

*Exxon Valdez* Oil Spill  
Restoration Project Annual Report

Herring Spawn Deposition and Reproductive Impairment

Restoration Project 96166  
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.

T. Mark Willette  
Greg S. Carpenter  
Karen Hyer

Alaska Department of Fish and Game  
Division of Commercial Fisheries Management and Development  
P.O. Box 669  
Cordova, AK 99574

April 1997

*Exxon Valdez* Oil Spill  
Restoration Project Annual Report

Herring Spawn Deposition and Reproductive Impairment

Restoration Project 96166  
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.

T. Mark Willette  
Greg S. Carpenter  
Karen Hyer

Alaska Department of Fish and Game  
Division of Commercial Fisheries Management and Development  
P.O. Box 669  
Cordova, AK 99574

April 1997

# Herring Spawn Deposition and Reproductive Impairment

## Restoration Project 96166 Annual Report

**Study History:** This project was initiated in 1989 as Natural Resources Damage Assessment Fish/Shellfish Study Number 11 under the title Injury to Prince William Sound Herring. 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. 1995). 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 Project 94166. This report covers the stock assessment component for spawn deposition biomass estimates. This project will be continued in FY97 as project 97166 with refinements to improve the accuracy and efficiency of herring biomass estimates.

**Abstract:** Underwater dive surveys of deposited eggs and acoustic techniques were used to estimate the 1996 adult spawning population of Pacific herring *Clupea pallasii* 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 pallasii*, *Exxon Valdez* oil spill, herring, Prince William Sound, spawn deposition surveys, spawning biomass, stock assessment.

**Project Data:** (will be addressed in the final report)

**Citation:**

Willette, T.M., G.S. Carpenter, and K. Hyer. 1997. Herring spawn deposition and reproductive impairment, *Exxon Valdez* Oil Spill Restoration Project Annual Report (Restoration Project 96166), Alaska Department of Fish and Game, Division of Commercial Fisheries Management and Development, Cordova, Alaska.

## TABLE OF CONTENTS

<b>List of Figures</b>	iii
<b>List of Tables</b>	iv
<b>List of Appendices</b>	v
<b>INTRODUCTION</b>	
Relation to Other Oil Spill Studies	1
<b>OBJECTIVES</b>	2
<b>METHODS</b>	3
Spawn Deposition Survey and Biomass Estimation	3
Spawn Deposition Survey Design	3
Spawn Deposition Survey Sampling Procedure	3
Biomass Estimation	4
Total Number of Eggs	5
Diver Calibration Sample Collection	7
Diver Calibration Modelling	8
Spawning Biomass per Billion Eggs	10
Herring Age, Weight, Length, Sex, and Fecundity	11
Mean Weight and Sex Ratio	12
Fecundity for Biomass Estimates	12
Egg Loss Study	13
Acoustic Survey and Biomass Estimation	14
Survey Design	14
Acoustic Parameters	14
Biomass Estimation	15
<b>RESULTS</b>	16
Biomass Estimation	16
Diver Calibration Modelling	16
Herring Age, Weight, Length, Sex, and Fecundity	17
Egg Loss Study	17
Acoustic Survey Estimation	17
<b>DISCUSSION</b>	18
<b>CONCLUSIONS</b>	20
<b>ACKNOWLEDGEMENTS</b>	20
<b>LITERATURE CITED</b>	21

## LIST OF FIGURES

### Figure

1. Location of spawning herring and kilometers of shoreline observed during aerial surveys, Prince William Sound, Alaska, 1996. 23
2. Spawn deposition transect locations in the Montague Island summary area, Prince William Sound, Alaska, 1996. 24
3. Spawn deposition transects in the Southeastern and Northeastern summary areas, Prince William Sound, Alaska, 1996. 25
4. Relationship between diver count and lab count for all divers, 1992-1996. Dashed line has intercept = 0 and slope = 1. 26
5. Regression of female weight and number of eggs per female for Pacific herring from Prince William Sound, Alaska, 1996. 27

## LIST OF TABLES

### Table

1.	Location and survey date of herring spawn deposition transects, Prince William Sound, Alaska, 1996.	28
2.	Calculation of spawning herring biomass by project summary area from spawn deposition surveys, Prince William Sound, Alaska, 1996.	29
3.	Variance of calculations of spawning herring biomass from spawn deposition surveys by project summary area, Prince William Sound, Alaska, 1996.	30
4.	Diver calibration model parameter estimates, 1996.	31
5.	Estimated mean weight and length and contributions of each age and year class to the herring biomass in Prince William Sound, Alaska, 1996.	32

## **LIST OF APPENDICES**

**APPENDIX A:** Rooper, C.N., et al. 1996. Physical and Biological Factors Affecting Pacific Herring Egg Loss in Prince William Sound, Alaska.

## INTRODUCTION

This project estimated the biomass of spawning adult Pacific herring *Clupea pallasii* in Prince William Sound (PWS) using underwater diver surveys of deposited eggs and hydroacoustic techniques. This measure of abundance is necessary for monitoring recovery of the injured herring population, including recovery to population levels sufficient for sustainable commercial harvest. In addition, this project collected information about natural losses of deposited eggs which will be used to improve spawner biomass estimates and to provide early life history abundance and survival information to improve understanding of the ecological importance of herring in the PWS ecosystem. Herring provide important forage for many species including some species severely injured by the *Exxon Valdez* oil spill. Predator species include humpbacked whales, seals, sea lions, gulls, sea ducks, shorebirds, halibut, salmon, rockfish, and other fish. In addition to their ecological value, herring are a major commercial resource in PWS. From 1969 to 1993, the average annual combined ex-vessel value of five commercial PWS herring fisheries was \$8.3 million. In addition, several thousand pounds of herring and herring spawn on kelp are harvested annually for subsistence purposes 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 1996. Spawn deposition surveys were not conducted in 1993, but an acoustic survey was conducted near Green and Montague Islands to obtain an updated estimate of the population size following the apparent high mortality of the previous winter.

## **OBJECTIVES**

1. Estimate the biomass of spawning herring in PWS using SCUBA diving spawn deposition survey techniques such that the estimate is within  $\pm 25\%$  of the true value 95% of the time, and describe the age, sex and size composition of the spawning population.
2. Test a model relating sound-wide embryo survival to habitat utilized, egg density and meteorological conditions.
3. Investigate the feasibility of estimating biomass of spawning herring using acoustic surveys and net sampling.

## **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.

Spawn Deposition Survey Design: Spawn deposition surveys were conducted to obtain biomass estimates within  $\pm 25\%$  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 (quadrates 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.

Spawn Deposition Survey Sampling Procedure: 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<sup>2</sup> 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.

Biomass Estimation: 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

$$B = TB' \quad (1)$$

where

- B = estimated spawning biomass in tonnes,
- T = 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)

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

where

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

Total Number of Eggs (T): 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 m<sup>2</sup> 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

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

where

L = the shoreline length of the spawn-containing stratum in meters,  
 N = L/0.1<sup>0.5</sup> = the total number of possible transects,  
 0.1<sup>0.5</sup> = 0.3162 m = width of transect strip,  
 $\hat{y}$  = average estimated total number of eggs (thousands) per transect,  
 10<sup>-6</sup> = 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

where

$$\hat{y}_i = M \bar{y}_i \quad (4)$$

and

$$\bar{y} = \frac{\sum_{i=1}^n \hat{y}_i}{n} \quad (5)$$

- $n$  = number of transects actually sampled,  
 $i$  = transect number,  
 $M_i$  =  $w_i/0.1^{0.5}$  = number of possible quadrates in transect  $i$ ,  
 $w_i$  = spawn patch width in meters measured as the distance along the transect between the first quadrate containing eggs and the last quadrate containing eggs, and  
 $\bar{y}_i$  = average quadrate egg count in transect  $i$  (in thousands of eggs).

Average quadrate egg count within a transect,  $\bar{y}_i$ , was computed as

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

where

- $j$  = quadrate number within transect  $i$ ,  
 $m_i$  = number of quadrates actually sampled in transect  $i$ , and  
 $y_{ij}$  = adjusted diver-estimated egg count (in thousands of eggs) from the diver calibration model for quadrate  $j$  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 (quadrates), 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

where

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

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

variance among transects,

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

variance among quadrates,

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

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

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

proportion of possible transects sampled, and

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

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

Diver Calibration Sample Collection: Spawn deposition survey methods for estimating spawning biomass utilize diver estimates of the number of eggs deposited within a systematically placed 0.1 m<sup>2</sup> quadrate. 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 quadrate. All egg-containing vegetation within the quadrate 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 90 calibration samples was set for each diver who had less than three years survey participation and 50 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 from each of four vegetation categories: eelgrass (EEL), fucus (FUC), large brown kelp (LBK), and hair kelp (HRK); and from each of four ranges of egg densities: low (0-20,000), medium (20,000-80,000), and high (80,000-160,000), within each vegetation category. In 1996 the very high (>160,000) category was added for eelgrass (EEL) and hair kelp (HRK) to better represent the density spread. 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).

