Exxon Valdez Oil Spill Restoration Project Annual Report

Herring Spawn Deposition and Reproductive Impairment

Restoration Project 95166 Annual Report

This annual report has been prepared for peer review as part of the *Exxon Valdez* Oil Spill Trustee Council restoration program for the purpose of assessing project progress. Peer review comments have not been addressed in this annual report.

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July 1997

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Study History: This project was initiated in 1989 as Natural Resources Damage Assessment Fish/Shellfish Study Number 11 under the title <u>Injury to Prince William Sound Herring</u>. Annual reports were issued in 1990 and 1991 and a number of contractor reports were submitted detailing individual research components. Project funding was continued in 1992, but was discontinued in 1993 and the project went into close out. A final report for research conducted from 1989 through 1992 was submitted in December 1994 (Brown, E.D., et al., 1995). <u>Injury to Prince William Sound Herring Following the *Exxon Valdez* Oil Spill). This final report was comprised of 8 chapters representing accepted or submitted journal articles covering most of the research topics investigated by this project. Due to an unanticipated decline in the abundance of spawning adults during 1993, stock assessment and genetic damage studies were reinitiated as Restoration Project 94166. This report covers the stock assessment component for spawn deposition biomass estimates. This project will be continued in FY96 as Restoration Project 96166.</u>

Abstract: Underwater dive surveys of deposited eggs and acoustic techniques were used to estimate the 1996 adult spawning population of Pacific herring *Clupea pallasi* in Prince William Sound (PWS). The spawn deposition estimate of the spawning biomass of herring was 25,101 tonnes with a 95% confidence interval ranging from 13,039 to 37,163 tonnes. This project also evaluated the feasibility of using acoustic echointegration techniques to estimate herring biomass immediately prior to spawning. However, all herring known to be in the area were not surveyed because herring had moved into shallow water and began to spawn while the survey was being conducted. Future acoustic surveys will be conducted earlier in the season to avoid this problem. Egg loss of PWS herring was studied during spawn deposition surveys in 1990, 1991, 1994, and 1995. The proportion of eggs lost through physical removal and mortality was investigated to improve diver survey biomass estimates and understanding of the mechanisms controlling early life history survival. Results indicated that egg loss rates are highly variable, site specific and are generally higher than previously estimated. Depth of spawn deposition and wave exposure accounted for much of the variation in instantaneous egg loss rates in the Montague Island area.

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

<u>Project Data</u>: (will be addressed in the final report)

Citation:

Willette, T.M., G.S. Carpenter, and E. Debevec. 1997. Herring spawn deposition and reproductive impairment, *Exxon Valdez* Oil Spill Restoration Project Annual Report (Restoration Project 95166), Alaska Department of Fish and Game, Division of Commercial Fisheries Management and Development, Cordova, Alaska.

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INTRODUCTION

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

Relation to Other Oil Spill Studies

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 will be 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 were continued in 1994 and 1995. 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.
- 2. Quantify egg loss rates (the proportion of eggs removed through time) from spawning areas due to wave action, predation, desiccation, or fungal infections between the time of egg deposition (spawning) and the time of hatching. Quantify egg loss by habitat type and egg density.
- 3. Incorporate egg loss and egg survival estimates with results from previous studies and revise the models as necessary.
- 4. Define herring spawning habitat types by similarities in temperature, salinity, depth, gradient, substrate, vegetation, and exposure to wave action. Characterize and map habitat utilized for spawning. Estimate the abundance and distribution of adult herring and eggs by habitat type. Test a model of the relationship of spawn timing, spawner density and abundance to egg distribution and density.

- 5. Incorporate egg loss and survival data with physical oceanographic and meteorological data to formulate and test a model of the relationship of meteorological conditions to wave height and egg desiccation.
- 6. Test a model of the relationship between predation, wave action, desiccation, fungal infections, habitat type, and egg density.
- 7. Test a model relating sound-wide embryo survival to habitat type, egg density, and meteorological conditions.
- 8. Test a model relating historic recruitment success to biological and environmental variables.

METHODS

Spawn Deposition Survey and Biomass Estimation

Biomass estimation based on spawn deposition surveys consisted of three major components: (1) a spawn deposition survey; (2) age-weight-length (AWL), sex ratio, and fecundity sampling; and (3) egg loss determination.

<u>Spawn Deposition Survey Design</u>: Spawn deposition surveys were conducted to obtain biomass estimates within ± 25% of the true biomass 95% of the time. Survey design was described in detail by Biggs and Funk (1988) and followed the two-stage sampling design of similar surveys in British Columbia (Schwiegert et al. 1985) and Southeast Alaska (Blankenbeckler and Larson 1982, 1987). Surveys consisted of random sampling for the first stage (transects) and systematic sampling for the second stage (quadrats within transects). Surveys were stratified by area to account for geographic differences and the potential for discrete herring stocks. Areas surveyed included Southeast, Northeast, and Montague Island (Figure 1).

Mean egg densities along each transect were combined to estimate average egg density by summary area. Spawning bed width along each of the transects was used to estimate average spawning bed width by summary area. Average width, average density, and total spawning bed shoreline length (judged from aerial surveys) were used to estimate total number of eggs deposited in each summary area. Average fecundity and sex ratio obtained from AWL sampling, and estimates of total number of eggs deposited from diver surveys were used to calculate herring population numbers and biomass. Confidence intervals were calculated assuming a normal distribution of total egg estimates.

<u>Spawn Deposition Survey Sampling Procedure</u>:-- The general location of spawning activity was determined from visible milt observed during aerial surveys (Figure 1). Spawning activity was summarized on maps showing spawning locations and the dates on which milt

was observed. Linear distances of shorelines over which herring spawned were estimated directly by aerial surveyors and were later measured from hand drawn aerial survey maps. Hand drawn maps were transcribed to computerized maps and linear distance estimated by the software was compared to surveyor estimates. Aerial observations were corrected using direct observations of eggs at the time of dive surveys.

Mapped shorelines containing herring spawn were divided into the shortest resolvable segments on the map scale (approximately 0.18 km) to aid in locating transects (Figures 2 and 3; Table 1). The total number of potential transects was calculated from the total of all shoreline where spawning was observed. A minimum sampling goal of 0.035 % of all potential transects within the spawning area was set to meet specified accuracy and precision based on variances obtained during 1984, and 1988 to 1992 surveys. Shoreline segments were assigned random numbers and the desired number of transects were randomly selected from among all possible shoreline segments. Each segment selected was assigned a sequential transect number and charted on waterproof field maps. Approximate locations for each transect were obtained from these field maps and exact locations were fixed as the dive skiff approached the shore before bottom profiles, bottom vegetation, or herring spawn became visible from the skiff. Typically, the skiff driver would choose an easily recognizable shoreline feature within the targeted shoreline segment as a reference point (e.g. a tree, rock, or cliff located above the high tide line) to locate the transect. The sampling transect extended seaward along a compass course perpendicular to shore from this fixed reference point.

Diving operations began several days after spawning ceased to allow water turbidity due to milt to decrease and for the large numbers of sea lions usually present near spawning herring to disperse. Two three-person dive teams consisted of a lead diver counting eggs (typically the person most experienced at this survey task), a second diver recording data, and a third diver on the surface serving as a dive tender. Diving and tending duties were rotated daily.

The number of herring eggs occurring within a standardized sampling quadrat was estimated at regular intervals along the length of the transect. The sampling quadrat consisted of a 0.1 m^2 frame constructed of PVC pipe with a depth gauge and compass attached. Location for the first quadrat placement along the transect was haphazardly selected within the first 5 meters of spawn. Succeeding quadrat placements were systematically spaced every 5 meters along the compass course until the apparent end of the spawn. At each quadrat placement, the lead diver estimated the number of eggs in units of thousands (K) within the quadrat and communicated the numbers through hand signals to the second diver. Number of eggs, vegetation type, percent vegetation cover, substrate, and depth were recorded by the second diver in pencil on water-proof plastic paper data forms attached to a clipboard. Divers verified the end of the spawn by swimming at least an additional 20 m past the end of the spawn until a steep drop-off was encountered or vegetation was no longer present.

<u>Biomass Estimation</u>: Analysis of the spawn deposition survey data was similar to methods used in 1988 (Biggs and Funk 1988), and 1989-1992 (Brown 1995). The biomass estimator was

$$B=TB',$$
 (1)

(m)

(m)

where

В	=	estimated spawning biomass in tonnes,
Т	=	estimated total number of eggs (billions) deposited in an area, and
B'	=	estimated tonnes of spawning biomass required to produce one billion eggs.

Estimates for T and B' were derived from separate sampling programs and were independent. The estimated variance for the product of the independent random variables T and B' was calculated according to Goodman (1960)

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

where

Var(B') = an unbiased estimate of the variance of B', and Var(T) = an unbiased estimate of the variance of T.

<u>Total Number of Eggs (T)</u>: The total number of eggs deposited in an area was estimated from a two-stage sampling design using random sampling at the primary stage and systematic sampling at the secondary stage, similar to the design described by Schwiegert et al. (1985). To compute variances based on systematic second stage samples, it was assumed that eggs were randomly distributed in spawning beds with respect to the 0.1 m² sampling unit. While this assumption was not examined, in practice the variance component contributed by the second sampling stage is much smaller than that contributed by the first stage and violation of this assumption has little effect on the overall variance. The total number of eggs (T), in billions, in an area was estimated as

$$T = N\hat{y} 10^{-6} / (1 - R),$$
 (3)

where

L	=	the shoreline length of the spawn-containing stratum in meters,
Ν	=	$L/0.1^{0.5}$ = the total number of possible transects,
$0.1^{0.5}$	=	0.3162 m = width of transect strip,
ŷ	=	average estimated total number of eggs (thousands) per transect,
10-6	=	conversion from thousands to billions of eggs, and
R	=	estimated proportion of eggs disappearing from the study area from the time of
		spawning to the time of the survey.

Average total number of eggs per transect (in thousands) was estimated as the mean of the total eggs (in thousands) for each transect using

$$\hat{y} = \frac{\sum_{i=1}^{n} \hat{y}_i}{n},$$
(4)

where

$$\hat{\mathbf{y}}_i = M_i \overline{\mathbf{y}}_i, \tag{5}$$

and

n	=	number of transects actually sampled,
i	=	transect number,
M _i	=	$w_i/0.1^{0.5}$ = number of possible quadrats in transect i,
w _i		spawn patch width in meters measured as the distance along the transect between the first quadrat containing eggs and the last quadrat containing eggs, and

$$\overline{y}_i$$
 = average quadrat egg count in transect i (in thousands of eggs).

Average quadrat egg count within a transect, $\overline{y}_{i},$ was computed as

$$\overline{y}_i = \frac{\sum_{j=1}^{m_i} y_{ij}}{m_i},\tag{6}$$

where

j =	quadrat	number	within	transect i,
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 m_i = number of quadrats actually sampled in transect i, and

= adjusted diver-estimated egg count (in thousands of eggs) from the diver calibration model for quadrat j in transect i.

The variance of T, ignoring the unknown variability in R, was similar to that given by Cochran (1963) for three stage sampling with primary units of equal size. In this case the expression was modified because the primary units (transects) did not contain equal numbers of secondary units (quadrats), and the variance term for the third stage comes from the regression model used in the diver calibration samples. Therefore the estimated variance of T, conditioned on R, was

$$[N^{2}(10^{-6})^{2}[\frac{(1-f_{1})}{n}s_{1}^{2} + \frac{f_{1}(1-f_{2})}{n}s_{2}^{2} + \frac{f_{1}f_{2}}{n}s_{3}^{2}]]$$

$$Var(T) = \frac{\sum_{i=1}^{n} m_{i}}{(1-R)^{2}},$$
(7)

where

y_{ii}

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

variance among transects,

$$s_{2}^{2} = \sum_{i=1}^{n} M_{i}^{2} \sum_{j=1}^{m_{i}} \frac{(y_{ij} - \bar{y}_{i})^{2}}{n(m_{i} - 1)} =$$
(9)

variance among quadrats,

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

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

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

proportion of possible transects sampled, and

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

proportion of quadrats sampled within transects (same for all transects).

