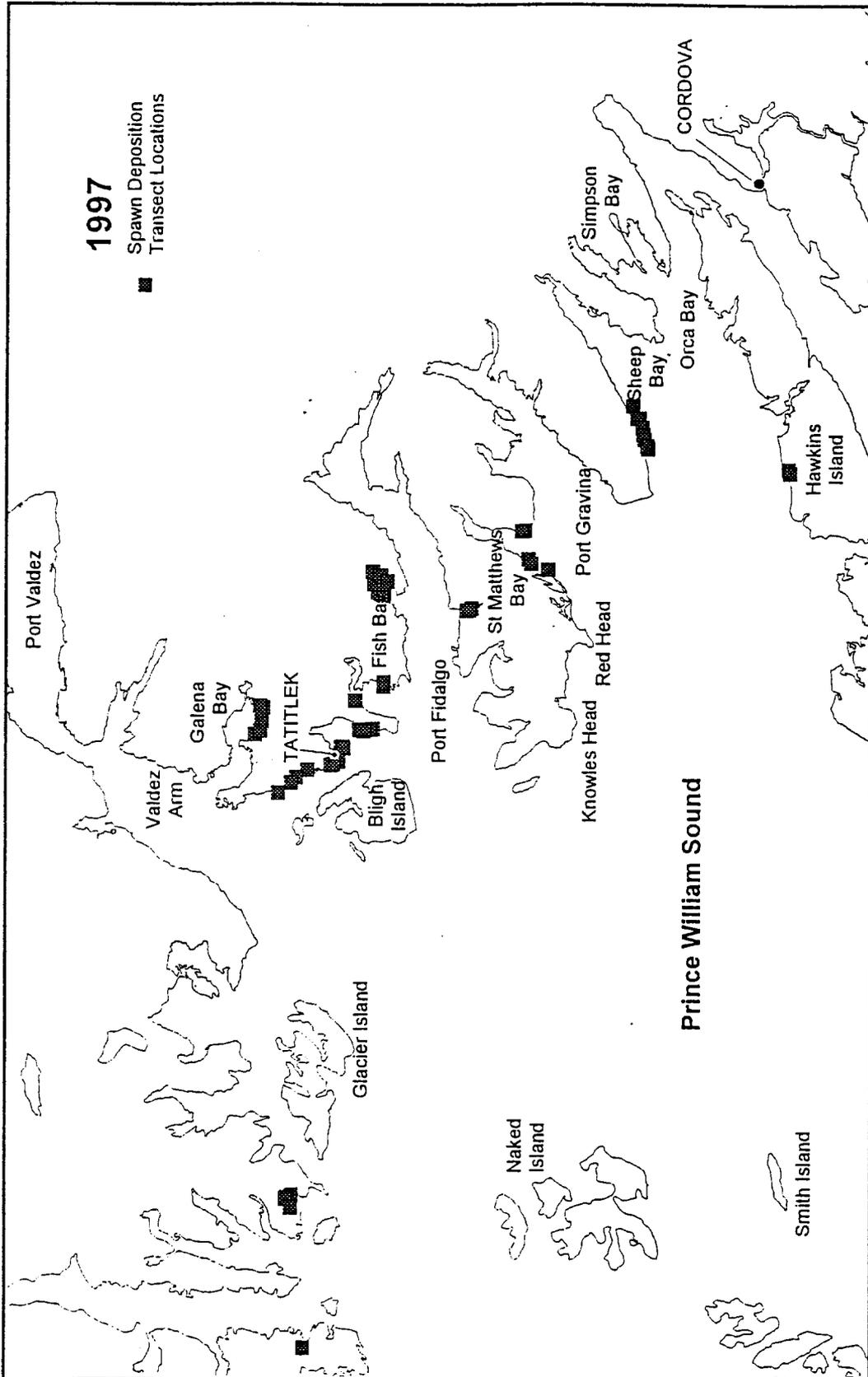


Figure 3. (continued).