Diver Calibration Modelling: Analysis of the 1996 spawn deposition diver calibration data was performed by Karen Hyer, ADF&G, Cordova, and is summarized here. Diver calibration was completed following the details outlined in Willette, Carpenter and Debevec (1996).

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.

Diver calibrations were calculated for all calibrated divers (Karl Becker, Beth Haley, and Matt Miller). The data set used in the analysis consisted of calibration samples from 1992, 1994, 1995 and 1996. This ensured that all divers had an equal number of years for the analysis. A diver's calibration data was pooled for all years and a single regression weighting each observation by the year was completed. The weights were calculated as

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

where  $year_i$  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  $\frac{1}{2}$ , those from 1992 had a weight of  $\frac{1}{4}$ , etc. 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. 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

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

where  $dc_{ijk}$  was the  $i$ th 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



$$adc_{ijk} = e^{\frac{\log(dc_{ijk})}{\hat{\beta}_{jk}}} \quad (15)$$

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:

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

Spawning Biomass per Billion Eggs (B'):-- 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

$$B' = \frac{\bar{W}S}{F(\bar{W}_f)} 10^3 \quad (17)$$

where

- $\bar{W}$  = 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,
- $F(\bar{W}_f)$  = estimated fecundity at the average weight of females in the spawning population in an area, in numbers of eggs, and

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

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:

$$\begin{aligned}
 \text{Var}(B') = & (10^3)^2 \left[ \left( \frac{S}{F(\bar{W}_p)} \right)^2 \text{Var}(\bar{W}) \right. \\
 & + \left[ \frac{\bar{W}}{F(\bar{W}_p)} \right]^2 \text{Var}(S) \\
 & + \left[ \frac{\bar{W}S}{F(\bar{W}_p)^2} \right]^2 \text{Var}(F(\bar{W}_p)) \\
 & + 2\text{Cov}(\bar{W}, S) \left[ \frac{S}{F(\bar{W}_p)} \right] \left[ \frac{\bar{W}}{F(\bar{W}_p)} \right] \\
 & - 2\text{Cov}[\bar{W}, F(\bar{W}_p)] \left[ \frac{S}{F(\bar{W}_p)} \right] \left[ \frac{\bar{W}S}{F(F(\bar{W}_p))^2} \right] \\
 & \left. - 2\text{Cov}[S, F(\bar{W}_p)] \left[ \frac{\bar{W}}{F(\bar{W}_p)} \right] \left[ \frac{\bar{W}S}{F(\bar{W}_p)^2} \right] \right].
 \end{aligned} \tag{18}$$

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,  $\text{Cov}(\bar{W}, S)$  and  $\text{Cov}[S, F(\bar{W}_p)]$ . Because the term involving  $\text{Cov}[\bar{W}, F(\bar{W}_p)]$  has been shown to be very small in previous analyses and probably contributes little to  $\text{Var}(B')$ , these covariance terms were not included in the estimate of  $\text{Var}(B')$ .

### 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 ( $F(\bar{W}_f)$ ). 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.

Mean Weight and Sex Ratio: 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

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

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

Fecundity for Biomass Estimates: Average fecundity for PWS was estimated from a fecundity-weight relationship as  $F(\bar{W}_f)$ , 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)

$$Var[F(\bar{W}_f)] = s^2 \left[ \frac{1}{n} + \frac{1}{q} + \frac{(\bar{W}_f - \bar{WF})^2}{\sum (W_i - \bar{WF})^2} \right] \quad (20)$$

where

- $s^2$  = the residual mean square from the fecundity-weight linear regression,
- $\bar{W}_f$  = the average weight of female fish in the spawning population,
- $\bar{WF}$  = 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, 1991, 1994, and 1995 to more accurately quantify loss rates. 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. 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. They also began investigating the modelling of egg loss to eventually construct an embryo survival model. The final report of the egg loss analysis studies is included as Appendix A

## 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. Acoustic signals were processed in real-time using the BioSonics ESP 221 Echo square integration software and stored on digital audio tape. 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.

Survey Design. 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.

Acoustic Parameters 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:

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

where  $\sigma$  is the mean acoustic backscattering coefficient,  $W$  is the mean weight (in kg),  $l$  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  $\log_{10}l$  versus  $10 \log(\sigma/w)$ , where  $10 \log(\sigma/w)$  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 ( $\sigma$ ). As a cross check, *in situ* measurements of target strength from dual beam acoustic data were generated and compared with Thorne's (1983a) empirical formula.

Biomass Estimation 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

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

where  $\beta_{jk}$  is the population density (mass per unit volume),  $\rho_{jk}$  is the density of scatterers,  $w_{jk}$  is mean weight of scatterers,  $C$  is acoustic constant (calibration settings ie., gain etc.)  $ei_{jk}$  is the mean of the voltage squared,  $P_{jk}$  is percentage of cell  $jk$  within the water column, and  $\sigma_{jk}$  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,

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

where  $nrs$  is number of reports (along the line transects),  $nst$  is number of depth strata, and  $A$  is survey area.

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

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

and the herring biomass B in an area is given as

$$B = \frac{C}{\gamma} \frac{\sum_j \sum_k (ei)_{jk} P_{jk}}{nrs} \cdot A \quad (25)$$

## RESULTS

### Biomass Estimation

The total biomass of herring spawning naturally in PWS during 1996 was estimated to be 25,101 tonnes from spawn deposition diver surveys (Table 2). The 95% confidence limits on the estimate were 13,039 to 37,163 tonnes (Table 3). Most of the estimated biomass was in the Montague Island summary area (21,964 tonnes), but small numbers of herring also spawned into the Southeastern (639 tonnes) and Northeastern (2,497 tonnes) summary areas (Figure 1). The total biomass in 1996 was approximately 6,938 tonnes more than the 1995 biomass which was primarily due to more spawn in the northeast area of PWS. The total miles of spawn in 1996 increased by approximately 33% from 1995 mainly due to the increases in the northeast.

Diver Calibration Modelling Diver estimates of the number of eggs in quadrates were adjusted using data from calibration samples collected in 1992, 1994, 1995, and 1996 (Table 4). Several recent years of calibration data were used because the range of the calibration data from 1996 only did not include the entire range of diver quadrate counts in 1996. Divers tended to under estimate egg counts below 65 K and over estimate egg counts greater than 400 K (Figure 4).

## **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 1996 PWS herring biomass is presented in Table 5. As expected from preseason forecasts, the total biomass consisted largely of age-8 herring from the 1988 year class (35.3% contribution by weight and 26.1% by number). Abundance of age 4 fish (33.3% by number) increased over 1995 indicating relatively strong recruitment of the 1992 year class.

The average weight of all sampled herring was 122.0 g and the average length was 209 mm, similar to average weights observed in 1995. Sex ratios varied between project summary areas, 2.32 for Montague, 2.04 for the Northeast and 2.29 for the Southeast areas. (Table 2). 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 2).

## **Egg Loss Study**

Analysis of egg loss data collected in 1990, 1991, 1994, and 1995 was conducted under a reimbursable services agreement with the University of Alaska. Their final report is included as Appendix A.

## **Acoustic Survey and Biomass Estimation**

Seven acoustic surveys were conducted in the spring of 1996 in the Montague Island area to estimate the biomass of herring. Sonar and aerial surveys indicated that this area represented the primary spawning concentration of herring in PWS. Two evening surveys were conducted in Rocky Bay and five evening surveys in Stockdale Harbor. The average length of herring from samples collected in Rocky Bay was 215 mm, resulting in a scaling factor of -32.3 dB/kg. Average length of herring samples in Stockdale Harbor was 210 mm, resulting in a scaling factor of -32.3 dB/kg. The resulting biomass estimates for Rocky Bay and Stockdale Harbor were 1,319 and 3,227 tonnes, respectively (Thomas et al. 1996). The acoustic survey was not initiated until after the herring had begun to spawn. As a result, an unknown portion of the stock was not included in the survey because the fish had moved into water too shallow for operation of the survey vessel.