<u>Diver Calibration Sample Collection</u>: Spawn deposition survey methods for estimating spawning biomass utilize diver estimates of the number of eggs deposited within a systematically placed 0.1 m^2 quadrat. It is possible or even likely that estimates of egg abundance vary considerably from the true abundance. A portion of that variability can be attributed to systematic effects which can be accounted for in a calibration model. Estimates of the effects of vegetation type and diver bias on egg counts were used to adjust the original counts, resulting in more accurate estimates of egg abundance.

Diver calibration samples were collected concurrently with spawn deposition surveys throughout the field season. Calibration samples were stratified by diver, vegetation type within four broad categories, and by egg density over three broad categories. Both divers independently estimated the number of eggs on removable vegetation in each calibration quadrat. All egg-containing vegetation within the quadrat was removed and placed in numbered mesh bags. The number of loose and attached eggs left after removal were estimated by the lead diver and recorded. Based on accuracy estimated for previous survey results, an approximate sample goal of 80 calibration samples was set for each diver who had less than three years survey participation and 40 for each calibrated diver who had participated in calibration sampling for three or more years of surveys. Calibration samples for each diver were to be taken equally from each of four vegetation categories: eelgrass (EEL), fucus (FUC), large brown kelp (LBK), and hair kelp (HRK); and equally from each of three ranges of egg densities: low (0-20,000), medium (20,000-80,000), and high (>80,000) within each vegetation category. Aboard the dive vessel, calibration samples were arranged within a sampling quadrat placed on the deck and all divers estimated the number of eggs within the quadrat to increase the number of calibration samples available for each diver and to simulate estimates conducted at low tide. Calibration samples were preserved in Gilson's solution and labelled as described by Becker and Biggs (1992). The actual number of eggs present in each calibration sample was later approximated gravimetrically in the laboratory using procedures also described in Becker and Biggs (1992).

<u>Diver Calibration Modelling</u>: Initial analysis of the 1995 spawn deposition diver calibration data was performed by Ed Debevec, ADF&G, Cordova, and is summarized here. More detailed information describing the motivation, methods, and results of his analysis are presented in his original paper as Appendix A.

The diver calibration analyses was done slightly different from that outlined in the 1995 Detailed Project Description. The purpose of the diver calibration is to adjust for systematic biases in the egg count and provide a more accurate estimate. This procedure considered diver and kelp type effects in that different divers may have had very different biases (e.g., one tended to overestimate while another underestimate) and different kelp types may have provided very different conditions for making the estimates. Calibration samples were collected throughout the dive survey and then counted in the lab. Diver calibration was then determined from the relationship between diver counts in the field (dependent variable) and the true lab counts (independent variable), assumed to be without errors. Covariates used in the model were diver and kelp type. Additional factors such as depth of sample, date, and time of day could also be important, but were assumed to be negligible.

Past analyses have used a two-step procedure: (1) pool like groups and (2) obtain calibration parameters for each group. Say we had calibration data for three years for four divers on four different kelp types, for a total of 48 possible groups $(3\times4\times4=48)$. The process was to determine which groups could be pooled so that we could "beef up" this years' sample sizes. Lab counts are fairly expensive in time and money making it impossible to collect a sufficient set of calibration samples each year. This process was a way to combine all available data to yield more precise adjustments from the resulting larger sample sizes.

In the present study, diver calibration regressions were calculated for each diver separately using data from all years combined where the observations were weighted by the year collected. This approach was taken because it appeared that earlier results from analyses of variance tests for differences in regression parameters among divers and years (Wilcock et al. 1995) may have been affected by differences in the samples sizes available for each group. As a result, the analysis of variance tests may not have always correctly indicated which groups should or should not be pooled. The weighted regression approach is appropriate regardless of whether the regression parameters differ among years within divers. This was intuitively appealing in that all data from past years were included in the analysis, but the most recent data were considered more important or perhaps more relevant to this year's calibration. The regressions were conducted for each diver separately because from talking with the divers it seemed that a single diver was more consistent between years than several divers were within the same year. Specifically, the regression weights were calculated as

$$weight_i = \frac{1}{96 - year_i}$$
(13)

where year_i is the year that observation i was taken (95, 94, etc.). Thus, observations from 1995 received a weight of 1, while those from 1994 had a weight of $\frac{1}{4}$, etc. Separate regressions were fit for each diver with kelp type used as a class variable in the analysis

Reparameterization was used to obtain directly relevant parameter estimates. For this analysis, each parameter estimate was the slope for a particular year, rather than having some parameters being the difference in slope between years as would be the case with the usual parameterization. The analyses were run with the intercept forced through zero, egg counts in actual number of eggs (i.e., 100 meant 100 eggs, not 100,000 eggs), and with years pooled. The diver calibration model used was

$$\log(dc_{ijk}) = \beta_{jk} \log(lc_{ijk}) + \epsilon_{ijk}$$
(14)

where dc_{ijk} was the ith count for diver j on kelp type k and lc_{ijk} was the associated lab count.

The egg count adjustment used the appropriate parameter estimate (for a given diver and kelp type) in an inverse prediction method of the form

$$adc_{ijk} = e^{\frac{\log(dc_{ijk})}{\beta_{jk}}}$$
(15)

where adc_{ijk} was the ith adjusted count for diver j on kelp type k. Note that the term adc replaced lc in equation (2) to represent the expected lab count, i.e., the adjusted diver count. Using the delta method, the variance for the adjusted count was determined to be as follows:

$$VAR(adc_{ijk}) = \left(\frac{\log(dc_{ijk})^2 VAR(\hat{\beta}_{jk})}{\hat{\beta}_{jk}^4}\right) e^{\frac{2\log(dc_{ijk})}{\hat{\beta}_{jk}}}$$
(16)

<u>Spawning Biomass per Billion Eggs (B')</u>:-- AWL, sex ratio, and fecundity data were used to estimate the relative relationship between spawning biomass and egg deposition. The

relationship between fecundity and female weight was used to calculate total number of eggs deposited and tonnes of herring spawners. The tonnes of spawning biomass required to produce one billion eggs (B') was estimated as

$$B' = \frac{\overline{WS}}{F(\overline{W}_{f})} 10^{3}, \tag{17}$$

where

 \overline{W} = estimated average weight in grams of all herring (male and female) in the spawning population in an area,

S

= estimated ratio of total spawning biomass (male and female) to female spawning biomass,

$$F(\tilde{W}_{f})$$

= estimated fecundity at the average weight of females in the spawning population in an area, in numbers of eggs, and

$$10^3$$
 = conversion factor = $\frac{10^{-6}}{10^{-9}}$ grams to tonnes
= $\frac{10^{-9}}{10^{-9}}$ eggs to billions

Because average weight, sex ratio and fecundity were all estimated from the same herring samples, the estimates were not independent. The variance of B' was approximately:

$$Var(B') = (10^{3})^{2} \left[\left[\frac{S}{F(\overline{W}_{f})}\right]^{2} Var(\overline{W}) + \left[\frac{\overline{W}}{F(\overline{W}_{f})}\right]^{2} Var(S) + \left[\frac{\overline{W}S}{F(\overline{W}_{f})}\right]^{2} Var(F(\overline{W}_{f})) + 2Cov(\overline{W},S)\left[\frac{S}{F(\overline{W}_{f})}\right]^{2} Var(F(\overline{W}_{f})) + 2Cov(\overline{W},S)\left[\frac{S}{F(\overline{W}_{f})}\right] \left[\frac{\overline{W}}{F(\overline{W}_{f})}\right] \left[\frac{\overline{W}S}{F(\overline{W}_{f})}\right] \left[\frac{\overline{W}S}$$

(18)

Because S was estimated from pooled or single AWL samples (depending on availability of fish), it was not possible to estimate the covariance terms containing S, $Cov(\overline{W},S)$ and $Cov[S,F(\overline{W}_f)]$. Because the term involving $Cov[\overline{W},F(\overline{W}_f)]$ has been shown to be very small in previous analyses and probably contributes little to Var(B'), these covariance terms were not included in the estimate of Var(B').

Herring Age, Weight, Length, Sex, and Fecundity

Biological samples were collected for age and sex composition, calculation of average weight and length, and estimation of fecundity. Most samples were captured by volunteer commercial seine vessels or vessels under short term contract as part of an existing ADF&G test fishing sampling program. Sampling generally occurred soon after concentrations of herring appeared in nearshore areas becoming accessible to purse seines and continued periodically throughout the spawning migration. Age and sex composition and average herring size were calculated using only AWL samples collected near the peak of spawning as determined from aerial survey sightings of milt and herring schools. AWL sampling was stratified by date and locality for test fishing catches in spawn deposition summary areas. Sample size for each stratum was set to simultaneously estimate proportions by age when sampling from a multinomial population (Thompson 1987). The goal was to select the smallest sample size for a random sample from a multinomial population such that the probability would be at least $1-\alpha$ (precision = 0.05) that all the estimated proportions were simultaneously within 5% (accuracy = 0.05) of the true population age proportions. A sample size of 450 herring per stratum was selected to ensure that this level of precision and accuracy would be obtained for any number of age classes and proportions when 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 *In press*).

Fecundity samples were subsampled from female herring in AWL samples and were stratified by fish length. Egg and gonad weights were measured and used to calculate average fecundity at the average female weight $(F(\overline{W_t}))$. Fecundity sampling goals were set such that fecundity estimates would contribute no more than 1% to the confidence interval width of the biomass estimate. It was determined that a sample size of 150 to 200 herring pooled across areas would be sufficient to maintain the coefficient of variation below 2.0%. To collect females across the range of all possible sizes, sample goals were 20 to 30 females within each 10 mm length category from 181 to 250 mm standard length, and 20 to 30 females 180 mm or smaller. The female gonad weight was the weight of the ovaries removed from each female.

<u>Mean Weight and Sex Ratio</u>: Average weight and sex ratio was estimated as a weighted average of estimates from each sampled locality based on observed aerial survey biomass at each locality. Because biological samples were collected only at Montague Island and because spawning observed in other areas was limited, AWL samples from Montague Island were used to estimate mean weight and sex ratio for all spawn deposition summary areas.

Sex ratio, S, was calculated as the ratio of the number of herring of both sexes in AWL samples to the number of females. The binomial distribution is applicable to estimating the proportion, p, of females in AWL samples, where S = 1/p. The variance of S is

$$Var(S) = \frac{S^2(S-1)}{n},$$
 (19)

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

<u>Fecundity for Biomass Estimates</u>: Average fecundity for PWS was estimated from a fecundity-weight relationship as $F(\overline{W}_t)$, and used in equation 17 to estimate biomass from

spawn deposition. The variance of estimated average fecundities was approximated by the variance of predicted means from the fecundity-weight linear regression (Draper and Smith 1981)

$$Var[F(\bar{W}_{f})] = S^{2}[\frac{1}{n} + \frac{1}{q} + \frac{(\bar{W}_{f} - \bar{W}\bar{F})^{2}}{\sum (\bar{W}_{i} - \bar{W}\bar{F})^{2}}],$$
(20)

where

s ²	=	the residual mean square from the fecundity-weight linear regression,
Ŵŗ WF	=	the average weight of female fish in the spawning population,
WF	=	the average weight of females in the fecundity sample,
W_i	=	the weights of individual females in the fecundity sample,
n	=	the total number of females in the fecundity sample from each area, and
q	=	the total number of females in the representative AWL sample or pooled
		samples from the corresponding area.