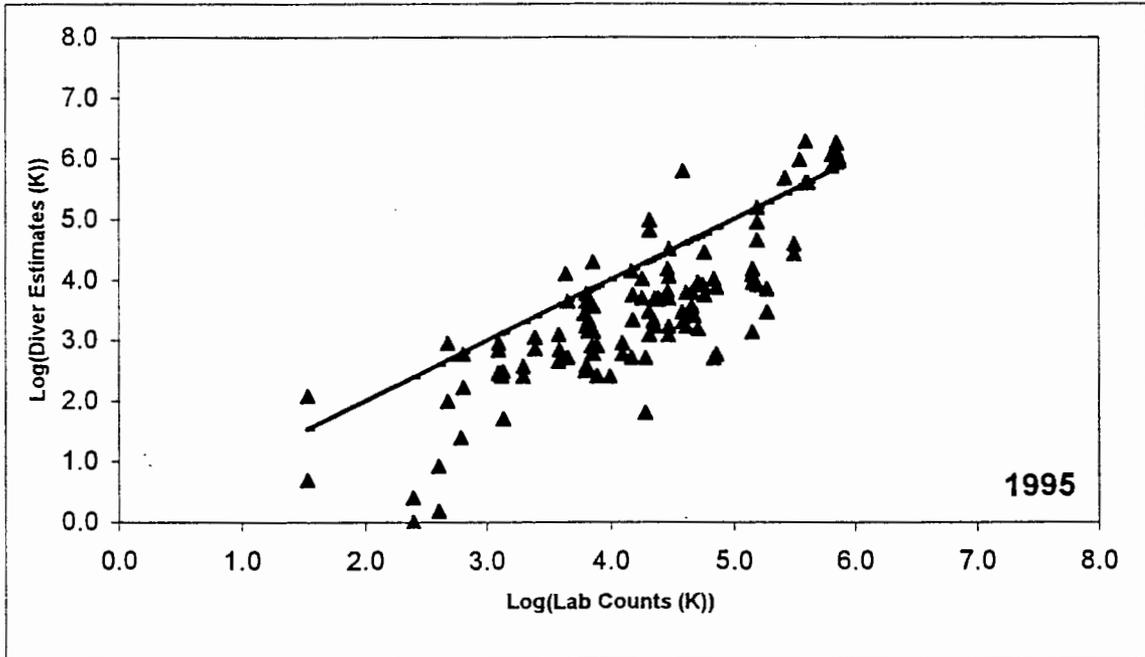
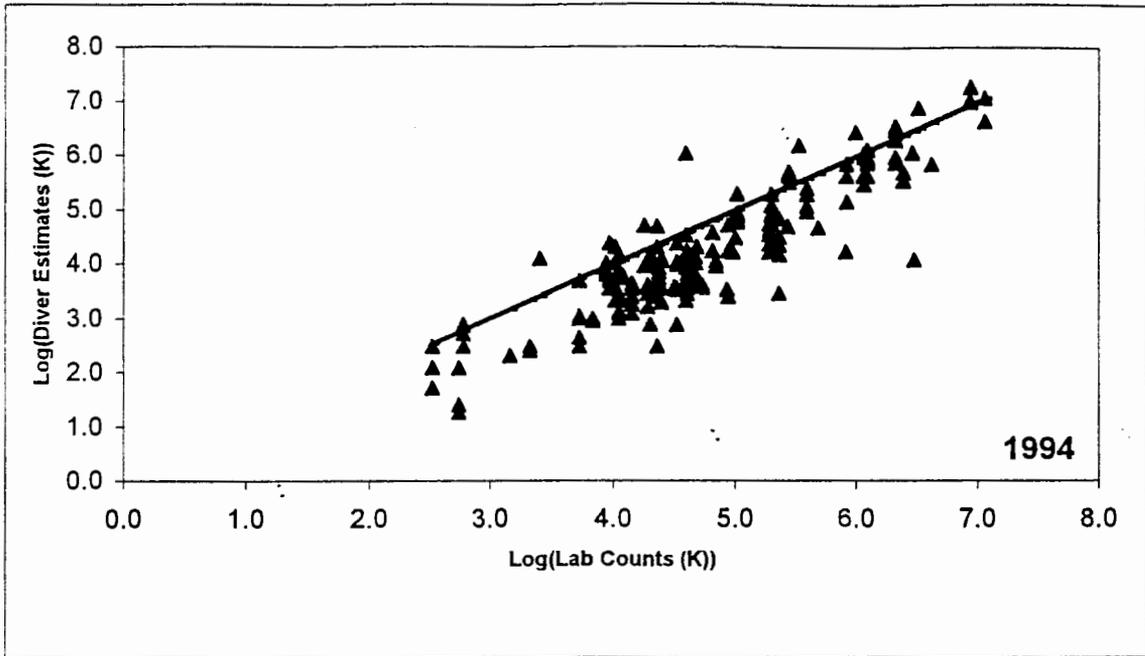


Figure 4. Relationship between diver count and lab count for all divers on all kelp types for 1994 to 1997. Line has intercept = 0 and slope = 1.