## DISCUSSION

Estimates from the 1996 spawn deposition surveys were incorporated into age structured assessment (ASA) models to project the herring biomass in 1997 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. 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 1996 were not as great as in these prior years. Biomass estimation based on spawn deposition surveys in 1996 were somewhat higher than 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 difficult because they are highly mobile and highly aggregated. 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 estimates are egg loss and calibration of divers. 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.

The spring 1996 acoustic biomass estimate for the Montague Island summary area was only 4,546 tonnes, while the spawn deposition survey estimate for this area was 21, 964 tonnes. The acoustic estimate was less than the spawn deposition estimate for several reasons. First, the acoustic surveys covered only Rocky Bay and Stockdale Harbor in the Montague Island area, because these bays contained the primary spawning concentrations of herring in the area. Second, the acoustic surveys did not include all of the fish known to be present Rocky Bay and Stockdale Harbor, because the fish moved into water too shallow for the survey vessel. Third, spawn deposition surveys covered several sites in the Montague Island summary area in addition to Rocky Bay and Stockdale Harbor. In the future, acoustic surveys will be conducted earlier in the season to avoid some of these problems. After FY98, a decision will be made to continue either spawn deposition or hydroacoustic surveys to estimate the biomass of herring in PWS.

The proportion of eggs lost through physical removal and mortality was investigated to improve diver survey biomass estimates and our understanding of the mechanisms controlling early life history survival. Prior to 1994, a 10% egg loss was assumed for surveys conducted 5-6 days after spawning (Biggs-Brown and Baker 1993). Results indicate 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.

## **CONCLUSIONS**

1. Results from the spawn deposition surveys indicated that 25,101 tonnes of herring spawned in Prince William Sound in 1996.
2. Spawn deposition surveys indicated that 21,964 tonnes of herring spawned in the Montague Island summary area; whereas, results from acoustic surveys indicated a herring biomass of only 4,546 tonnes in this same area. Acoustic estimates were likely negatively biased due to movement of fish outside of the survey area.
3. 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.

## **ACKNOWLEDGEMENTS**

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

## LITERATURE CITED

- Baker, T.T., J.A. Wilcock, and B.W. McCracken. 1991. Stock Assessment and management of Pacific herring in Prince William Sound, Alaska, 1990. Alaska Department of Fish and Game, Division of Commercial Fisheries, Technical Data Report No. 91-22, Juneau.
- Becker, K.E., and E.D. Biggs. 1992. Prince William Sound Herring Spawn Deposition Survey Manual. Regional Informational Report 2A92-05, 2C92-02, Alaska Department of Fish and Game, Anchorage, 35 pp.
- Biggs, E.D., and F. Funk. 1988. Pacific herring spawning ground surveys for Prince William Sound, 1988, with historic overview. Regional Information Report 2C88-07, Alaska Department of Fish and Game, Anchorage, 73 pp.
- Biggs-Brown, E.D. and T.T. Baker. 1993. Estimates of egg loss for Pacific herring in Prince William Sound, 1990-1991. NRDA Damage Assessment, Fish/Shellfish Study 11: 22p.
- Blankenbeckler, W.D., and R. Larson. 1982. Pacific herring (*Clupea harengus pallasii*) spawning ground research in Southeastern Alaska, 1978, 1979, and 1980. Alaska Department of Fish and Game Technical Report No. 69, Juneau, Alaska.
- Blankenbeckler, W.D., and R. Larson. 1987. Pacific herring (*Clupea harengus pallasii*) harvest statistics, hydroacoustic surveys, age, weight, and length analysis, and spawning ground surveys for Southeastern Alaska, 1980-1983. J. Fish Dis., 202p.
- Brown, E.D. 1995. Studies on Pacific Herring *Clupea pallasii* spawning in Prince William Sound following the 1989 *Exxon Valdez* oil spill, 1989-1992. Final Report for Natural Resource Damage Assessment Fish/Shellfish Study Number 11. Alaska Department of Fish and Game, Anchorage, Alaska.
- Cochran, W.G. 1963. Sampling techniques. John Wiley and sons, New York.
- Draper, N.R., and H. Smith. 1981. Applied regression analysis. John Wiley and Sons, New York.
- Funk, F. 1995. Age-structured assessment of Pacific herring in Prince William Sound, Alaska and forecast of abundance for 1994. Regional Informational Report 5J92-xx, Alaska Department of Fish and Game, Juneau, Alaska.
- Goodman, L.A. 1960. On the exact variance of products. Journal of the American Statistical Association 55:708-713.

- Haegele, C.W., R.D. Humphreys, and A.S. Hourston. 1981. Distribution of eggs by depth and vegetation type in Pacific herring (*Clupea harengus pallasii*) spawnings in Southern British Columbia. *Can. J. Fish. Aquat. Sci.* 38:381-386.
- Hourston, A.S., V. Haist, and R.D. Humphreys. 1981. Regional and temporal variation in the fecundity of Pacific herring in British Columbia waters. *Canadian Technical Report of Fisheries and Aquatic Sciences*, No. 1009. 31 pp.
- Meyers, T. R., S. Short, K. Lipson, W. N. Batts, J. R. Winton, J. Wilcock, and E. Brown. 1994. Epizootic hemorrhages of the skin in Pacific herring *Clupea pallasii* from Prince William Sound and Kodiak Island, Alaska, USA associated with the isolation of North American viral hemorrhagic septicemia (VHSV). *Diseases of Aquatic Organisms* (in press).
- Reid, G.M. 1971. Age composition, weight, length and sex of herring, (*Clupea pallasii*), used for reduction in Alaska, 1929-66., 1-25.
- Schweigert, J.F., C.W. Haegele, and M. Stocker. 1985. Optimizing sampling design for herring spawn surveys on the Strait of Georgia, B.C. *Can. J. Fish. Aquat. Sci.* 42: 1806-1814.
- Thomas, G.L., J. Kirsch, P. Salomone, and J.A. Wilcock. 1995. Pacific herring biomass in the Knowles Head and Green Island areas of Prince William Sound, Alaska, in the fall of 1994. Alaska Department of Fish and Game Regional Information Report No.2A95-43.
- Thomas, G.L., J. Kirsch, D. Thorne, J. Wilcock. 1996. Acoustic estimate of herring biomass in Rocky Bay and Stockdale Harbor, Prince William Sound, in the spring of 1996. Prince William Sound Science Center, P.O. Box 705, Cordova, AK 99574.
- Thompson, S.K. 1987. Sample size for estimating multinomial proportions. *The American Statistician* 41:42-46.
- Wilcock, J.A., T.T. Baker, and E.B. Brown. In Press. Stock assessment and management of Pacific herring in Prince William Sound, Alaska, 1991. Technical Fishery Report 93-xx, Alaska Department of Fish and Game, Juneau.
- Wilcock, J.A., E.D. Brown, and D. Evans. 1995 Herring spawn deposition and reproductive impairment, Annual report to the *Exxon Valdez* Trustee Council, project 94166, Alaska Department of Fish and Game, Cordova, Alaska.
- Willette, T. M., G.S. Carpenter, and E. Debevec. 1996. Herring spawn deposition and reproductive impairment, *Exxon Valdez* Oil Spill Restoration Project Annual Report (Restoration Project 95166), Alaska Department of Fish and Game, Cordova, Alaska.