A linear relationship between female body weight and fecundity was used because Hourston et al. (1981) found that female body weight at spawning explained 70% of the variation in fecundity among individuals, but length and age only explained another 2% of the variation.

Egg Loss Study

The proportion of eggs lost through physical removal and the mortality rate of remaining eggs was investigated to improve diver survey biomass estimates and to improve understanding of the mechanisms controlling early life history survival. The total number of eggs estimated from diver surveys (term T, equation 1) was corrected for eggs lost between the time of herring spawning and diver surveys as term R in equation 3. In prior spawn deposition studies for PWS, an assumed constant egg loss rate of 10% was used to correct spawn deposition estimates based on values recommended in the literature (Haegele et al. 1981, Blankenbeckler and Larson 1982). This estimated loss was based on the assumption that surveys were generally conducted 5-6 days after spawning. Egg loss was studied during spawn deposition surveys of PWS in 1990 and 1991 to more accurately quantify loss rates (Brown 1995). These studies indicated that egg loss varied substantially over time and between sites and suggested that using a constant rate of 10% may be inappropriate in some instances. These studies also suggested that spawning habitat may play a key role in determining egg loss rates, but the study design did not include collection of data to relate egg loss to habitat type, environmental conditions, or predation. The 1995 study included measurements of 1) slope, substrate, and vegetation to describe habitat characteristics; and 2) temperature and salinity to describe environmental conditions. In addition, information was collected about bird predators in collaboration with EVOS Project 95320Q, Avian Predation on Herring Spawn. A Reimbursable Services Agreement (RSA) was initiated with the University of Alaska to investigate the factors important for estimating egg loss using the

results from previous studies and the 1995 study. They also began investigating the modelling of egg loss to eventually construct an embryo survival model. A progress report for this work is included as Appendix B. More detailed descriptions of their analytical methods and results for egg loss studies will be included in their final report, anticipated for late FY96.

Egg Loss Sampling Procedure. Eight transects were established in 1995 on Montague Island to study egg loss (Figure 2; Table 2). Transect locations were chosen to represent typical spawning beach habitat characteristics within the spawn deposition summary area and to cover the range of potential exposures to wave action during incubation. Similar to spawn deposition transects, egg loss transects were established perpendicular to shore following a compass course. Three sampling stations were located along each transect line at depths within the range of usual herring spawn (+1.65 m to -9.90 m). Sampling stations were set at (1) 1.0 m above MLLW, (2) 1.0 m below MLLW, and (3) 3.0 m below MLLW based on information from previous egg loss and egg distribution studies. Station depths for some transects were adjusted according to actual deposition of eggs. Depth at each station was initially determined using SCUBA diver depth gauges and later corrected for tide level. During transect establishment, beach gradient, substrate, and vegetation present at the site were recorded.

A grid of 5 x 2 permanent 0.1 m^2 quadrats was placed along transect lines at each depth station. Grids were generally oriented perpendicular to the transect and parallel to the shoreline, but actual placement was adjusted to conform to bottom contour, occurrence of spawn, and to represent vegetation typical of the site at that depth.

To collect information on egg loss due to predation and wave action, predator exclusion frames were placed at each of the three depth stations along each transect line. Exclusion devices were constructed from steel shrimp trap frames approximately 1 m^3 in volume and enclosed in mesh. Placement at each depth included: (1) one frame covered with small mesh intended to retain all eggs lost from wave action and to exclude large predators, (2) one frame covered with mesh large enough to exclude avian predators, but which would allow physical egg removal by wave action, and (3) a control plot marked by steel spikes, but without frames or mesh.

Transects were generally visited every three to four days. During each site visit, divers estimated egg density within each of five 0.1 m² quadrats along the bottom row of the fixed quadrat grid and the top row was reserved in case of destruction of any quadrats in the bottom row. Divers also collected eggs and vegetation within a separate 0.1 m² quadrat haphazardly placed near the egg loss grid for calibration samples. Diver calibration samples were preserved and processed in the same manner as those collected for spawn deposition surveys. During each site visit, measurements were made of air temperature, water temperature, and salinity. In addition, precipitation, tide height, wind speed and direction were noted. To investigate the range of temperatures to which incubating eggs would be exposed, mechanical temperature recorders were installed at two egg loss sites. However, recorders were not activated properly and only temperatures measured during site visits were collected.

An additional sample containing over 200 eggs, was haphazardly selected from vegetation adjacent to the frames during each visit and depth. For each such sample, live/dead ratios were estimated and the eggs were examined for signs of desiccation or other signs of morbidity. Subsamples of live embryos were also collected just prior to hatch and preserved for later evaluation of morphological abnormalities and cytogenetics. Subsequent funding for processing of these samples was not included in the FY95 work plan.

Near the mid-point date of the incubation period, a sample of potential herring egg predators within an approximately $1 m^2$ patch of spawning area adjacent to each egg loss transect was collected for species identification. Eggs and vegetation collected for this sample were preserved in Gilson's solution and all vertebrate and invertebrate animals were frozen. Frozen samples were submitted to nearshore researchers at the University of Alaska Fairbanks for identification.

Acoustic Survey and Biomass Estimation

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 scientific echosounding equipment was located aboard the ADF&G research vessel *Montague* for acoustic mapping of the biomass. The acoustics vessel was outfitted with a BioSonics 120 Khz echo sounder with a dual beam pre-amplified transducer mounted on a 1.2 m BioSonics Biofin in a down-looking configuration. The Biofin was towed at a depth of about 2 m at approximately 5 m off to one side of the vessel. The catching vessel was equipped with a seine approximately 30 m deep typical of the gear-type used in the commercial sac roe herring fishery.

<u>Survey Design</u>. The acoustic survey followed a multistage sampling design (Cochran 1967). Historical information about location of spawning, aerial surveys of herring schools, and wide scale searches using ship's searchlight (sweeping) and down-looking echosounders was used to locate concentrations of herring schools in a first stage search. The second stage of sampling involved mapping the school groups and measuring the density using the scientific

echosounder. Acoustic survey transects were run in a zigzag fashion over the school groups and were replicated during both day and night for large school groups.

<u>Acoustic Parameters</u> Target strength information for herring was derived from average length to target strength (in decibels) per kg fish after Thorne (1983a). Thorne's (1983a) empirical relationship assumes the following logistical equation:

$$\gamma = \frac{\overline{\sigma}}{\overline{W}} = a\overline{l}^{-b}$$
(21)

where σ is the mean acoustic backscattering coefficient, W is the mean weight (in kg), 1 is the mean length (in cm), and a and b are constants. Values for the constants (a and b) are obtained from data for a variety of fisheries presented by Thorne using a linear regression of \log_{10} versus 10 log (σ /w), where 10 log (σ /w) is referred to in Thorne (1983a) as "target strength per kg." Average herring length and weight data was compiled from samples obtained by the purse seine catcher vessel. These measured data were applied to Thorne's (1983a) empirical relationship to obtain the ratio $\gamma = \sigma$ /w and the mean backscatter coefficient (σ). As a cross check, *in situ* measurements of target strength from dual beam acoustic data were generated and compared with Thorne's (1983a) empirical formula.

<u>Biomass Estimation</u> Herring biomass was calculated for each zigzag survey. The general calculation of the population density using echointegration for a single cell jk on a transect is given as

$$\beta_{jk} = \rho_{jk} \overline{w}_{jk} = \frac{C(ei)_{jk} \cdot P_{jk}}{\frac{\overline{\sigma}_{jk}}{\overline{w}_{jk}}}$$
(22)

where β_{jk} is the population density (mass per unit volume), ρ_{jk} is the density of scatterers, w_{jk} is mean weight of scatterers, C is acoustic constant (calibration settings ie., gain etc.) e_{ijk} is the mean of the voltage squared, P_{jk} is percentage of cell *jk* within the water column, and σ_{jk} is mean backscattering coefficient for targets within cell *jk*.

The biomass for a region of surface area A is determined by using a set of line transects along which a total of nrs point estimates of biomass per unit area is obtained. Specifically, where nrs is number of reports (along the line transects), nst is number of depth strata, and A is survey area.

$$B = \frac{\sum_{j=1}^{nrs} \sum_{k=1}^{nst} \beta_{jk}}{nrs} \cdot A$$
(23)

Herring biomass estimates followed Thorne (1983a), assuming that σ_{jk}/w_{jk} is independent of cell *jk*, hence, for all *jk* σ_{jk}/w_{jk} is a constant γ , and γ is given by equation 21. With this assumption, equation 22 simplifies to:

$$\beta_{jk} = \frac{C}{\gamma} \cdot (ei)_{jk} P_{jk}$$
(24)

and the herring biomass B in an area is given as

$$B = \frac{C}{\gamma} \frac{\sum_{j} \sum_{k} (ei)_{jk} P_{jk}}{nrs} A$$
(25)

RESULTS

Biomass Estimation

The total biomass of herring spawning naturally in PWS during 1995 was estimated to be 18,163 tonnes from spawn deposition diver surveys (Table 3). The variance of this estimated total was high, and the 95% confidence limits ranged from 11,410 tonnes to 24,916 tonnes (Table 4). Most of the estimated biomass spawned in the Montague Island summary area (16,463 tonnes), but small biomasses of spawning herring were calculated for the Southeastern (1390 tonnes) and Northeastern (309 tonnes) summary areas (Figure 1). The total biomass from 1995 was approximately 3,175 tonnes more than the 1994 biomass which was primarily due to more spawn in the northeast and southeast areas of PWS. The total miles of spawn in 1995 increased by approximately 40% from 1994 mainly due to the increases in the northeast and southeast.

<u>Diver Calibration Modelling</u>: The diver calibration method was implemented with adjusted egg counts calculated for the 1995 data. The range of diver calibration counts for 1995 was 0.6 K to 530 K, while it was 0.6 K to 1442 K for all years. The range of diver estimates on

sampled quadrats in 1995 was 0 to 2800 K, almost double the maximum calibration point from any year. This raised the concern that we were using the calibration model on points well outside the range of data used to build the model. We could assume the trend continues to these high counts, but that may not be realistic. There appeared to be a tendency for high counts to be more accurate than moderate counts. This can be seen in a plot of all calibration points where the mean diver count is decidely underestimated below around 5.5 on the X-axis, while points greater than 5.5 appear to be centered on the unity line (Figure 4).

Without calibration points to cover the range of the data, it is difficult to model these extreme counts with any kind of certainty. The model over the range of available calibration points resulted in an adjustment that becomes more severe for larger diver estimates. For extremely large estimates, such as 2800 K which is five times the maximum calibration point for 1995, the resulting adjustment would be quite substantial. Based on what little supporting data we have, this does not seem to be realistic.

Several options regarding large diver estimates were considered. The first was to leave the model as it was and run the adjustment. As just stated, this was not considered a realistic option and the resulting five or six extremely large estimates had a substantial effect on the final biomass estimate, varying the result by several thousand tons depending on whether they were included in the analysis or not. The second option was to use the calibration model on diver counts up to some threshold number of eggs, but no adjustment on counts above the threshold. However, this also seemed to be rather extreme. Additionally, there would be an unrealistic discontinuity in the model around the threshold.