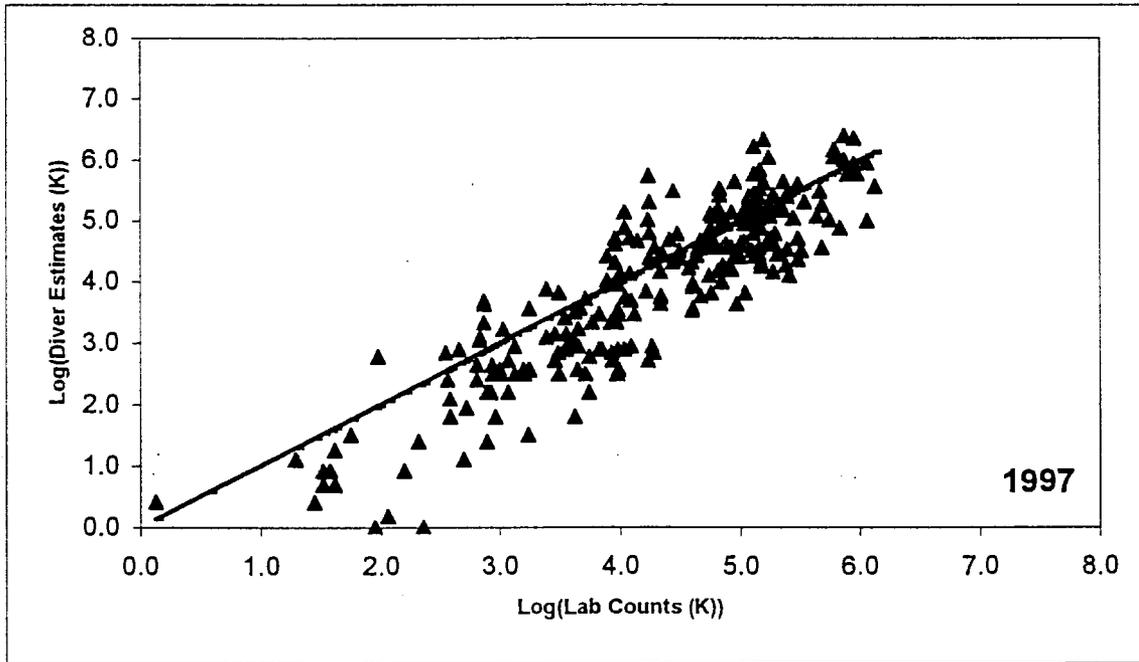
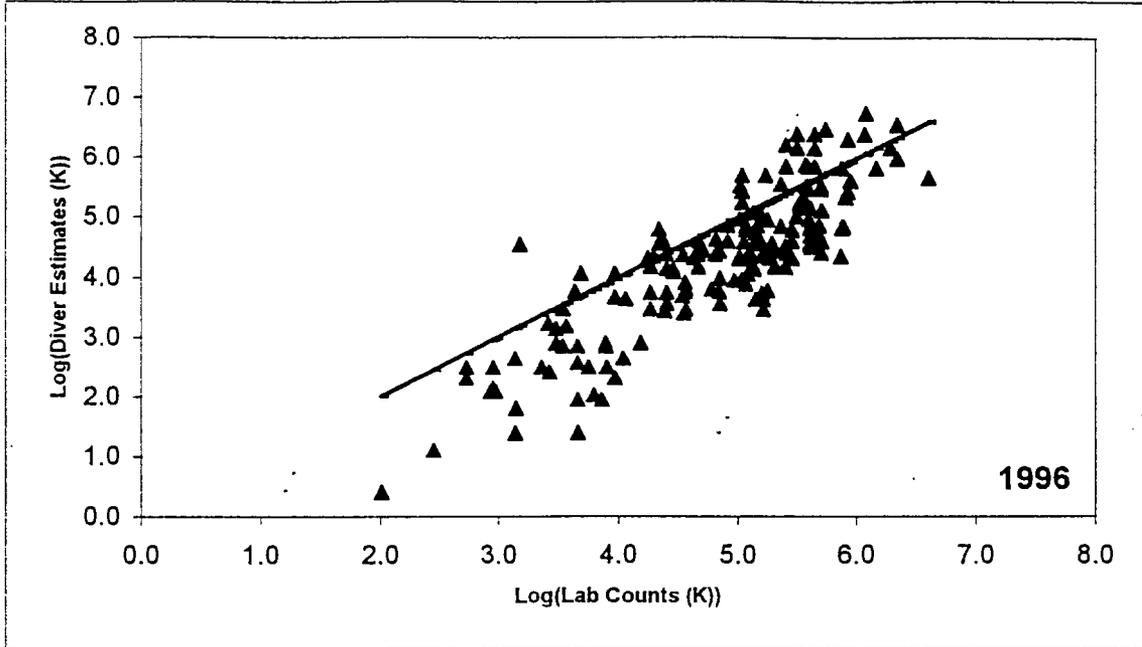