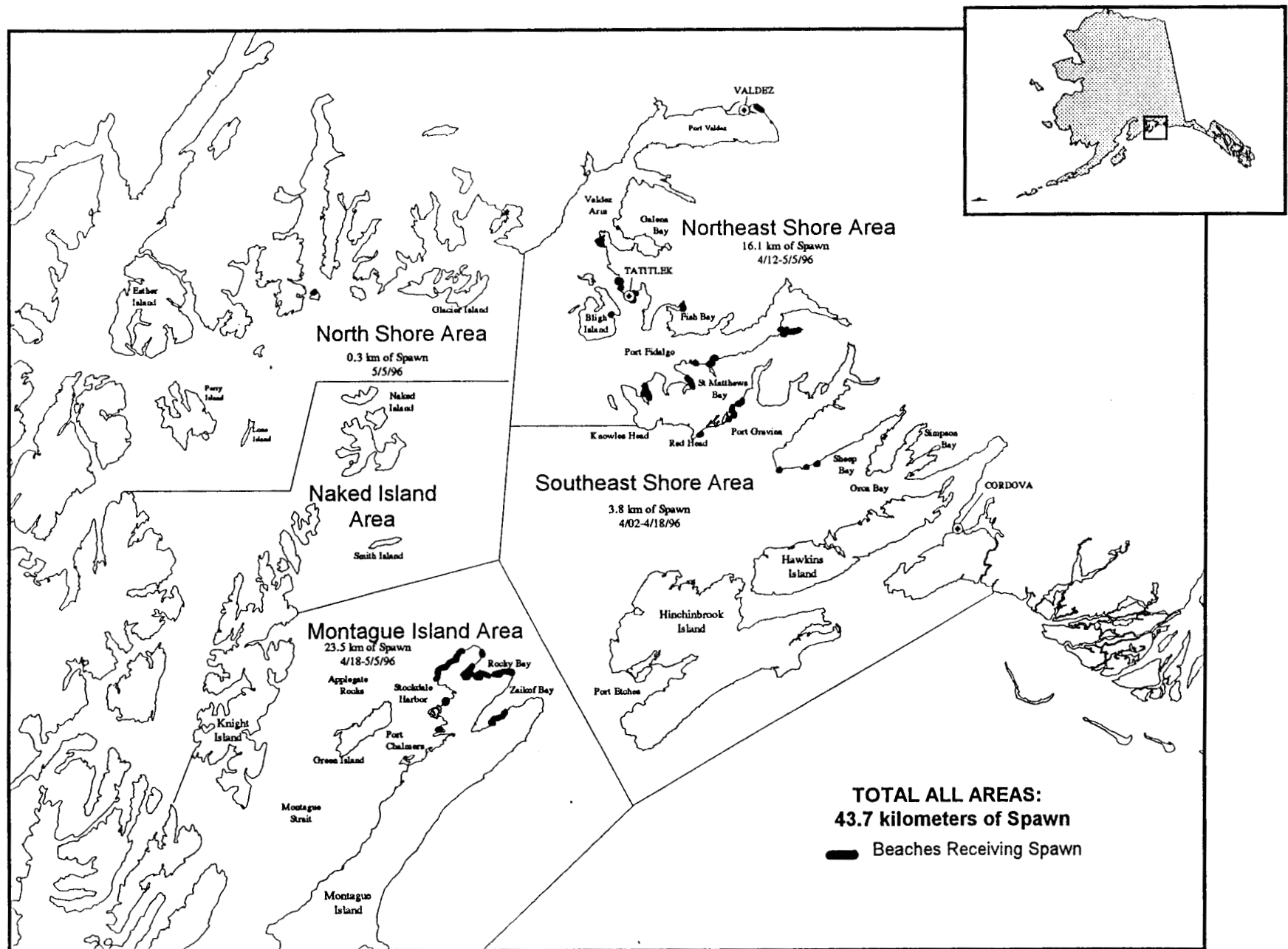


Figure 1. Location of spawning herring and kilometers of shoreline observed during aerial surveys in Prince William Sound, Alaska, 1996.

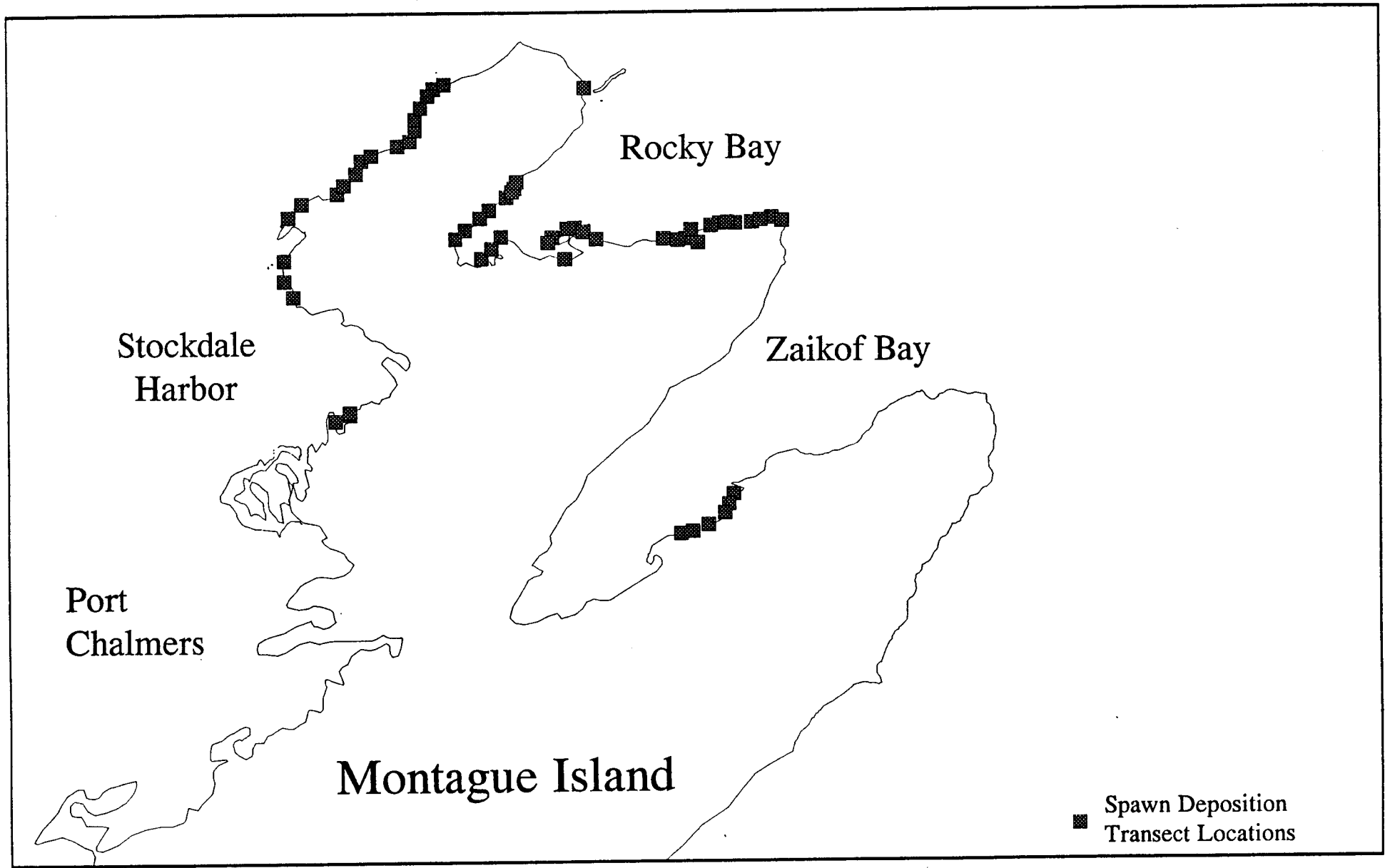


Figure 2. Spawn deposition transect locations in the Montague Island summary area, Prince William Sound, Alaska, 1996.