A third option was used that was a compromise between the first two. Again, the calibration model was used on diver counts up to a threshold number of eggs. However, instead of switching to the unity line for points above the threshold, a line parallel to the unity line was used that was continuous with the calibration line. The resulting calibration tended to follow the apparent curve suggested in Figure 4 where estimates seemed to be more accurate at the higher counts. Perhaps non-linear regression could be used to better model the relationship. More essential, though, is the need for more calibration points for higher diver counts.

Herring Age, Weight, Length, Sex, and Fecundity

Age and sex composition and average size at each locality is estimated as part of ongoing ADF&G fishery management activities. These data will be published separately in a regular Commercial Fisheries Management and Development Division reporting series (personal communication, D. Sharp, Alaska Department of Fish and Game, Cordova; unpublished data, J. Wilcock, Alaska Department of Fish and Game, Cordova). The average size at age of all sampled herring and the estimated contribution by age to the 1995 PWS herring biomass is presented in Table 5. As expected from preseason forecasts (Funk 1995), the total biomass consisted largely of age-7 herring from the 1988 year class (52.7% contribution by weight and 44.9% by number). The abundance of herring from the 1989 year class continued to be low

and comprised only 2.5% of the total number of fish. Abundance of age 3 fish (24.1% by number) increased over 1994 indicating relatively strong recruiment of the 1992 year class.

The average weight of all sampled herring was 123.0 g and the average length was 211 mm, similar to average weights observed in 1994 (Wilcock et al. 1995). Sex ratios varied between project summary areas, 2.65 for Montague, 2.27 for the Northeast and 2.89 for the Southeast areas. (Table 3). Regression results for the weight to fecundity relationship are presented in Figure 5. Average fecundity of female herring by summary area was similar to fecundity estimated for previous years (Table 3).

Egg Loss Study

Sites for 8 egg loss transects established on Montague Island during 1995 (Figure 2; Table 2) were chosen to represent a range of habitat characteristics over which herring spawn occurred. All sites were visited at least eight times during incubation. Exposures varied from very protected shoreline near the head of Rocky Bay at site 2, to extremely exposed rocky oceanic shoreline at site 6 on Montague Point. Rocky substrates were most frequent (6) at egg loss sites reflecting the selection of this substrate by spawning herring, while sand or mud bottoms occurred at only one site.

Avian predation exclusion frames were installed at all sites, but a number of frames were dislodged by wave action over the course of incubation, particularly the frames enclosed in small mesh. It was also found that algal and detrital build-up was severe on the small mesh frames and that loose eggs tended to drift into the frame from outside the enclosure and accumulate. Because of these shortcomings, small mesh enclosures were not felt to accurately represent egg loss and were dropped from the analysis. Large mesh frames were less frequently dislodged, and data from these frames will be included in the egg loss completion report. More detailed discussion of avian predator methods and results is included in the annual report for project 95320Q.

Preliminary analysis of egg loss data collected for 1995 was conducted under a reimbursable services agreement with the University of Alaska (Appendix B). They graphically examined 1995 egg loss results as well as results from previous studies to identify factors important for modelling egg loss. More detailed descriptions of their methods and results will be included in the final report for that project component.

Acoustic Survey and Biomass Estimation

The spring 1995 acoustic biomass estimation consisted of five surveys in the Montague Island summary area. Sonar and aerial surveys indicated that this area represented the primary spawning concentration of herring in PWS. Two daytime surveys were conducted in both Rocky Bay and Zaikof Bay, and two night time 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 samples in Zaikof Bay was 184 mm, resulting in a

scaling factor of -31.9 dB/kb. The resulting biomass estimates for Rocky Bay was 9,265 tonnes and Zaikof Bay was 2,735 tonnes. Historically, herring acoustic surveys have used -33 dB/kg as the scaling factor regardless of the length of the fish. Using the -33db/kg scaling estimate would have increased the biomass estimate for Rocky Bay by 18% and Zaikof Bay by 29%, respectively. The 1995 spring biomass estimate of 12,000 tonnes for the two areas was similar to the 12,500 tonnes of herring estimated the previous fall (Thomas et al. 1995). The final report on the 1995 spring acoustic survey has not been received from the contractor. Detailed descriptions of their methods and results will be included in the 1996 annual report.

DISCUSSION

Preliminary estimates from the 1995 spawn deposition surveys were incorporated into age structured assessment (ASA) models to project the returning run biomass in 1996 as part of ongoing Department stock assessment and management functions (Funk 1995). ASA modelling generally incorporates other stock abundance estimates including aerial surveys of peak biomass of herring schools and kilometers of visible milt, estimated biomass from fall acoustic surveys, and information about age structure and average fish size to calculate projected returns. During the years of high abundance for herring (1988-1992), spawn deposition surveys provided abundance estimates that varied considerably from these other indicators of population size and spawn deposition estimates were accorded minimal weighting in ASA modelling. In general, differences between spawn deposition survey estimates and other stock assessment methods in 1995 were not as great as in these prior years. Biomass estimates based on aerial surveys of peak abundance, although it is generally felt that aerial surveys typically tend to underestimate abundance because not all fish schools or milt releases are visible to surveyors.

Accurately estimating the magnitude of herring populations is made difficult because they are a highly mobile species and exhibit large changes in distribution and abundance over a wide range of spatial and temporal scales. Spring spawning migrations provide perhaps the best opportunity to estimate abundance because herring are more aggregated and more visible than at other times of the year. Acoustics and other spectral technologies (e.g. LIDAR, CASI) could provide accurate and cost effective means of quantifying herring abundance, but these methods are limited in the amount of area that can be surveyed and occurrence of herring beyond areas surveyed is difficult to reconcile. Species verification of the quantified targets is also required.

Spawn deposition surveys are designed to estimate spawning abundance for all observed spawning herring, but the accuracy of the method is constrained on several points. It is assumed 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 surveyors attempt to minimize the occurrence of unobserved spawning through frequent surveys. Two other important factors which can affect the accuracy of spawn deposition using revised loss rates. Revised biomass estimates will continue to provide information useful to fine tuning of ASA population models. Formulation and application of diver calibration models was investigated for this study, and a logical alternative was chosen from among the various possible approaches. Of all terms included in biomass calculations from spawn deposition surveys, diver calibration models may have the greatest potential for affecting population abundance estimates. Investigation of diver calibration models should continue as an integral part of project operations. Because these and other constraints to the accuracy of spawn deposition surveys cannot be cost effectively eliminated, other potential methods of herring stock assessment should continue to be studied in conjunction with spawn surveys. In particular, acoustic surveys during herring spawning migrations may have the potential for estimating spring biomass at lower cost and take advantage of the aggregative behavior of herring at this time of year.

After FY98 a decision will be made to continue either spawn deposition surveys or hydroacoustic biomass estimates of the herring population. The spring 1995 acoustic biomass estimate was 12,000 tonnes while the spawn deposition survey estimate was 16,463 tonnes. The biomass estimation from the acoustic surveys covered only Rocky Bay and Zaikof Bay on Montague Island since these areas represent the primary spawning concentration of herring in PWS. The acoustic surveys generally are conducted prior to spawning when the herring begin to aggregate in the bays where as spawn depositon surveys begin 5 to 7 days after spawning has occurred. In addition to Rocky Bay and Zaikof Bay the herring spawn deposition surveys covered several other sites in the Montague Island summary area. For a direct comparison between the two methods the acoustic survey may need to be extended to additional spawning areas on Montague Island. During the spring of 1996 acoustic surveys will be conducted in the Montague Island area and compared to the spawn deposition biomass estimates.

CONCLUSIONS

- 1. Results from the spawn deposition surveys indicated that 18,163 tonnes of herring spawned in Prince William Sound in 1995.
- 2. Acoustic and spawn deposition techniques indicated that 12,000 and 16,463 tonnes of herring spawned in the Montague Island summary area, respectively.

ACKNOWLEDGEMENTS

We would like to thank the staff of the Alaska Department of Fish and Game, Prince William Sound Science Center, and University of Alaska Juneau who endured difficult field conditions to obtain the samples needed for this study.

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Figure 1. Location of spawning herring and kilometers of shoreline observed during aerial surveys in Prince William Sound, Alaska, 1995.

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Figure 2. Spawn deposition and egg loss transect locations in the Montague Island summary area, Prince William Sound, Alaska, 1995.



Figure 3. Spawn deposition transects in the Southeastern and Northeastern summary areas, Prince William Sound, Alaska, 1995.



Figure 4: Relationship between diver count and lab count for all divers and all years. Dashed line has intercept = 0 and slope = 1.



Number of Observations	312
Degrees of Freedom	310
Slope of Regression	182.45
Standard Error	6.16
Intercept of Linear Regression	-2531.2
Standard Error of Y Estimate	4345.62
R Squared	0.738

Figure 5. Regression of female weight and number of eggs per female for Pacific herring from Prince William Sound, Alaska, 1995.

Table 1. Location and survey date of herring spawn deposition transects, Prince William Sound, Alaska, 1995.

		Transect		ſ			Transect	Date
Summary Area	Transect Location	Number	Surveyed		Summary Area	Transect Location	Number	Surveyed
Montague Island	Rocky Bay	51	5/9/95		Montague Island	Port Chalmers	96	5/14/95
	Rocky Bay	52	5/11/95		(continued)	Port Chalmers	97	5/13/95
	Rocky Bay	53	5/11/95			Port Chalmers	98	5/14/95
	Rocky Bay	54	4/23/95			Port Chalmers	99	5/14/95
	Rocky Bay	56	5/11/95		Southeast	St. Matthews	1	4/20/95
	Rocky Bay	57	5/11/95			Hell's Hole	2	4/20/95
	Montague Point	58	5/10/95			Olsen Bay	3	4 / 21/95
	Rocky Bay	59	5/10/95			Olsen Bay	4	4/21/95
	Rocky Bay	60	5/11/95			Hell's Hole	5	4/20/95
	Montague Point	61	5/10/95			Hell's Hole	6	4/20/95
	Montague Point	63	5/9/95			St. Matthews	7	4/20/95
	Montague Point	64	5/9/95			St. Matthews	8	4/20/95
	Montague Point	65	5/8/95			St. Matthews	9	4/20/95
ł	Graveyard Point	66	5/8/95			St. Matthews	10	4/20/95
	Montague Point	67	5/10/95			Olsen Bay	11	4/21/95
	Montague Point	68	5/10/95			Olsen Bay	12	4/21/95
	Montague Point	69	5/10/95			Olsen Bay	13	4/21/95
	Montague Point	70	5/10/95			Olsen Bay	14	4/21/95
	Montague Point	71	5/10/95			Olsen Bay	15	4/21/95
	Graveyard Point	72	5/12/95			Olsen Bay	16	4/21/95
	Montague Point	73	5/12/95			Gravina Pt.	17	4/21/95
	Graveyard Point	74				Gravina Pt.	18	4/21/95
	Graveyard Point	75				Gravina Pt.	19	4/21/95
	Graveyard Point	76				Gravina Pt.	20	4/21/95
	Graveyard Point	77	5/15/95			Gravina Pt.	21	4/21/95
	Graveyard Point	78	5/15/95			Gravina Pt.	22	4/21/95
	Graveyard Point	79	5/15/95			Gravina Pt.	23	4/21/95
	Graveyard Point	81	5/8/95			Gravina Pt.	24	4 / 21/95
	Graveyard Point	82				Canoe Passage	35	4/23/95
	Stockdale Harbor	83			Northeast	Fish Bay	25	4/22/95
	Stockdale Harbor	84				Fish Bay	26	4/22/95
	Gilmour Pt.	85				Fish Bay	27	4/22/95
	Port Chalmers	86				Fish Bay	28	4/22/95
	Port Chalmers	88				Fish Bay	29	4/22/95
	Port Chalmers	89				Ellamar	30	4/22/95
	Port Chalmers	90				Ellamar	31	4/22/95
	Port Chalmers	91	5/14/95			Ellamar	32	4/22/95
	Port Chalmers	93				Ellamar	33	4/22/95
	Port Chaimers	94				Ellamar	34	4/22/95
	Port Chalmers	95	5/14/95					
Transect No.	Location	Date Installed	Date Removed	Number of Site Visits	Spawning Begin	Substrate	Exposure	
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1	Rocky Bay-Inner	1-May	21-May	12	28-Apr	Boulders	S. facing: semi protected	
2	Rocky Bay-Inner	2-May	24-May	12	28-Apr	Rocky	NW facing: protected	
11	Montague Reef	1-May	24-May	10	27-Apr	Rocky	SE. facing exposed	
14	S. Port Chalmers	4-May	22-May	9	27-Apr	Sand	W. facing: semi protected	
13	N. Port Chalmers	4-May	23-May	9	27-Apr	Rocky	NE facing: semi protected	
12	N. Graveyard Point	2-May	23-May	12	27-Apr	Rocky	N. facing exposed	
9	Graveyard Point	2-May	22-May	9	27-Apr	Rocky	NW facing: exposed	
6	Montague Point	30-Apr	21-May	11	27-Apr	Rocky	NE facing: exposed	