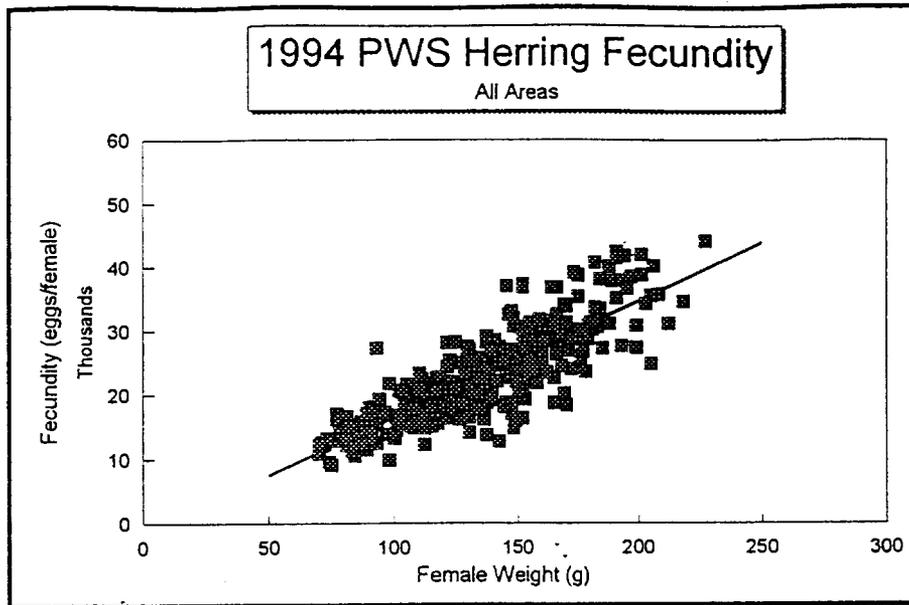
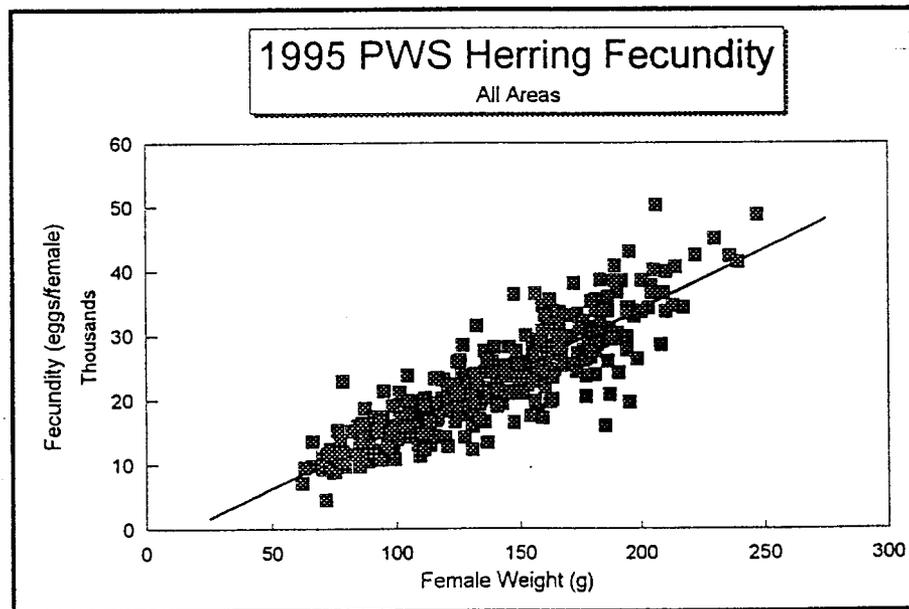