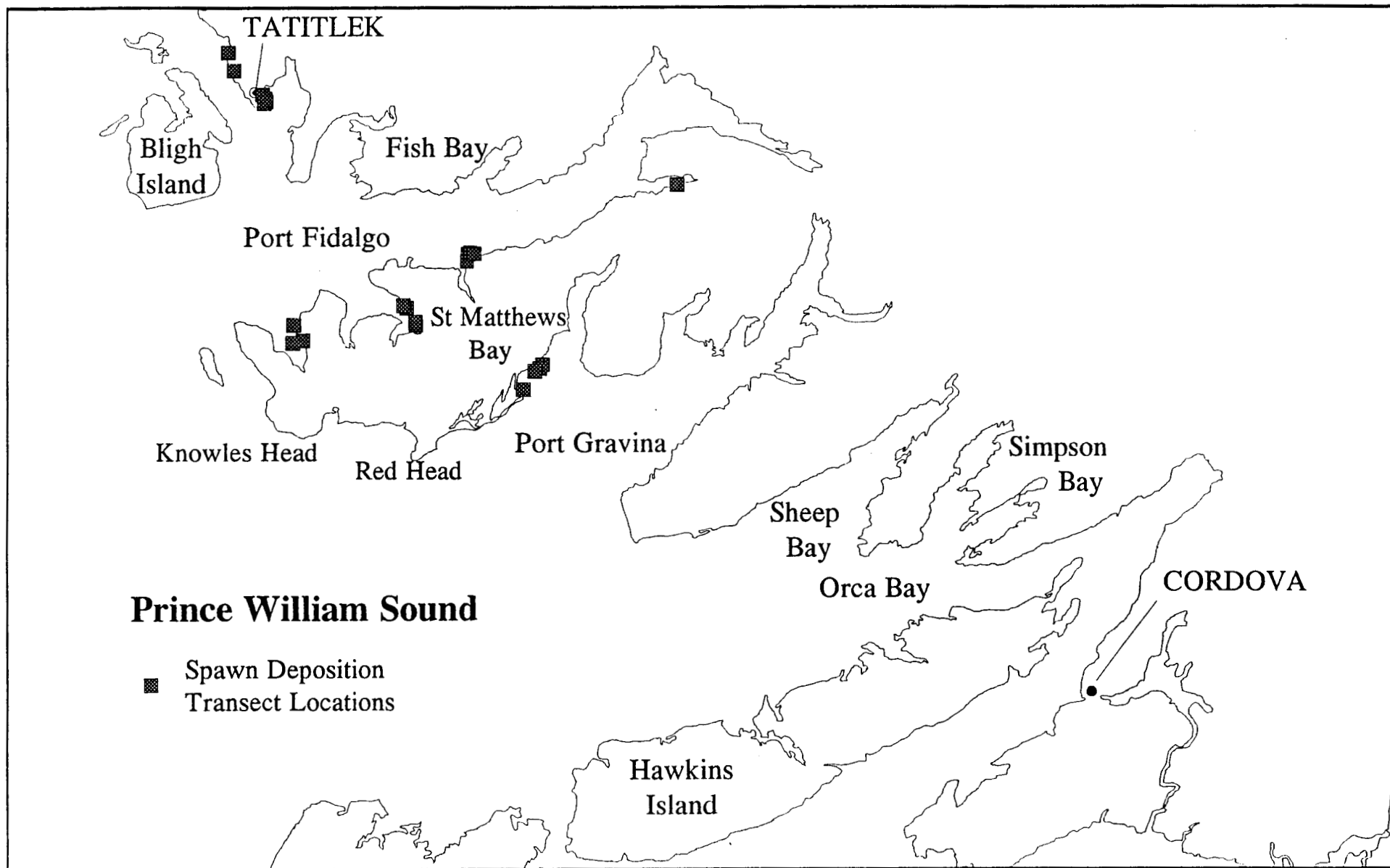


Figure 3. Spawn deposition transects in the Southeastern and Northeastern summary areas, Prince William Sound, Alaska, 1996.



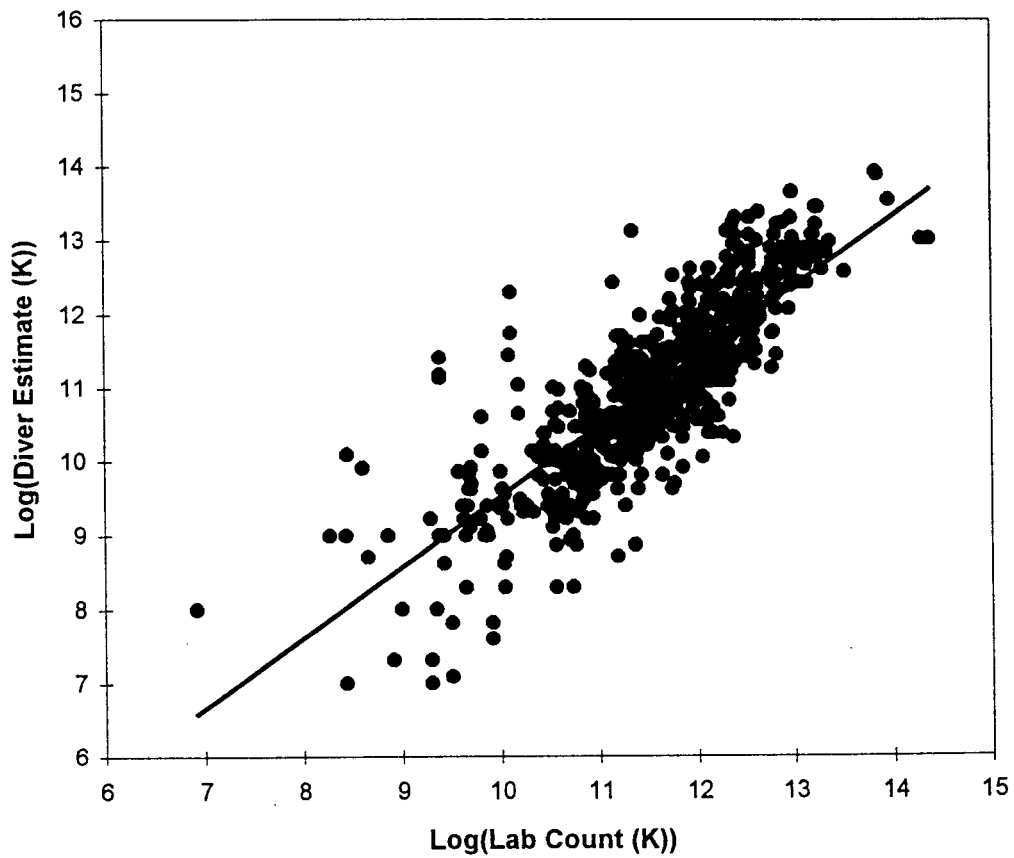


Figure 4. Relationship between diver count and lab count for all divers on all kelp types for years 1992 to 1996. Line has intercept = 0 and slope = 1.

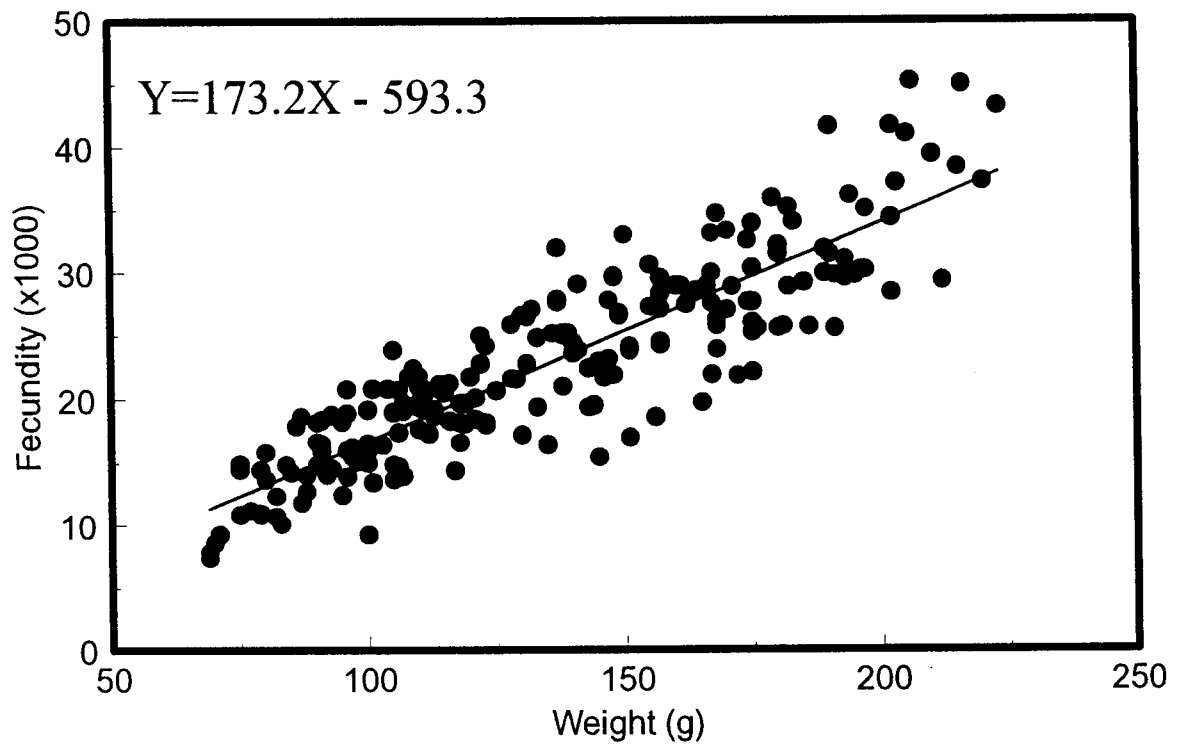


Figure 5: Regression of female weight and number of eggs per female for Pacific herring from Prince William Sound, Alaska 1996.

Table 1. Location and survey date of herring spawn deposition transects, Prince William Sound, Alaska, 1996.