 Table 2.
 Location and spawn dates for herring egg loss study transects at Montague Island, 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	64123	10178	29517	103819
Number of transects sampled	n	52	10	25	87
Number of quadrats sampled	Σm_i	1089	142	302	1533
Proportion of transects sampled	f_1	0.00081	0.00098	0.00085	0.00084
Proportion of quadrats sampled	f_2	0.06325	0.06325	0.06325	0.06325
Average spawn patch width (m)		104.71	71.00	60.40	
Total area of spawn patches (km ²)		2.123	0.229	0.564	2.916
Unweighted average density (1000/m ²)		355.66	114.95	122.27	
Average total eggs per transect (K)	ŷ	14951	2079	2411	
Proportion of eggs lost before survey	R	0.1	0.1	0.1	
Total eggs in area (G)	Т	1065.22	23.51	79.06	1167.79
Average herring weight from AWL (g)	W	123	154	118	
Average weight of females (g)	\overline{W}_{f}	130	160	121	
Number of females in AWL sample	q	839	544	303	
Number of fish in AWL sample		2223	1238	877	
Sex ratio	S	2.650	2.276	2.894	
Fecundity of average female	$F(W_{f})$	21,086	26,643	19,419	
Fecundity regression slope		185.239	185.239	185.239	
Fecundity regression intercept		-2995.04	-2995.04	-2995.04	
Tonnes per billion eggs	B'	15.456	13.154	17.588	
Estimated biomass in tonnes	В	16,463.7	309.2	1,390.5	18,163.4
Estimated biomass in short tons		18,148.0	340.9	1,532.7	20,021.5
Short tons per statute mile		1,440.3	170.4	264.3	981.4
Millions of pounds per statute mile		2.88	0.34	0.53	1.96
Distribution (percent miles of spawn)		61.76%	9.80%	28.43%	100.00%
Distribution (percent biomass)		90.64%	1.70%	7.66%	100.00%

Table 3. 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
Egg Counts					
Variance - among transects	s_l^2	4.866×10 ⁸	5.202×10 ⁶	1.719×10 ⁷	
Variance - within transects	s ₂ ²	8.617×10 ⁹	1.182×10 ⁷	1.537×10 ⁸	
Variance - individual quadrats	S3 ²	30295	648	2770	
Variance of estimated total eggs	Var(T)	47494	66	739	48300
AWLS Sampling					
Variance of average weight		2.289	2.795	9.497	
Variance of sex ratio	Var(S)	0.0052	0.0053	0.0181	
MSE from fecundity regression	s ²	1.787×10 ⁷	1.787×10 ⁷	1.787×10^{7}	
Mean weight in fecundity sample		139.5	139.5	139.5	
Number of fish in fecundity sample		311	311	311	
Variance of est. average fecundity		8.203×10 ⁴	1.056×10 ⁵	1.289×10 ⁵	
Variance of B'	Var(B)	0.257	0.224	0.985	
Biomass Estimate					
Variance of biomass	Var(B)	1.163×10 ⁷	1.162×10 ⁴	2.341×10 ⁵	1.187×10 ⁷
Standard error of B	SE(B)	3409.5	107.8	483.9	3445.4
Coefficient of variation for B		0.207	0.348	0.348	0.190
95% confidence interval as % of B		40.59%	68.30%	68.21%	37.18%
Confidence limits on estimated biomass					
Lower 95% (tonnes)		9,781.0	98.0	442.1	11,410.4
Upper 95% (tonnes)		23,146.5	520.4	2,338.9	24,916.4
Lower 95% (short tons)		10,781.6	108.0	487.3	12,577.7
Upper 95% (short tons)		25,514.3	573.7	2,578.2	27,465.4

Table 4. Variance of calculations of spawning herring biomass from spawn deposition surveys by project summary area, Prince William Sound, Alaska, 1995.

Year Class	Age Class	Mean Weight (g)	Mean Standard Length (mm)	Weight (tonnes)	Biomass by A Percent by Weight	ge Class Number of Fish (x 1,000)	Percent by Number
1994	1			0.0	0.0	0.0	0.0
1993	2	20	163	37.8	0.2	767.4	0.5
1992	3	76	184	2,724.0	15.0	35,679.2	24.1
1991	4	96	197	534.8	2.9	5,597.4	3.8
1990	5	112	208	2,477.2	13.6	22,136.2	15.0
1989	6	133	218	482.3	2.7	3,636.5	2.5
1988	7	144	222	9,568.8	52.7	66,521.0	44.9
1987	8	164	229	170.7	0.9	1,038.4	0.7
1986	9	156	230	241.8	1.3	1,557.8	1.1
1985	10	168	234	824.5	4.5	4,906.9	3.3
1984	11	177	237	1,060.3	5.8	6,002.5	4.1
1983	12	166	236	28.8	0.2	173.0	0.1
1982	13+			0.0	0.0	0.0 12,640.2	0.0
Tot	tal	123	211	18,151.0	100.0	148,016.2	100.0

Table 5.Estimated mean weight and length and contributions of each age class to the
herring biomass in Prince William Sound, Alaska, 1995.

APPENDIX A.: DIVER CALIBRATIONS, 1995 SPAWN DEPOSITION SURVEY

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1995 herring spawn deposition diver calibration and biomass estimation

by

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25 October 1995

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Introduction

The 1995 herring spawn deposition survey followed procedures and analyses described in the detailed project description for project number 95166. The diver calibration, however, was done slightly different from that outlined in the DPD. The purpose of the diver calibration was to adjust for systematic biases in the egg count and provide a more accurate estimate. This procedure considered diver and kelp type effects in that different divers may have had very different biases (e.g., one tended to overestimate while another underestimated) and different kelp types may have provided very different conditions for making the estimates. Calibration samples were made throughout the cruise, collected, and counted in the lab. Diver calibration was then determined from the relationship between the divers' counts in the field (dependent variable) and the true lab counts (independent variable), assumed to be without errors. Covariates used in the model were diver and kelp type. Additional factors such as depth of sample, date, and time of day could also be important, but were assumed to be negligible.

Past analyses have used a two-step procedure: (1) pool like groups and (2) obtain calibration parameters for each group. Say we had calibration data for three years for four divers on four different kelp types, for a total of 48 possible groups $(3 \times 4 \times 4 = 48)$. The process was to determine which groups could be pooled so that we could "beef up" this years' sample sizes. Lab counts are fairly expensive in time and money making it impossible to collect a sufficient set of calibration samples each year. This process was a way to combine all available data to yield more precise adjustments from the resulting larger sample sizes.

The philosophy of these past analyses was that all years, divers, and kelp types should be assumed to be the same unless we had sufficient evidence to keep them separate. In the procedure described above, the null hypotheses were that factor effects were zero. From looking at the data, it seemed likely that some groups were found to be not different primarily because of small sample sizes, not necessarily because they really were the same. An argument could be made for the philosphy that all divers and kelp types should be assumed to be different and only pooled if we had sufficient evidence that they were the same. From talking with the divers, it seemed that a single diver was more consistent between years than several divers were within the same year. This led to the desire to build separate calibration models for each diver using weighted regression where the weights related to how recent the sample was taken. The current year's data were weighted the heaviest with each preceeding year receiving less and less weight.

Diver Calibration: Methods and Results

Calibration data from all previous years as well as 1995 were extracted from Rbase and MS Excel and imported as a data frame in S-plus. Divers included were bb (Bill Bechtol), bh (Beth Halley), eb (Evelyn Brown), kb (Karl Becker), and mm (Matt Miller). Data for each diver were then separated into individual data frames with a label prefix of 'dc' for diver calibration followed by the diver's initials. For example, the first few rows of dc.bb are as follows:

> dc.1	bb[]	L:10,]			
Y	ear	diver	veg	est	lab
256	91	bb	1	40.0	20.024390
258	91	bb	4	6.5	4.482627
259	91	bb	3	48.0	46.559540
261	91	bb	3	38.0	41.889230
263	91	bb	4	220.0	134.648300
266	91	bb	2	65.0	49.621430
268	91	bb	4	114.0	52.425000
278	91	bb	3	140.0	207.247600
310	91	bb	4	34.0	65.000000
312	91	bb	2	52.0	80.206670

Kelp types were listed as veg and were coded as 1 (eelgrass), 2 (hair kelp), 3 (fucus), or 4 (large brown kelp). Every diver had at least three years worth of calibration data with most divers having four. The number of available calibration samples for each diver, year, and kelp type were as follows:

bh					bb				
<u>yr</u>	1	2	3	4	yr_	1	2	3	4
90	19	19	21	25	90	21	5	4	9
91	24	42	24	30	91	15	32	17	19
92	33	38	26	27	92	28	34	36	28
94	6	6	10	13	94	5	5	10	15
95	9	9	5	6	95	11	9	7	6
kb					eb				
yr	1	2	3	4	yr	1	2	3	<u>4</u> 9
91	19	33	23	25	88	6	7	7	9
92	34	32	20	23	89	19	20	16	26
94	15	9	8	14	90	22	25	22	33
95	7	5	8	3	91	9	5	9	9
					92	35	28	24	24
mm					94	18	7	10	14
	1	2	-	4	95	10	12	8	4
<u>yr</u>	1	2	3	4					
92	22	37	32	27					
94	6	8	9	15					
95	1	5	8	4					

As can be seen, the number of samples collected in the past two years has dropped off considerably from previous levels. The intention was to collect 20 samples over a range of densities for each of the four kelp types. No matter what method of calibration is to be used, it will be difficult to make reasonably precise adjustments with so few current data.

A series of scatterplots was made for an initial look at the calibration data (Appendix 2). A separate plot was made for each diver, year, and kelp type with the reliability code used as the plotting symbol. A dashed line with a slope of 1 was also added as an aid for viewing the

relationship between diver and lab counts. Points above the line represented overestimation, while points below the line represented underestimation. There seemed to be a tendency to underestimate most of the time. This pattern was fairly consistent for all kelp types and all years. Additionally, the highest egg counts seemed to be clustered closer to the unity line, indicating the possibility that extremely high counts of eggs were more accurate than those from typical densities. For example, diver bb on kelp type 1 in 1995 had five counts in the range of 20,000 to 150,000 eggs that were all somewhat underestimated. Five other counts of approximately 400,000 were extremely accurate with only one of the five not on the unity line itself.