Figure 4. Continued.

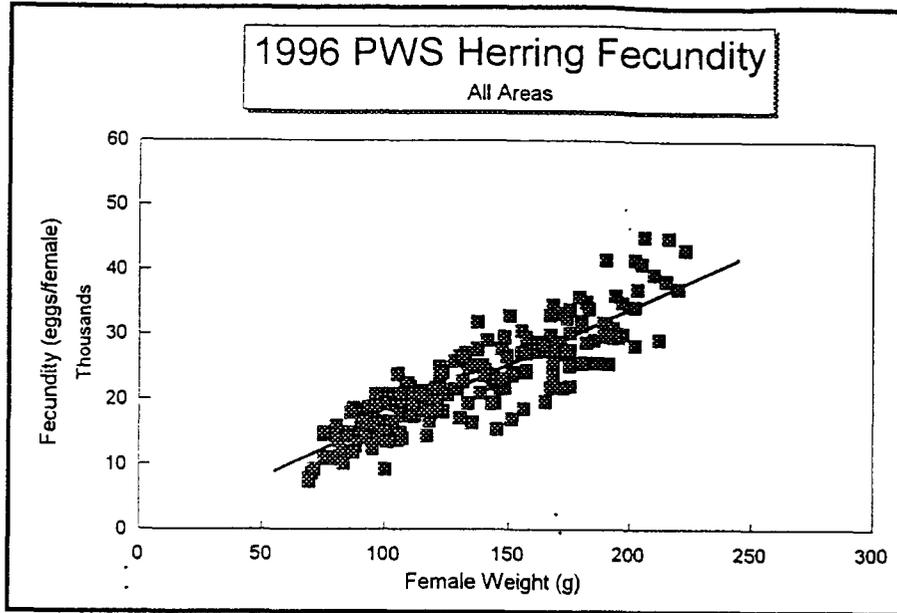


Number of Observations	342
Degrees of Freedom	340
Slope of Regression	182.462
Standard Error	6.448306
Intercept of Linear Regression	-1592.53
Standard Error of Y Estimate	3980.06
R Squared	0.701931