Summary Area	Transect Location	Transect Number	Date Surveyed	Summary Area	Transect Location	Transect Number	Date Surveyed	
Montague Island	Zaikof Bay	23	4/26/96	Montague Island (continued)	Middle Point	64	4/30/96	
	Zaikof Bay	24	4/26/96		Middle Point	65	4/30/96	
	Zaikof Bay	25	4/26/96		Stockdale Harbor	66	4/28/96	
	Zaikof Bay	26	4/26/96		Graveyard Point	67	4/28/96	
	Zaikof Bay	27	4/26/96		Montague Point	68	5/1/96	
	Zaikof Bay	28	4/26/96		Graveyard Point	69	5/1/96	
	Stockdale Harbor	29	4/28/96		Montague Point	70	5/1/96	
	Stockdale Harbor	30	4/28/96		Graveyard Point	71	5/1/96	
	Graveyard Point	31	4/28/96		Rocky Bay	72	5/3/96	
	Graveyard Point	32	4/27/96		Rocky Bay	73	4/29/96	
	Graveyard Point	33	4/28/96		Rocky Bay	74	5/3/96	
	Graveyard Point	34	4/28/96		Rocky Bay	75	5/3/96	
	N. of Graveyard	35	4/27/96		Rocky Bay	76	5/3/96	
	Graveyard Point	36	4/27/96		Rocky Bay	77	5/3/96	
	N. of Graveyard	37	4/27/96		Rocky Bay	78	5/2/96	
	N. of Graveyard	38	4/27/96		Rocky Bay	79	5/2/96	
	N. of Graveyard	39	4/27/96		Rocky Bay	80	5/1/96	
	Graveyard Point	40	4/28/96		Middle Point	81	4/30/96	
	N. of Graveyard	41	4/28/96		Southeast	St. Matthews Bay	1	4/19/96
	SW Montague Point	42	5/1/96			St. Matthews Bay	2	4/19/96
	SW Montague Point	43	5/1/96			St. Matthews Bay	3	4/19/96
	Rocky Bay	44	5/1/96			Hell's Hole	4	4/19/96
	Rocky Bay	45	5/1/96	Northeast	Snug Corner Cove	5	4/21/96	
	Rocky Bay	46	5/2/96		Snug Corner Cove	6	4/21/96	
	Rocky Bay	47	5/2/96		Snug Corner Cove	7	4/21/96	
	Rocky Bay	48	4/29/96		Two Moon Bay	8	4/21/96	
	Rocky Bay	49	4/29/96		Two Moon Bay	9	4/21/96	
	Rocky Bay	50	4/29/96		Two Moon Bay	10	4/21/96	
	Rocky Bay	51	5/3/96		Two Moon Bay	11	4/21/96	
	Rocky Bay	52	5/3/96		Irish Cove	12	4/22/96	
	Rocky Bay	53	5/3/96		Irish Cove	13	4/22/96	
	Rocky Bay	54	5/3/96		Irish Cove	14	4/22/96	
	Rocky Bay	55	5/3/96		Irish Cove	15	4/22/96	
	Rocky Bay	56	5/2/96		Whalen Bay	16	4/22/96	
	Rocky Bay	57	4/29/96		Boulder Bay	17	4/23/96	
	Rocky Bay	58	4/29/96		Boulder Bay	18	4/23/96	
	Rocky Bay	59	4/29/96		Boulder Bay	19	4/23/96	
	Rocky Bay	60	5/1/96		Boulder Bay	20	4/23/96	
	Rocky Bay	61	5/2/96		Tatitlek Narrows	21	4/23/96	
	Rocky Bay	62	4/30/96		Ellamar	22	4/23/96	
	Middle Point	63	4/30/96					

Table 2. Calculation of spawning herring biomass by project summary area from spawn deposition surveys and comparison with aerial surveys of fish schools and visible milt, Prince William Sound, Alaska, 1996.

Calculation	Symbol	Summary Area			
		Southeast	Northeast	Montague	Total
Area of Spawn	Kilometers of Visible Milt	3.86 <sup>#</sup>	16.09 <sup>#</sup>	23.49 <sup>2</sup>	43.44
	Number of Transects Possible	(N) 12,214	50,892	74,302	137,379
	Number of Transects Sampled	(n) 3	18	52	73
	Proportion of Transects Sampled	(f1) 0.00025	0.00035	0.00070	0.00053
	Quadrats Sampled in Spawn Patches	(sum of mi) 25	303	1,083	1,411
	Proportion of Quadrats Sampled	(f2) 0.06325	0.06325	0.06325	
	Avg. Width of Spawn Patch (m)	31.2	84.2	92.7	
	Total Area of Spawn Patches (km <sup>2</sup> )	0.12	1.35	2.18	3.65
Deposited Eggs	Average Eggs/Transect (1,000's)	(y hat) 1,797	2,307	8,641	
	Proportion of Eggs Lost Before Survey	(R) 10%	10%	10%	
	Total Eggs in Area (billions)	(T) 46.90	219.20	1,657.00	
Eggs per Female (AWL Sampling)	Avg. Herring Weight in AWL Samples (g)	(W) 130	136	120	
	Number of Fish in AWL Sample	447	2,090	1,770	
	Number of Females in AWL Sample	(q) 195	1,023	763	
	Number of females for average weight	195	643	738	
	Sex Ratio	(S) 2.2923	2.0430	2.3198	
	Average Weight of Females (g)	(Wf) 130	145	125	
	Fecundity of Female at Average Weight	F(Wf) 21,849	24,393	21,001	
	Slope of Fecundity Regression	169.58	169.58	169.58	
Intercept of Fecundity Regression	-195.74	-195.74	-195.74		
Herring Biomass	Tonnes per Billion Eggs	(B') 13.64	11.39	13.26	38.3
	Estimated Biomass (tonnes)	(B) 639.7	2,496.8	21,964.1	25,100.5
	Short tones per statute mile	705.1	2,752.2	24,211.0	27,668.3
	Peak Aerial Survey Biomass (tonnes)	181.0	1,085.0	9,410.0	10,676.0

<sup>1</sup> Sum of aerial surveyor estimates of the length of visible spawn adjusted for skiff surveys.

<sup>2</sup> Sum of line segment lengths using hand drawn aerial surveyor shoreline observations redrawn in computer mapping software (MapInfo).

<sup>3</sup> Sum of aerial surveyor estimates of the length of visible spawn.

Table 3. Variance of calculations of spawning herring biomass from spawn deposition surveys by project summary Prince William Sound, Alaska, 1996.

Calculation	Symbol	Summary Area				
		Southeast	Northeast	Montague	Total	
Egg Counts	Among Transect Variance	(s1 <sup>2</sup> )	1.39E+07	1.32E+07	1.60E+09	
	Within Transect Variance	(s2 <sup>2</sup> )	2.61E+07	3.85E+07	3.43E+10	
	Sum of Variance of Ind. Pred. Obs.	(s3 <sup>2</sup> )	352	1,832	117,146	
	Variance of Estimated Total Eggs	Var(T)	852	2,336	210,098	2.13E+05
AWL Sampling	Variance of Average Herring Weight	Var(W)	7.020	3.015	2.063	
	Variance of Sex Ratio	Var(S)	0.015	0.002	0.004	
	MSE from Fecundity Regression		1.470E+07	1.470E+07	1.470E+07	
	Mean Weight in Fecundity Sample		136.5	136.5	136.5	
	Number of Fish in Fecundity Sample		206	206	206	
	Variance of Est. Avg. Fecundity	Var(F(Wff))	148,695	89,145	96,780	
Biomass	Variance of Tonnes per Billion Eggs	Var(B')	6.73E-01	1.05E-01	1.95E-01	
	Variance of Estimated Biomass (tonnes)	Var(B)	1.60E+05	3.08E+05	3.74E+07	3.79E+07
	Standard Error of B		399	554	6,116	6,154
	Coefficient of Variation of B		0.62	0.22	0.28	0.25
	Interval Width as +/- % of B		122%	43%	55%	48%
	Lower Bound (tonnes)		(142)	1,411	9,977	13,038
	Upper Bound (tonnes)		1,422	3,583	33,951	37,163
	Lower 95% limit, short tons		(156.9)	1,555.3	10,997.3	14,372.2
	Upper 95% limit, short tons		1,567.2	3,949.2	37,424.6	40,964.4

Table 4: Diver calibration model parameter estimates, 1996.