It seemed reasonable to combine a diver's calibration data for all years and run a single regression where the observations were weighted by the year it was collected. Specifically, the weights were calculated as

$$weight_i = \frac{1}{96 - year_i},\tag{1}$$

where *year*, is the year that observation *i* was taken (95, 94, etc.). The result of this is that observations from 1995 received a weight of 1, while those from 1994 had a weight of 1/2, those from 1992 had a weight of ¹/₄, etc. This was intuitively appealing in that all data from past years were included in the analysis, but that the most recent data were considered more important or perhaps more relevant to this year's calibration. Separate regressions were fit for each diver with kelp type used as a class variable in the analysis. The S-plus functions used to perform these analyses were divcal2 and repar and are listed in Appendix 1. Divcal2 was the primary function used to do the weighted regressions, while repar was a function called by divcal2 to do a reparameterization. Arguments passed to divcal2 were the dataframe to be used (e.g., dc.bb) and two logical parameters: one to indicate whether intercept terms were to be included in the model and the other to indicate whether egg counts were to be expressed as eggs or thousands of eggs. Once the model was fit, the function went on to produce residual plots for each year. Arguments passed to repar were the dataframe being used, the parameter from divcal2 to indicate whether an intercept term should be included, and a parameter to indicate whether years should be pooled. The purpose of the reparametrization was to obtain directly relevant parameter estimates. For this analysis, each parameter estimate was the slope for a particular year, rather than having some parameters being the difference in slope between years as would be the case with the usual parameterization. The analyses were run with the intercept forced through zero, egg counts in actual number of eggs (i.e., 100 meant 100 eggs, not 100,000 eggs), and with years pooled. The diver calibration model used was

$$\log(dc_{ijk}) = \beta_{jk} \log(lc_{ijk}) + \varepsilon_{ijk}, \qquad (2)$$

where dc_{ijk} was the i^{th} count for diver j on kelp type k and lc_{ijk} was the associated lab count. A summary of the results follows with full results and residual plots included in Appendix 3.

Diver (j)	Kelp Type (k)	Slope Estimate $(\hat{\beta}_{jk})$	Standard Error
BB	1 = eelgrass	0.9779	0.0062
	2 = hair kelp	0.9819	0.0062
	3 = fucus	0.9447	0.0066
	4 = large brown kelp	0.9554	0.0068
BH	1 = eelgrass	0.9704	0.0065
	2 = hair kelp	0.9530	0.0059
	3 = fucus	0.9112	0.0067
	4 = large brown kelp	0.9462	0.0064
EB	1 = eelgrass	0.9742	0.0058
	2 = hair kelp	0.9678	0.0061
	3 = fucus	0.9456	0.0067
	4 = large brown kelp	0.9728	0.0066
KB	1 = eelgrass	0.9340	0.0065
	2 = hair kelp	0.9607	0.0068
	3 = fucus	0.9026	0.0074
	4 = large brown kelp	0.9435	0.0074
MM	1 = eelgrass	0.9431	0.0111
	2 = hair kelp	0.9617	0.0079
	3 = fucus	0.9167	0.0079
	4 = large brown kelp	0.9397	0.0082

 Table 1:
 Parameter estimates for weighted regression

The egg count adjustment used the appropriate parameter estimate (for a given diver and kelp type) in an inverse prediction method of the form

$$adc_{ijk} = e^{\frac{\log(dc_{ijk})}{\hat{\beta}_{jk}}},$$
(3)

:

where adc_{ijk} was the i^{th} adjusted count for diver j on kelp type k. Note that the term adc replaced lc in equation (2) to represent the expected lab count, i.e., the adjusted diver count. Using the delta method, the variance for the adjusted count was determined to be as follows:

$$\operatorname{VAR}(adc_{ijk}) = \left(\frac{\log(dc_{ijk})^2 \operatorname{VAR}(\hat{\beta}_{jk})}{\hat{\beta}_{jk}^4}\right) e^{\frac{2\log(dc_{ijk})}{\hat{\beta}_{jk}}}.$$
(4)

This diver calibration method was implemented with adjusted egg counts calculated for the 1995 data. The range of diver calibration counts for 1995 was 0.6 K to 530 K, while it was 0.6 K to 1442 K for all years. The range of diver estimates on sampled quadrats in 1995 was 0 to 2800 K, almost double the maximum calibration point from any year. This raised the concern that we were using the calibration model on points well outside the range of data used to build the model. We could assume the trend continues to these high counts, but that may not be realistic. As mentioned earlier, there appeared to be a tendency for high counts to be more accurate than moderate counts. This can be seen in a plot of all calibration points where the mean diver count is decidely underestimated below around 5.5 on the X-axis, while points greater than 5.5 appear to be centered on the unity line.



log(Lab Count (K))

Figure 1: Relationship between diver count and lab count for all divers and all years. Dashed line has intercept = 0 and slope = 1.

Without calibration points to cover the range of the data, it is difficult to model these extreme counts with any kind of certainty. The model over the range of available calibration points resulted in an adjustment that becomes more severe for larger diver estimates. For extremely large estimates, such as 2800 K that is five times the maximum calibration point for 1995, the resulting adjustment would be quite substantial. Based on what little supporting data we have, this does not seem to be realistic.

Several options regarding large diver estimates were considered. The first was to leave the model as it was and run the adjustment. As just stated, this was not considered a realistic option and the resulting five or six extremely large estimates had a substantial effect on the final biomass estimate, varying the result by several thousand tons depending on whether they were included in the analysis or not. The second option was to use the calibration model on diver counts up to some threshold number of eggs, but no adjustment on counts above the threshold. This seemed to be rather drastic to the other extreme. Additionally, there would be an unrealistic discontinuity in the model around the threshold.

A third option was used that was a compromise between the first two. Again, the calibration model was used on diver counts up to a threshold number of eggs. However, instead of switching to the unity line for points above the threshold, a line parallel to the unity line was used that was continuous with the calibration line. The following figure best describes what was done. The resulting calibration tended to follow the apparent curve suggested in Figure 1 where estimates seemed to be more accurate at the higher counts. Perhaps non-linear regression could be used to better model the relationship. More essential, though, is the need for more calibration points for higher diver counts.



log(Lab Count)

Figure 2: Final calibration adjustment scheme. Unity line has slope = 1, threshold is some determined egg count. The calibration line has a slope determined from multiple linear regression for lab counts less than the threshold and a slope of 1 for greater counts.

A threshold of 90 K eggs (log(Lab Count) = 4.5) was chosen based on Figure 1. Putting this in terms of a threshold for the diver counts resulted in a threshold of $\hat{\beta}$ log(90,000). The inverse prediction and variance estimate formulas for counts less than the threshold remained unchanged from equations (3) and (4). The inverse prediction for counts greater than the threshold were simply 90 K plus some constant determined as the difference between the actual diver count and the expected diver count for a lab count of 90 K.

$$adc_{ijk} = e^{\log(90,000) + \log(d_{ijk}) - \hat{\beta} \log(90,000)}$$
(5)

Since in this case a constant was added to the adjusted count for 90 K, the variance estimate would be the same as the variance estimate from equation (4) for a diver count of 90 K.

The resulting calibration models are shown for each diver and kelp type (Figure 3). The size of the plotting symbol represents its weight in the linear regression, i.e., the largest symbols are from 1995, etc. Again, there may well be better ways to model this relationship. Some sort of non-linear regression should be explored as well as spline regression. For the time being, this seemed to be a reasonable and workable approach. To fully model these extremes in the data, we are absolutely going to need some data in these ranges. Without that, it is purely guesswork.



Figure 3: Calibration model curves for each diver and kelp type combination. Size of plotting symbol represents weight in the linear regression analysis.

Biomass Estimation: Methods and Results

Egg count adjustments were made for all diver counts from all samples: single visit transects, repeated visit transects, deca-frame sites, and predator exclusion frames. Single visit transects were used to estimate total herring biomass in areas designated Northeast PWS, Southeast PWS and Montague Island. An initial three-stage process was used to finalize the data set.

- (1) Several transects had leading or trailing quadrats with egg counts of zero. Since the length of a transect was used to calculate spawn patch width, these quadrats needed to be removed. The S-plus function *trim* was used to do this (Appendix 1).
- (2) Frequently, piles of loose eggs and eggs on detached vegetation were washed up on shore a long way from attached vegetation and the spawn patch itself. These piles were included in the transects where they existed and were recorded as vegetation win or wind row. Usually there was a long gap with no eggs between the wind row and the spawn patch. It was felt that these empty quadrats should not be included in the sample as they would falsely inflate the patch width. A protocol was determined whereby empty quadrats were deleted when there were four or more of them in a row following wind row. These quadrats were deleted manually in a text editor.
- (3) Each quadrat was identified with a primary vegetation code as defined in the database documentation. Each of these codes related to one of four kelp types, corresponding to the four types used in the diver calibration. A column was added to the dataframe to indicate the kelp type, which together with the diver, specified which egg count adjustment to use.

The final dataset was read into an S-plus data frame called herring, a portion of which follows:

> ł	nerrir	ng[1:10,]								
	year	transect	station	veg	eggs	loose	left	diver	area	kelp
1	95	1	1	win	0.04	0.00	0	bb	Southeast	FUC
2	95	1	18	bfr	0.00	0.05	0	bb	Southeast	HRK
3	95	1	19	sd	0.00	0.00	0	bb	Southeast	EEL
4	95	1	20	sd	0.00	0.00	0	bb	Southeast	EEL
5	95	1	21	ul	0.00	0.00	0	bb	Southeast	LBK
6	95	1	22	ul	0.00	0.00	0	bb	Southeast	LBK
7	95	1	23	rib	0.00	0.00	0	bb	Southeast	LBK
8	95	1	24	rib	0.00	0.00	0	bb	Southeast	LBK
9	95	1	25	rib	0.00	0.00	0	bb	Southeast	LBK
10	95	1	26	cob	0.00	0.00	0	bb	Southeast	FUC

Once the data were finalized, a series of S-plus functions was used to do the biomass estimation (Appendix 1). The function *adjust* did the actual adjustment on the diver egg counts. Arguments were the dataframe (*herring*) and a logical variable to set whether the high count adjustment was to be done. If so, the term *limit* within the function set the threshold (90,000). The output of this function was input to the *by.transect* function, which did calculations at the transect level. The output of this was then input to the *by.area* function, which did the final calculations for each area. Lastly, this output was input to the function *total*, which did all

necessary calculations to produce the standard summary output obtained in past years. This output includes appropriate statistics for each area separately as well as for all areas combined. The S-plus functions can be used in a couple ways. Each step can be done separately with the output from each saved and then input to the next function:

herring.by.transect <- by.transect(herring)
herring.by.area <- by.area(herring.by.transect)
herring.total <- total(herring.by.area)</pre>

Alternately, the functions can be nested and performed in one step:

herring.total <- total(by.area(by.transect(herring)))</pre>

Table 2a:	Summary of Prince	William Sound Herrin	g Egg Deposition Survey for 1995
	Summary of Lime		