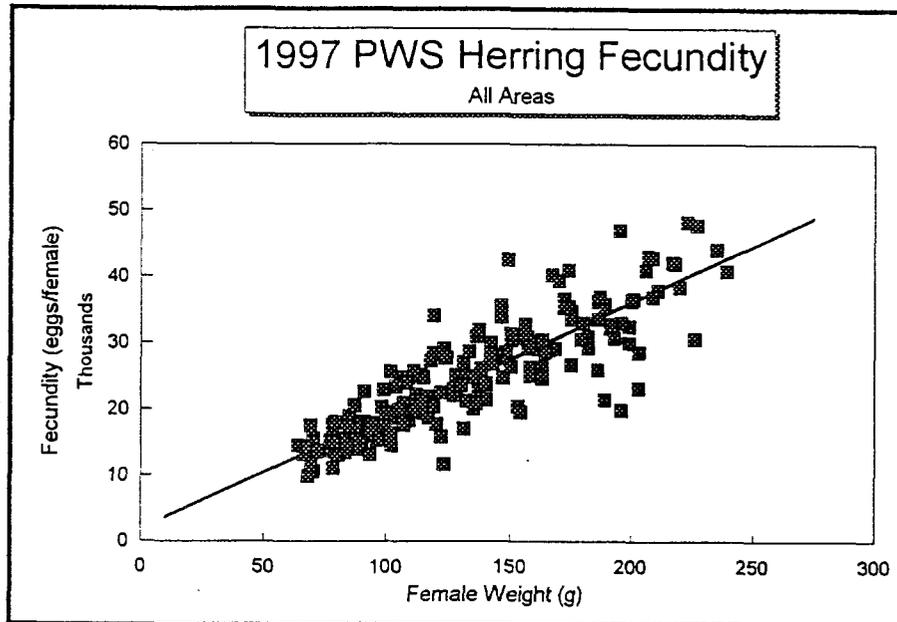


Number of Observations	310
Degrees of Freedom	308
Slope of Regression	185.413
Standard Error	5.842
Intercept of Linear Regression	-2941.69
Standard Error of Y Estimate	4095.207
R Squared	0.765822

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.

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
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.

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
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	$\Sigma m_i$	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 <sup>2</sup> )		2.56	0.01	0.02	2.60
Unweighted average density (1000/m <sup>2</sup> )		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)	$\bar{W}$	126	126	126	
Average weight of females (g)	$\bar{W}_f$	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	$s_1^2$	1.67x10 <sup>9</sup>	2.73x10 <sup>5</sup>	3.21x10 <sup>6</sup>	
Variance - within transects	$s_2^2$	6.39x10 <sup>9</sup>	1.34x10 <sup>6</sup>	7.25x10 <sup>6</sup>	
Variance - individual quadrats	$s_3^2$	1.29x10 <sup>6</sup>	59.74	94.22	
Variance of estimated total eggs	$Var(T)$	1.54x10 <sup>6</sup>	0.10168	1.97762	1.54x10 <sup>6</sup>
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	$s^2$	1.48x10 <sup>7</sup>	1.48x10 <sup>7</sup>	1.48x10 <sup>7</sup>	
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	$Var(B)$	6.34x10 <sup>7</sup>	20.52	3.42x10 <sup>2</sup>	6.34x10 <sup>7</sup>
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 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	$\Sigma m_i$	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 <sup>2</sup> )		2.56	0.01	0.02	2.60
Unweighted average density (1000/m <sup>2</sup> )		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)	$\bar{W}$	126	126	126	
Average weight of females (g)	$\bar{W}_f$	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 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	$\Sigma m_i$	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 <sup>2</sup> )		3.05	0.38	1.28	4.72
Unweighted average density (1000/m <sup>2</sup> )		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)	$\bar{W}$	123	154	118	
Average weight of females (g)	$\bar{W}_f$	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	$s_1^2$	2.48x10 <sup>9</sup>	2.27x10 <sup>7</sup>	5.75x10 <sup>7</sup>	
Variance - within transects	$s_2^2$	1.34x10 <sup>10</sup>	2.47x10 <sup>8</sup>	4.17x10 <sup>8</sup>	
Variance - individual quadrats	$s_3^2$	1.87x10 <sup>6</sup>	2.45x10 <sup>4</sup>	4.72x10 <sup>4</sup>	
Variance of estimated total eggs	$Var(T)$	1.88x10 <sup>5</sup>	2.35x10 <sup>2</sup>	1.72x10 <sup>3</sup>	1.90x10 <sup>5</sup>
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	$s^2$	1.78x10 <sup>7</sup>	1.78x10 <sup>7</sup>	1.78x10 <sup>7</sup>	
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	$Var(B)$	1.16x10 <sup>8</sup>	5.35x10 <sup>4</sup>	8.97x10 <sup>5</sup>	1.17x10 <sup>8</sup>
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	$\Sigma m_i$	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 <sup>2</sup> )		3.21	1.94	0.24	5.39
Unweighted average density (1000/m <sup>2</sup> )		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)	$\bar{W}$	120	136	130	
Average weight of females (g)	$\bar{W}_f$	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	$s_1^2$	$2.31 \times 10^9$	$2.52 \times 10^7$	$4.76 \times 10^7$	
Variance - within transects	$s_2^2$	$3.94 \times 10^{10}$	$9.76 \times 10^7$	$1.61 \times 10^8$	
Variance - individual quadrats	$s_3^2$	$7.47 \times 10^5$	$4.01 \times 10^3$	$1.26 \times 10^3$	
Variance of estimated total eggs	$Var(T)$	$2.16 \times 10^5$	$3.63 \times 10^3$	$1.77 \times 10^3$	$2.21 \times 10^5$
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	$s^2$	$1.46 \times 10^7$	$1.46 \times 10^7$	$1.46 \times 10^7$	
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	$Var(B)$	$1.33 \times 10^8$	$1.50 \times 10^6$	$3.47 \times 10^5$	$1.35 \times 10^8$
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	$\Sigma m_i$	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 <sup>2</sup> )		3.22	0.19	2.81	1.53	7.76
Unweighted average density (1000/m <sup>2</sup> )		417.39	87.68	67.62	222.86	
Average total eggs per transect (K)	$\bar{y}$	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)	$\bar{W}$	120	130	130	130	
Average weight of females (g)	$\bar{W}_f$	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	$s_1^2$	$3.42 \times 10^3$	$1.66 \times 10^6$	$1.54 \times 10^7$	$7.10 \times 10^8$	
Variance - within transects	$s_2^2$	$2.51 \times 10^9$	$1.13 \times 10^7$	$8.04 \times 10^7$	$1.25 \times 10^{10}$	
Variance - individual quadrats	$s_3^2$	$3.86 \times 10^5$	$2.48 \times 10^2$	$4.95 \times 10^3$	$1.84 \times 10^3$	
Variance of estimated total eggs	$Var(T)$	$4.20 \times 10^4$	$3.0 \times 10^1$	$2.94 \times 10^3$	$5.94 \times 10^4$	$1.04 \times 10^5$
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	$s^2$	$1.77 \times 10^7$	$1.77 \times 10^7$	$1.77 \times 10^7$	$1.77 \times 10^7$	
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	$Var(B)$	$3.37 \times 10^7$	$9.3 \times 10^3$	$1.09 \times 10^6$	$9.13 \times 10^6$	$4.39 \times 10^7$
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.