Diver (j)	Kelp Type (k)	Slope Estimate ( $\hat{\beta}_{jk}$ )	Standard Error
KB	1 = eelgrass	0.9596	0.0074
	2 = hair kelp	0.9533	0.0070
	3 = fucus	0.9452	0.0081
	4 = large brown kelp	0.9369	0.0083
BH	1 = eelgrass	0.9682	0.0064
	2 = hair kelp	0.9588	0.0059
	3 = fucus	0.9310	0.0078
	4 = large brown kelp	0.9601	0.0071
MM	1 = eelgrass	0.9633	0.0084
	2 = hair kelp	0.9709	0.0071
	3 = fucus	0.9301	0.0090
	4 = large brown kelp	0.9237	0.0073

Table 5. Estimated mean weight and length and contributions of each age and year class to the herring biomass in Prince William Sound, Alaska, 1996.

Year Class	Age Class	Mean Weight (g)	Mean Standard Length (mm)	Biomass by Age Class			
				Weight (tonnes)	Percent by Weight	Number of Fish (x 1,000)	Percent by Number
1995	1			0.0	0.0	0.0	0.0
1994	2	45	156	95.5	0.4	2,144.7	1.0
1993	3	79	185	3,062.8	12.2	38,811.6	18.8
1992	4	101	200	6,965.5	27.7	68,630.8	33.3
1991	5	119	211	879.3	3.5	7,379.5	3.6
1990	6	133	217	2,677.8	10.7	20,082.9	9.7
1989	7	149	226	1,049.0	4.2	7,021.3	3.4
1988	8	164	230	8,857.1	35.3	53,949.9	26.1
1987	9	168	233	220.1	0.9	1,313.5	0.6
1986	10	179	236	267.4	1.1	1,495.7	0.7
1985	11	188	239	714.2	2.8	3,802.9	1.8
1984	12	180	236	312.6	1.2	1,733.1	0.8
1983	13+			0.0	0.0	0.0	0.0
Total		122	209	25,101.3	100.0	206,365.9	100.0

**APPENDIX A: EGG LOSS STUDY**



**Physical and Biological Factors Affecting Pacific Herring Egg Loss in  
Prince William Sound, Alaska.**

**by Christopher N. Rooper, Lewis J. Haldorson, and Terrance J. Quinn II**

Juneau Center, School of Fisheries and Ocean Sciences  
University of Alaska Fairbanks  
11120 Glacier Highway  
Juneau AK 99801-8677

Report to Alaska Department of Fish and Game  
Commercial Fisheries Management and Development Division  
P.O. Box 669  
Cordova AK 99574

May 28, 1996

## Table of Contents

Summary Report.....	iv
List of Figures.....	xiv
List of Tables.....	xvii
Introduction.....	1
Chapter 1. Factors affecting Pacific herring egg loss	
1.1. Introduction.....	3
1.2. Materials and Methods.....	5
1.3. Results.....	12
1.3.1. 1990 analysis.....	12
1.3.2. 1991 analysis.....	15
1.3.3. 1994 analysis.....	17
1.3.4. 1995 analysis.....	21
1.3.5. Combined 1990-1991 analysis.....	24
1.3.6. Combined 1994-1995 analysis.....	28
1.3.7. Combined Montague Island analysis.....	31
1.3.8. Kelp type analysis.....	33
1.3.9. Air exposure versus depth.....	34
1.3.10. Model comparisons.....	35
1.4. Discussion.....	37
Chapter 2. Calculations of egg loss at selected 1995 transects	
2.1. Introduction.....	41

2.2. Materials and Methods.....	42
2.3. Results.....	43
2.4. Discussion.....	44
Chapter 3. Wave energy analysis	
3.1. Introduction.....	46
3.2 Materials and Methods.....	46
3.3. Results.....	47
3.4. Discussion.....	50
Literature Cited.....	52
Figures.....	54
Tables.....	110
Appendix A. Results of factorial analyses of individual years.....	154
Appendix B. Results of factorial analyses of combined years.....	176
Appendix C. Avian predator exclusion experiments.....	191

## **INTRODUCTION - Summary**

The Prince William Sound herring (*Clupea pallasii*) population did not support commercial harvests in 1993-1996 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, invertebrates, marine mammals and fish are predators of herring eggs and juveniles. Finally, the *Exxon Valdez* oil spill of 1989 may have affected herring adult and juvenile health, egg viability, and genetic composition.

In Prince William Sound estimates of the number of eggs spawned are used to estimate spawning biomass of the herring population. Because the survey occurs some days after spawning, some egg loss 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 herring egg loss 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 Biggs-Brown and Baker 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 air exposure, 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 habitat variables depth, air exposure, vegetation type, wave exposure, and substrate type were available for all years. The 1994 and 1995 data came from transects located in previously oiled areas only, so a variable for presence or absence of oil was only used for the 1990 and 1991 data sets. Additional data collected in 1994 allowed classification of the data

by the covariates average bird abundance, average glaucous winged gull abundance and cumulative loose eggs observed at each transect. The 1995 data were analyzed using both of the bird abundance measurements, as well as an another covariate, fish predation measured by gillnetting.

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

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

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

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

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

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

$$Z = \mu + \alpha_i + \beta_j + \gamma_k + (\alpha\beta)_{ij} + \dots + \varepsilon$$

The independent variables were the habitat factors, covariate terms and year. Factorial analyses of these variables were performed, sequentially removing insignificant factors. 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. 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.

Wave energy was measured at three egg loss transects in 1995. Wave energies were then compared to changes in egg abundance observed at these transects, with the objective of measuring the effects of wave action on egg loss.

## **RESULTS - Summary**

Egg loss rates ( $Z$ ) in 1990 averaged 0.078, and about 62.5% of the egg loss regressions of  $\ln(\text{egg abundance})$  versus days since spawn were significant (Table I). 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 85.4% of the variability in egg loss rates in 1990 was explained by a model containing three variables; the presence or absence of oil, wave exposure and depth. (Table II). The average egg loss rate (Z) at oiled transects in 1990 was 0.125 while the average in unoiled transects was only 0.019. At wave exposed transects the average egg loss rate was 0.091, slightly higher than at wave protected transects, 0.070. Egg loss rates were also higher at shallower depths in 1990.

In 1991 egg loss rates (Z) averaged 0.042, with about 58% of the egg loss regressions significant (Table I). 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 exposure variable (Table II). 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 air exposure, with higher egg loss rates occurring at shallower 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 I). 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 II). As before, egg loss rates increased with decreased depth, and also decreased as a function of bird abundance.

About 66% of the egg loss regressions were significant in 1995, with an average egg loss rate (Z) of 0.096 (Table I). Factorial analysis of the 1995 egg loss rates resulted in a model explaining 53.9% of the variability in egg loss rates, containing only the depth term (Table II). As in previous years, egg loss rates increased with decreasing depth.

The best model explained about 73.4% of the variability in egg loss rates for the combined years 1990 and 1991 (Table III). Significant habitat variables included in the model were depth, wave exposure, year, 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 increased with decreasing depth, and the average egg loss rate was higher for oiled transects (0.074, 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. Egg loss rates in 1990 were higher than in 1991, with averages of 0.086 and 0.042 respectively. Average egg loss rate was also higher for protected transects (0.079, 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 III). Data from the rocky substrate only was used, and the only significant term is depth. The model is very consistent with the previous analyses of egg loss rates, with egg loss rates increasing with decreasing 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 71.5% of the variability, and contains three significant terms, depth, wave exposure and year, with depth explaining the majority of the variation in egg loss rates (Table III).

The average egg loss rate in protected areas was 0.116 (SE= 0.015) while in exposed areas the average was lower at 0.071 (SE= 0.012), the opposite of the expected result. The year with the highest egg loss on Montague Island was 1990 (Z= 0.154, SE= 0.029); however, the following year had the lowest average egg loss (Z= 0.003, SE= 0.015). Egg loss rates increased with decreasing depth, a consistent pattern within all the egg loss data sets.

For each of the data sets examined, 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 1990 and 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 R<sup>2</sup> values for habitat models developed from factorial analyses were compared to R<sup>2</sup> values for three other models for each data set examined. The three models were: a model containing only the depth variable, a model containing only the 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<sup>2</sup> value of 0.769 (SE=0.049). Models from factorial analysis had an average R<sup>2</sup> value of 0.679 (SE=0.044), while average R<sup>2</sup> values from the depth only models and the air exposure models were 0.344 (SE=0.057) and 0.257 (SE=0.056). 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 air exposure models were compared for just 1994 and 1995, they performed much better, with average R<sup>2</sup> values of 0.425 (SE=0.107) and 0.362 (SE=0.107) respectively.