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	64123	10178	29517	103819
Number of transects sampled	n	52	10	25	87
Number of quadrats sampled	Σm_i	1089	142	302	1533
Proportion of transects sampled	f_l	0.00081	0.00098	0.00085	0.00084
Proportion of quadrats sampled	f_2	0.06325	0.06325	0.06325	0.06325
Average spawn patch width (m)		104.71	71.00	60.40	
Total area of spawn patches (km ²)		2.123	0.229	0.564	2.916
Unweighted average density (1000/m ²)		355.66	114.95	122.27	
Average total eggs per transect (K)	ŷ	14951	2079	2411	
Proportion of eggs lost before survey	R	0.1	0.1	0.1	
Total eggs in area (G)	T	1065.22	23.51	79.06	1167.79
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Average weight of females (g)	\overline{W}_{f}	130	160	121	
Number of females in AWL sample	q	839	544	303	
Number of fish in AWL sample		2223	1238	877	······································
Sex ratio	S	2.650	2.276	2.894	
Fecundity of average female	$F(W_{\theta})$	21086	26643	19419	
Fecundity regression slope		185.239	185.239	185.239	
Fecundity regression intercept		-2995.04	-2995.04	-2995.04	
Tonnes per billion eggs	B'	15.456	13.154	17.588	
Estimated biomass in tonnes	В	16463.7	309.2	1390.5	18163.4
Estimated biomass in short tons		18148.0	340,9	1532.7	20021.5
Short tons per statute mile		1440.3	170,4	264.3	981.4
Millions of pounds per statute mile		2.88	0.34	0.53	1.96
Distribution (percent miles of spawn)		61.76%	9.80%	28.43%	100.00%
Distribution (percent biomass)		90.64%	1.70%	7.66%	100.00%

Quantity Estimated	Symbol	Montague	Northeast	Southeast	Total
Egg Counts					
Variance - among transects	s_l^2	4.866×10^{8}	5.202×10 ⁶	1.719×10 ⁷	
Variance - within transects	s_2^2	8.617×10 ⁹	1.182×10 ⁷	1.537×10 ⁸	
Variance - individual quadrats	S3 ²	30295	648	2770	
Variance of estimated total eggs	Var(T)	47494	66	739	48300
AWLS Sampling					
Variance of average weight		2.289	2.795	9.497	
Variance of sex ratio	Var(S)	0.0052	0.0053	0.0181	
MSE from fecundity regression	5 ²	1.787×10^{7}	1.787×10^{7}	1.787×10^{7}	
Mean weight in fecundity sample		139.5	139.5	139.5	
Number of fish in fecundity sample		311	311	311	
Variance of est. average fecundity		8.203×10 ⁴	1.056×10 ⁵	1.289×10 ⁵	
Variance of B'	Var(B)	0.257	0.224	0.985	
Biomass Estimate					
Variance of biomass	Var(B)	1.163×10 ⁷	1.162×10 ⁴	2.341×10 ⁵	1.187×10^{7}
Standard error of B	SE(B)	3409.5	107.8	483.9	3445.4
Coefficient of variation for B		0.207	0.348	0.348	0.190
95% confidence interval as % of B		40.59%	68.30%	68.21%	37.18%
Confidence limits on estimated biomass					
Lower 95% (tonnes)		9781.0	98.0	442.1	11410.4
Upper 95% (tonnes)		23146.5	520.4	2338.9	24916.4
Lower 95% (short tons)		10781.6	108.0	487.3	12577.7
Upper 95% (short tons)		25514.3	573.7	2578.2	27465.4

 Table 2b:
 Variances of Egg Deposition Survey Estimates for 1995

Appendix 1: S-plus Functions

```
divcal2 function(df,I=T,K=F) {
if(!K) { df$est df$est*1000: df$lab df$lab*1000 }
fit lm(log(dfSest)--1+repar(df,I,vy=F),na.action=na.omit,singular.ok=T,weight=1/(96-dfSyear))
u.y sort(unique(df$year))
if(length(u,y)=7 | length(u,y)=8) par(mfrow=c(2,4))
if(length(u,y)=5 \mid length(u,y)=6) par(mfrow=c(2,3))
if(length(u,y)=3 \mid length(u,y)=4) par(mfrow=c(2,2))
if(length(u.y)=2) par(mfrow=c(1.2))
par(mgp=c(2,1,0),omi=rep(0.5,4),mar=c(5,3,2,2))
x.max max(fitted(fit).na.rm=T); x.min min(fitted(fit).na.rm=T)
y.max max(abs(resid(fit)),na.rm=T)
for(y in u.y) {
        ind df$year--y
        plot(fitted(fit)[ind].resid(fit)[ind].xlim=c(x.min,x.max).ylim=c(-y.max.y.max).
                xlab=paste("Fitted Values -".1900+y).ylab="Residuals".type="n".cex=0.65)
        abline(0)
        text(fitted(fit)[ind].resid(fit)[ind].df$veq[ind].cex=0.5)
        }
mtext(paste(*Residual plots for*.substring(deparse(substitute(df)).4)).side=1.line=-
2.outer=T.adj=1.cex=0.7)
par(mfrow=c(1.1))
return(summary(fit,F))
}
```

```
repar function(df.int=T.vy=T) {
attach(df.2)
if(vy) x veg*10 + year%%10
       else x veg
u.x < - sort(unique(x))
tmp <- matrix(x, nrow = length(u.x), ncol = length(x), byrow = T)
il <- t(tmp == u.x) * 1
dimnames(i1) <- list(dimnames(x)[[1]], paste("i", u.x, sep = ""))</pre>
i2 i1 \times \log(lab)
dimnames(i2)[[2]] <- paste("s", u.x. sep = "")
detach(2)
if(int) {
        imat numeric(0)
        for(col in 1:ncol(i1)) {
                tmp dimnames(imat)[[2]]
                imat_cbind(imat,i1[.col].i2[.col])
                dimnames(imat)_list(NULL.c(tmp.paste(c("i"."s").u.x[col].sep="")))
                }
        return(imat)
        }
else return(i2)
}
```

```
trim_function(df) {
ord_order(df$transect.df$station)
df df[ord.]
df$eggs[is.na(df$eggs)] 0: df$loose[is.na(df$loose)] 0: df$left[is.na(df$left)] 0
eggs df$eggs+df$lcose+df$left
ind_!duplicated(df$transect)
first_c((1:nrow(df))[ind],nrow(df)+1)
keep_rep(T,nrow(df))
for(trans in first) {
        if(trans<nrow(df)+1) {
                i trans
                while(eggs[i]--0 & i<=nrow(df)) { keep[i]_F; i_i+1 }</pre>
                }
        if(trans>1) {
                i trans-1
                while(eggs[i]==0 & i>=1) { keep[i]_F: i_i-1 }
                }
        }
return(df[keep.])
}
adjust_function(df.high.adj=F) {
attach(df.2)
d_c(rep("bb",5).rep("bh",5).rep("eb",5).rep("kb",5).rep("mm".5))
k_rep(c("EEL"."HRK","FUC","LBK","NA"),5)
s_c(.9779..9819..9447..9554.1.
    .9704..9530..9112..9462.1.
    .9742..9678..9456..9728.1.
    .9340..9607..9026..9435.1.
    .9431..9617..9167..9397.1)
v_c(.0062..0062..0066..0068.0.
    .0065..0059..0067..0064.0.
    .0058..0061..0067..0066.0.
    .0065..0068..0074..0074.0.
    .0111..0079..0079..0082.0)
v_v^2
pos1 match(paste(as.character(diver).as.character(kelp)).paste(d.k))
slope s[pos1]: variance v[pos1]
eggs[is.na(eggs)]_0: loose[is.na(loose)]_0: left[is.na(left)]_0
est (eggs+left)*1000
adjegg_rep(0,nrow(df))
```

Appendix 1: continued

```
ind est>0
adjegg[ind] exp(log(est[ind])/slope[ind]) # estimates for egg count < limit
varegg rep(0,nrow(df))
varegg[ind]_(adjegg[ind]^2)*((log(est[ind]))^2)*variance[ind]/(slope[ind]^4)
if(high.adj) {
        limit 90000
        ind adjegg>limit
        adjegg[ind] exp(log(limit)+log(est[ind])-slope[ind]*log(limit)) # egg count > limit
        varegg[ind]_exp(2*log(limit)/slope[ind])*((log(limit))^2)*variance[ind]/(slope[ind]^4)
        }
adjtot adjegg/1000+loose
varegg varegg/le6
detach(2)
return(data.frame(df.adjtot.varegg))
}
by.transect function(df) {
year tapply(df$year.df$transect.unique)
transect_tapply(df$transect.df$transect.unique)
diver_tapply(df$diver.df$transect.unique)
area tapply(df$area.df$transect.unique)
length.na_function(x) { sum(!is.na(x)) }
mi_tapply(df$station,df$transect.length.na)
wi mi*5
Mi wi/sqrt(0.1)
f2_mi/Mi: f2[is.na(f2)]_mean(f2.na.rm=T)
yi.bar_tapply(df$adjtot.df$transect.sum)/mi; yi.bar[is.na(yi.bar)] 0
yi.hat Mi*yi.bar
pos_tapply(df$adjtot.df$transect)
s3i_tapply(df$varegg.df$transect.sum)
ss (df$adjtot-yi.bar[pos])^2
s2i tapply(ss.df$transect.sum)
return(data.frame(year.transect.diver.area.mi.wi.Mi.f2.yi.bar.yi.hat.s3i.s2i))
}
by.area_function(df) {
```

```
df$area_as.character(df$area)
areas_c("Montague","Southeast","Northeast","Total")
miles_c(12.6.5.8.2.0.20.4)
kmeter_miles*1.609344
```

```
year_tapply(df$year.df$area.unique)
area_tapply(df$area.df$area.unique)
R_rep(0.10.length(area))
n_tapply(df$transect.df$area.length)
```

Appendix 1: continued

```
mi.of.spawn miles[match(as.character(area), areas)]
km.of.spawn kmeter[match(as.character(area),areas)]
N km.of.spawn*1000/sqrt(0.1)
mean.w tapply(dfSwi,dfSarea,mean)
spawn.area km.of.spawn*mean.w/1000
avg.density_tapply(df$yi.bar*10.df$area,mean)
y.hat tapply(dfSyi.hat.dfSarea.sum)/n
T.est_N*y.hat*le-6/(1-R)
s3 tapply(df$s3i,df$area.sum)
ind df$mi>1
s2 tapply(dfsMi[ind]^2*dfss2i[ind]/(dfsmi[ind]-1).dfsarea[ind].sum)/n
pos tapply(df$yi.hat.df$area)
ss (df$yi.hat-y.hat[pos])^2
sl_tapply(ss.dfSarea.sum)/(n-1)
fl n/N
f2 tapply(df$f2.df$area,mean)
sum.mi_tapply(df$mi.df$area.sum)
T.var_N^2*1e-12*((1-f1)*s1/n + f1*(1-f2)*s2/sum.mi + f1*f2*s3/sum.mi)/(1-R)^2
point.est data.frame(year.mi.of.spawn.km.of.spawn.N.n.sum.mi,fl.f2.mean.w.spawn.area.avg.density.y.hat
.R.T.est)
var.est data.frame(s1,s2,s3,T.var)
w.bar c(123.154.118)
wf.bar c(130.160.121)
n.fish c(2223.1238.877)
n.female_c(839.544.303)
w.bar.var c(40^2/699.30^2/322.41^2/177)
fec.mse rep((4227.147)^2.length(area))
fec.wf.bar_rep(139.499.length(area)); sum.wt2_rep(6543458.35.length(area));
fec.n rep(311.length(area))
fec.slope_rep(185.239,length(area)); fec.int_rep(-2995.04,length(area))
sex.ratio n.fish/n.female
sex.ratio.var sex.ratio<sup>2*</sup>(sex.ratio-1)/n.fish
avg.fec fec.int+fec.slope*wf.bar
avg.fec.var fec.mse*( 1/fec.n + 1/n.female + (wf.bar-fec.wf.bar)^2/(sum.wt2-fec.m*fec.wf.bar^2) )
B.prime w.bar*sex.ratio*1e3/avg.fec
B.prime.var_le6*((sex.ratio/avg.fec)^2*w.bar.var + (w.bar/avg.fec)^2*sex.ratio.var +
(w.bar*sex.ratio/avg.fec^2)^2*avg.fec.var )
B T.est*B.prime
B.var T.est<sup>2</sup>*B.prime.var + B.prime<sup>2</sup>*T.var - T.var*B.prime.var
B.se sqrt(B.var); B.cv_B.se/B
B.short_B*1.1023; ton.per.mile_B.short/mi.of.spawn; Mlb.per.mile_ton.per.mile*2e-3
percent.miles_100*mi.of.spawn/sum(mi.of.spawn); percent.biomass_100*8/sum(B)
tonnes.lower B-1.96*B.se; tonnes.upper B+1.96*B.se
short.lower tonnes.lower*1.1023; short.upper tonnes.upper*1.1023
percent.B 100*1.96*B.cv
```