Summary Area	Management Year	Spawn Deposition Est.		Aerial Survey Est.		Acoustic Est.
		10% Egg Loss (tonnes)	Variable Egg Loss (tonnes)	Peak Biomass (tonnes) <sup>a</sup>	Shoreline Spawn (km) (tonnes) <sup>b</sup>	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	

<sup>a</sup> Largest single day aerial estimate of herring biomass.

<sup>b</sup> 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 A: 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 pallasii*) 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  $\varepsilon$  is a random error term with mean 0 and constant variance. Taking the logarithm of this equation, one obtains

$$\ln N(t) = \ln N_0 - Zt + \varepsilon$$

showing that a linear regression of  $\ln(\text{egg abundance})$  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

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

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  $\ln(\text{egg abundance})$  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 <sup>2</sup>
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 <sup>2</sup>
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		

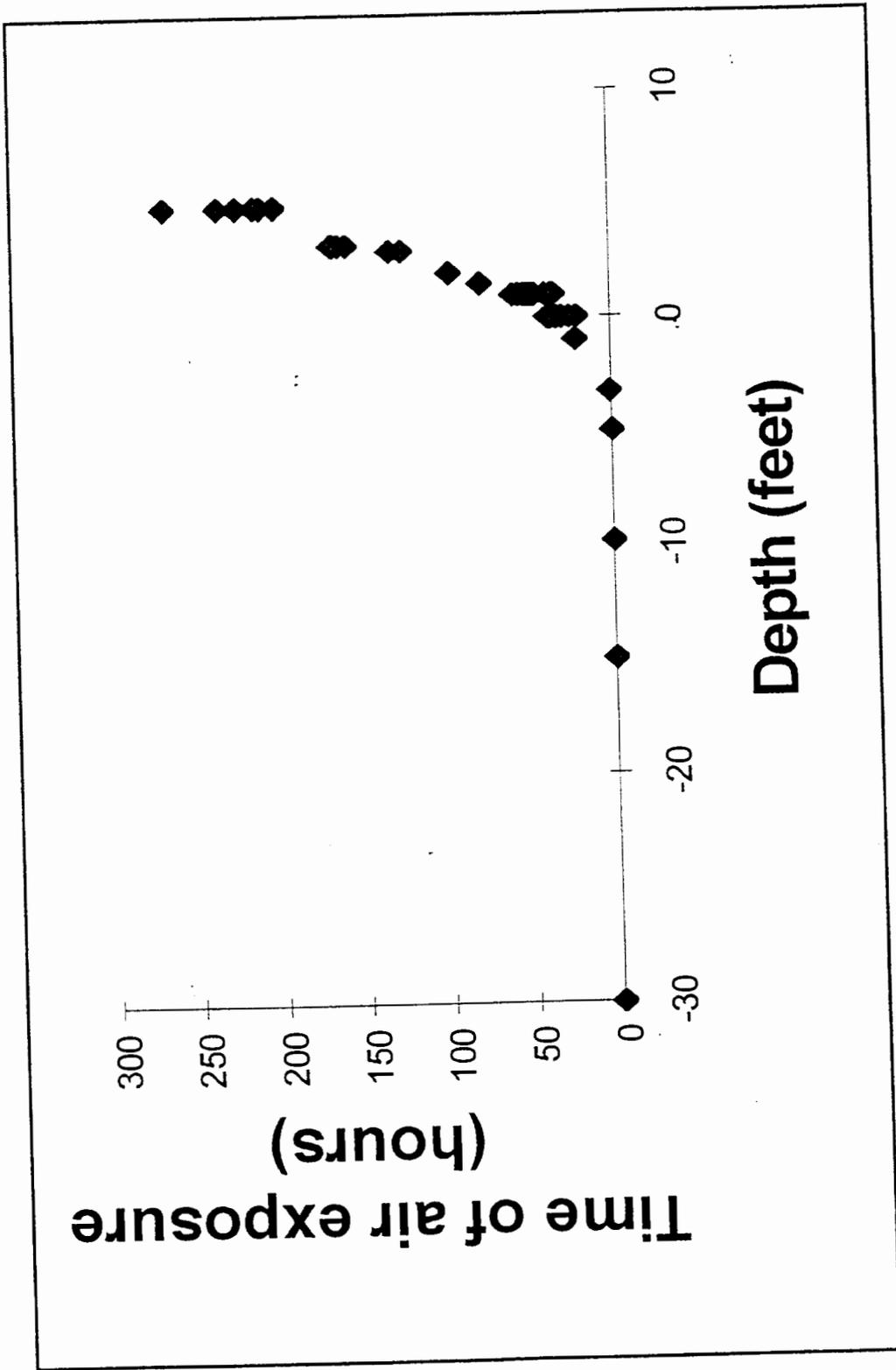


Figure 1. Total time of air exposure over the egg incubation period for each depth sampled at egg loss transects.

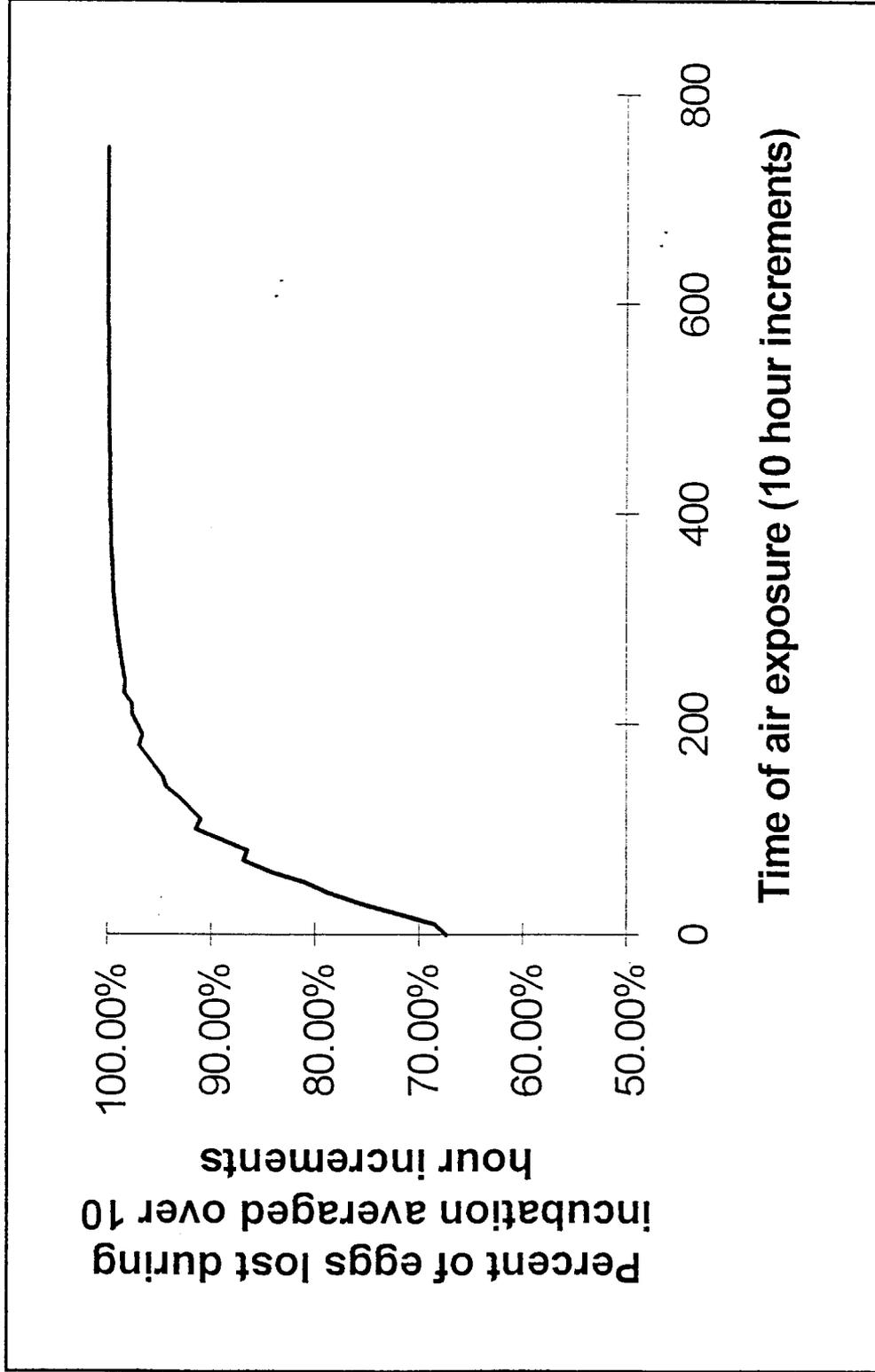
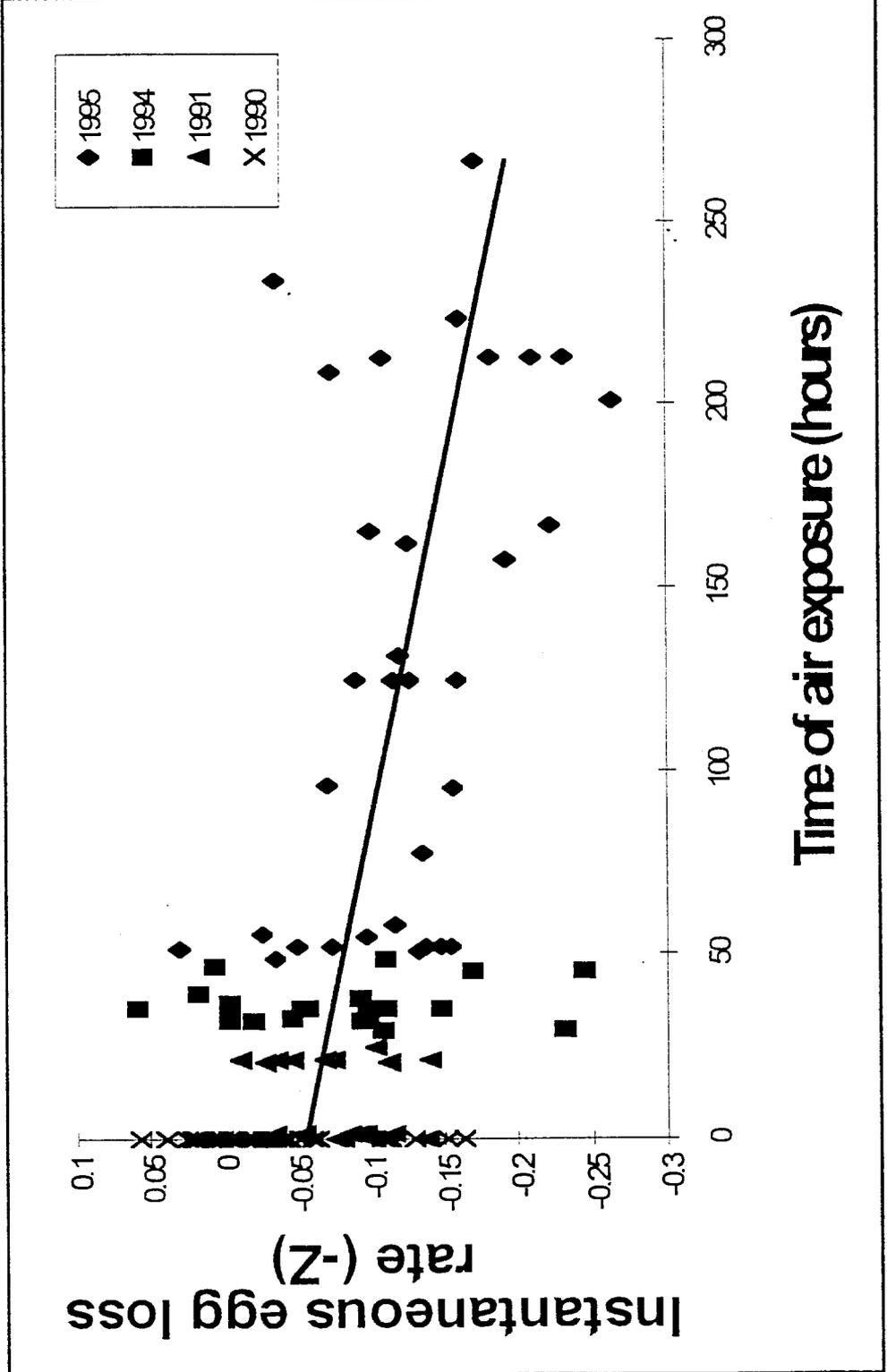


Figure 2. Percentage of eggs lost from time of spawning to time of hatching at spawn deposition transects in 1995, as predicted by the time of air exposure model.



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