Appendix 1: continued

point.est_data.frame(point.est,w.bar.wf.bar.n.female.n.fish.sex.ratio.avg.fec.fec.slope.fec.int.B.prim e.B.B.short.ton.per.mile.Mlb.per.mile.percent.miles.percent.biomass) var.est_data.frame(var.est,w.bar.var.sex.ratio.var.fec.mse.fec.wf.bar.sum.wt2.fec.n.avg.fec.var.B.prim e.var.B.var.B.se.B.cv.percent.B.tonnes.lower.tonnes.upper.short.lower.short.upper)

```
return(point.est.var.est)
}
```

```
total_function(df) {
r nrow(df$point.est)+1
attach(df$point.est.2)
year[r] mean(year): mi.of.spawn[r] sum(mi.of.spawn): km.of.spawn[r] sum(km.of.spawn): N[r] sum(N):
n[r] sum(n)
sum.mi[r] sum(sum.mi); f1[r] n[r]/N[r]; f2[r] mean(f2); mean.w[r] NA: spawn.area[r] sum(spawn.area);
avg.density[r] NA
y.hat[r]_NA; R[r]_NA; T.est[r]_sum(T.est); w.bar[r]_NA; wf.bar[r]_NA; n.female[r]_NA; n.fish[r] NA;
sex.ratio[r] NA
avg.fec[r]_NA; fec.slope[r]_NA; fec.int[r] NA; B.prime[r]_NA; B[r]_sum(B); B.short[r]_1.1023*B[r]_
ton.per.mile[r] B.short[r]/mi.of.spawn[r]; Mlb.per.mile[r] ton.per.mile[r]*2e-3:
percent.miles[r]_sum(percent.miles); percent.biomass[r]_sum(percent.biomass)
point.est data.frame(year,mi.of.spawn,km.of.spawn,N,n,sum.mi,f1,f2,mean.w.spawn.area.avg.density.y.hat
.R.T.est.
w.bar,wf.bar,n.female,n.fish,sex.ratio,avg.fec,fec.slope,fec.int,B.prime,B.B.short,ton.per.mile,Mlb.pe
r.mile.
        percent.miles.percent.biomass)
dimnames(point.est)[[1]][r]_"Total"
detach(2)
attach(df$var.est.2)
s1[r] NA: s2[r] NA: s3[r] NA: T.var[r] sum(T.var): w.bar.var[r] NA: sex.ratio.var[r]_NA:
fec.mse[r]_NA: fec.wf.bar[r]_NA
sum.wt2[r]_NA; fec.n[r]_NA; avg.fec.var[r]_NA; B.prime.var[r]_NA; B.var[r]_sum(B.var);
B.se[r] sqrt(B.var[r])
B.cv[r]_B.se[r]/B[r]; percent.B[r] 100*1.96*B.cv[r]; tonnes.lower[r]_B[r]-1.96*B.se[r];
tonnes.upper[r] B[r]+1.96*B.se[r]
short.lower[r] tonnes.lower[r]*1.1023; short.upper[r] tonnes.upper[r]*1.1023
var.est_data.frame(s1,s2,s3,T.var,w.bar.var,sex.ratio.var,fec.mse,fec.wf.bar.sum.wt2,fec.n.avg.fec.var
        B.prime.var.B.var.B.se.B.cv.percent.B.tonnes.lower.tonnes.upper.short.lower.short.upper)
dimnames(var.est)[[1]][r]_"Total"
detach(2)
return(point.est,var.est)
}
```



Year 1995 - Diver bb











log(Lab Count)

22

bb - 2







Year 1990 – Diver bb

Appendix 2: continued

6

6





6





0

2

log(Lab Count)

bh - 2















bh - 2



6

6





6





N

0

Ċ

2

4

log(Lab Count)








6

6







eb - 2



6





eb - 2

0

2

4

log(Lab Count)

A-32

log(Diver Count)

log(Diver Count)

3

















log(Lab Count)











kb - 2

3²

4

1

4

log(Lab Count)

log(Lab Count)

6

6

2

2









2 2

6

6



Appendix 3: Weighted regression results

> fit.bb Call: lm(formula = log(dfsest) - -1 + repar(df. I. vy = F). weights = 1/(96 - dfsyear)) Residuals: Min 10 Median 3Q Max -1.079 -0.2 0.03442 0.2126 1.407 Coefficients: Value Std. Error t value Pr(>|t|) repar(df. I, vy = F)s1 0.9779 0.0062 156.5127 0.0000 repar(df. I. vy = F)s2 0.9819 0.0062 158.1247 0.0000 repar(df. I. vy = F)s3 0.9447 0.0066 143.5101 0.0000 repar(df, I, vy = F)s4 0.9554 0.0068 141.3030 0.0000 Residual standard error: 0.3719 on 308 degrees of freedom Multiple R-Squared: 0.9966 F-statistic: 22520 on 4 and 308 degrees of freedom, the p-value is 0 > fit.bh Call: lm(formula = log(df\$est) ~ -1 + repar(df, I, vy = F), weights = 1/(96 - df\$year))Residuals: Min 10 Median 3Q Max -1.951 -0.1672 0.03479 0.2636 1.334 Coefficients: Value Std. Error t value Pr(>[t]) repar(df, I, vy = F)s1 0.9704 0.0065 148.7689 0.0000 0.0000 repar(df, I, vy = F)s2 0.9530 0.0059 160.8673 repar(df, I, vy = F)s3 0.9112 0.0067 135.8535 0.0000 repar(df, I, vy = F)s4 0.9462 0.0064 148.8917 0.0000 Residual standard error: 0.3835 on 385 degrees of freedom Multiple R-Squared: 0.9957 F-statistic: 22160 on 4 and 385 degrees of freedom, the p-value is 0 ... > fit.eb Call: lm(formula = log(dfsest) - -1 + repar(df, I, vy = F), weights = 1/(96 - dfsyear))Residuals: Min 10 Median 3Q Max -1.377 -0.1926 0.02275 0.2481 2.083 Coefficients: Value Std. Error t value Pr(>|t|) repar(df. I. vy = F)s1 0.9742 0.0058 168.2514 0.0000 repar(df. I. vy = F)s2 0.9678 0.0061 158.3826 0.0000 repar(df, I. vy = F)s3 0.9456 0.0067 140.3626 0.0000 repar(df, I, vy = F)s4 0.9728 0.0066 147.4523 0.0000 Residual standard error: 0.3975 on 429 degrees of freedom Multiple R-Squared: 0.9955 F-statistic: 23710 on 4 and 429 degrees of freedom, the p-value is 0

> fit.kb Call: lm(formula = log(dfsest) - -1 + repar(df. I. vy = F). weights = 1/(96 - dfsyear))Residuals: 10 Median 3Q Max Min -1.79 -0.1813 0.002978 0.2299 1.135 Coefficients: Value Std. Error t value Pr(>|t|) repar(df. I. vy = F)sl 0.9340 0.0065 143.1624 0.0000 repar(df. I. vy = F)s2 0.9607 0.0068 142.1444 0.0000 repar(df, I, vy = F)s3 0.9026 0.0074 121.5971 0.0000 0.0000 repar(df, I, vy = F)s4 0.9435 0.0074 127.2015 Residual standard error: 0.3814 on 271 degrees of freedom Multiple R-Squared: 0.9962 F-statistic: 17920 on 4 and 271 degrees of freedom, the p-value is 0 > fit.mm Call: lm(formula = log(df\$est) ~ -1 + repar(df, I, vy = F), weights = 1/(96 - df\$year)) Residuals: 10 Median 3Q Max Min -0.9311 -0.2408 0.03588 0.241 1.293 Coefficients: Value Std. Error t value Pr(>[t]) repar(df. I. vy = F)s1 84.9122 0.0000 0.9431 0.0111 repar(df, I, vy = F)s2 0.9617 0.0079 121.1885 0.0000 0.0000 repar(df. I. vy = F)s3 0.9167 0.0079 115.8717 repar(df, I. vy = F)s4 0.9397 0.0082 114.5988 0.0000 Residual standard error: 0.3956 on 168 degrees of freedom Multiple R-Squared: 0.9965 F-statistic: 12110 on 4 and 168 degrees of freedom, the p-value is 0



Residual plots for bb

Appendix 3: continued







.



Appendix 3: continued

A-46

:

Residual plots for kb





Residual plots for mm

APPENDIX B: FACTORS AFFECTING EGG LOSS

.

Summary Report of Results from Prince William Sound Egg Loss Modeling

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April 11, 1996

INTRODUCTION - Summary

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

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

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

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

MATERIALS AND METHODS - Summary

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

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

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

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

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

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

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

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

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

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

Data from individual years as well as combinations of years were analyzed to attain the best possible model of egg loss for Prince William Sound. The years 1990 and 1991 and

years 1994 and 1995 were combined; in addition, data from Montague Island transects only were combined over all four years.

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

RESULTS - Summary

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

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

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

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

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

The best model explained about 60.0% of the variability in egg loss rates for the combined years 1990 and 1991 (Table 3). Significant habitat variables included in the model were depth, wave-exposed/protected, oiled/unoiled and the interaction between oiled/unoiled and year. Depth and the interaction term accounted for the most variability in egg loss

rates, suggesting that these two terms were the most important factors affecting egg loss in 1990 and 1991. The average egg loss rate decreased with increasing depth, and the average egg loss rate was higher for oiled transects (0.070, SE=0.016) than unoiled transects (0.052, SE=0.013) when both years are combined. Average egg loss rates were higher in oiled areas only in 1990, in 1991 egg loss rates were marginally higher in unoiled areas. Average egg loss rate is also higher for protected transects (0.077, SE=0.012) than for exposed transects (0.021, SE=0.018), a counterintuitive result since transects that were exposed to higher wave forces over the incubation period would be expected to have higher egg loss.

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

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

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

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

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

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

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

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

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

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

Dataset	<u>n</u>	Term	Sum of Squares	DF	<u>p-value</u>	R ²
1990	26	Oiled/unoiled Error	0.064 0.095	1 24	0.001	0.401
1991	26	Depth Wave exposed/protected Error	0.025 0.049 0.040	4 1 20	0.036 0.000	0.653
1994	30	Depth*Bird abundance Dep	0.063	5	0.000	0.736

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

Dataset	<u>n</u>	Tem	Sum of Squares	DF	<u>p-yalue</u>	R ²
1990-1991 combined	52	Year*Oiled/unoiled	0.043	1	0.000	0.600
		Depth	0.043	5	0.017	
		Wave exposed/protected	0.039	1	0.000	
		Oiled/unoiled	0.028	1	0.002	
		Error	0.118	43		
1994-1995 combined	41	Depth	0.076	8	0.001	0.524
	71	Error	0.069	32	0.001	0.524
		Death	0.004			
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		

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





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



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