To calculate the initial number of eggs spawned at spawn deposition transects for 1995 a model using only air exposure was used. Time of air exposure can be calculated for 1995 spawn deposition for transects at each depth above -3.5 feet 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. At depths below -3.5 feet time of air exposure is zero. The egg loss rate for each depth in 1995 can then be calculated using

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

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

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

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

The average eggs lost from the time of spawning to the time at which the spawn deposition survey took place was 6.69% per day at selected spawn deposition transects in 1995. Egg loss increased from 4.61% per day at subtidal depths to 21.61% per day at higher depths, which experienced more hours of air exposure. About 33% of the total eggs spawned were lost from the time of spawning to the time of the survey. 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. The average percentage of eggs lost over the entire incubation period at all transects was 76.06%.

Wave energy per day had a significant effect on egg abundance, with higher egg loss at greater wave energy. However, this effect was highly influenced by a storm event with wave energies of  $8229 \text{ j}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$  which resulted in large amounts of egg loss. Excluding the storm event wave energies ranged from  $2\text{-}561 \text{ j}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ , and these energy levels had no effect on egg loss. This suggests that a wave energy threshold exists, beyond which egg loss can be great, but typical wave energies do not have a large effect on egg abundance.

## 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 data sets, and was the predominant variable in all models of 1994 and 1995 data. 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. The results of wave energy measurements suggest there is a threshold energy level beyond which large egg losses may occur, but typical wave energies do not have a significant effect on egg loss.

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 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 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. This point is illustrated in Figure I, where egg loss rates from all years are plotted against air exposure (Figure I).

Using the air exposure model, egg loss from the time of spawn to the time of spawn deposition surveys was estimated at 33%, much higher than originally thought. The results of Biggs-Brown and Baker (1993) suggested that 10 to 15% of eggs were lost from the time of spawn to the time of survey; however, they excluded the highest depth when making their estimates. We found no reason to exclude higher depths from our analysis, since high egg loss at shallower depths was a consistent pattern throughout all our analyses of egg loss data.

Interannual variability is an important factor that must be considered when estimating egg loss. The time of air exposure over incubation changes each year depending on both timing of spawning events and tidal cycles. The results of this study also show that egg loss rates are not constant with depth every year. Therefore, a combination of spawn deposition transects and egg loss transects are needed in order to accurately estimate the spawning biomass of herring in Prince William Sound each year.

**Table I.** 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	40	0.078	0.011	0.244 to -0.025	0.63
1991	26	0.042	0.013	0.263 to -0.059	0.58
1994	30	0.096	0.012	0.242 to -0.112	0.90
1995	32	0.096	0.011	0.231 to -0.007	0.66

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

Dataset	n	Term	Sum of Squares	DF	p-value	R <sup>2</sup>
1990	21	Oiled/unoiled	0.057	1	0.000	0.854
		Wave exposure	0.016	1	0.005	
		Depth	0.042	5	0.005	
		Error	0.019	13		
1991	26	Depth	0.025	4	0.036	0.653
		Wave exposure	0.049	1	0.000	
		Error	0.040	20		
1994	30	Depth*Bird abundance	0.063	5	0.000	0.736
		Depth	0.047	5	0.002	
		Error	0.032	19		
1995	32	Depth	0.067	5	0.001	0.539
		Error	0.057	26		

**Table III.** Summary of egg loss models resulting from factorial analysis of combined Prince William Sound data sets.

<b>Dataset</b>	<b>n</b>	<b>Term</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>p-value</b>	<b>R<sup>2</sup></b>
1990-1991 combined	51	Year*Oiled/unoiled	0.046	1	0.000	0.734
		Depth	0.054	5	0.000	
		Wave exposure	0.036	1	0.000	
		Oiled/unoiled	0.025	1	0.001	
		Year	0.009	1	0.034	
		Error	0.077	41		
1994-1995 combined	41	Depth	0.076	8	0.001	0.524
		Error	0.069	32		
Montague Island combined	59	Depth	0.098	9	0.000	0.715
		Year	0.068	3	0.000	
		Wave exposure	0.018	1	0.005	
		Error	0.091	45		

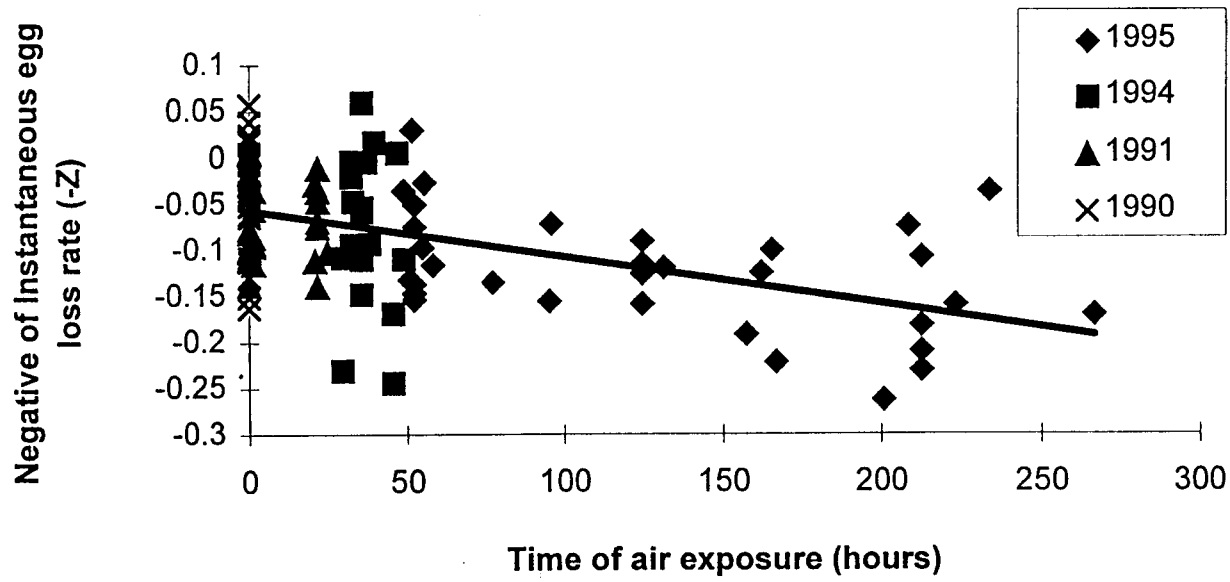


Figure I. Negative of instantaneous egg loss rate (-Z) versus air exposure for all years, from rocky and boulder substrates only.

## **List of Figures.**

- Figure 1. Map of Prince William Sound, Alaska showing egg loss transects.
- Figure 2. Regressions of  $\ln(\text{egg abundance})$  against days since spawn for 1990 transects.
- Figure 3. Egg loss rates for wave-exposed and wave-protected transects in 1990.
- Figure 4. Egg loss rates for previously oiled and unoiled transects in 1990.
- Figure 5. Egg loss rates for each substrate type sampled in 1990.
- Figure 6. Egg loss rates in each kelp type category for 1990.
- Figure 7. Egg loss rates against both depth and air exposure in 1990.
- Figure 8. Regressions of  $\ln(\text{egg abundance})$  against days since spawn for 1991 transects.
- Figure 9. Egg loss rates for wave-exposed and wave-protected transects in 1991.
- Figure 10. Egg loss rates for previously oiled and unoiled transects in 1991.
- Figure 11. Egg loss rates in each kelp type category for 1991.
- Figure 12. Egg loss rates against depth and air exposure in 1991.
- Figure 13. Regressions of  $\ln(\text{egg abundance})$  against days since spawn for 1994 transects.
- Figure 14. Egg loss rates for wave-exposed and wave-protected transects in 1994.
- Figure 15. Egg loss rates for each substrate type sampled in 1994.
- Figure 16. Egg loss rates in each kelp type category in 1994.
- Figure 17. Egg loss rates against depth and air exposure in 1994.
- Figure 18. Egg loss rates against loose eggs observed at transects in 1994.
- Figure 19. Egg loss rates against average glaucous winged gull abundance at 1994 transects.

Figure 20. Egg loss rates against average number of birds observed at 1994 transects.

Figure 21. Regressions of  $\ln(\text{egg abundance})$  against days since spawn for 1995 transects.

Figure 22. Egg loss rates for wave-exposed and wave-protected transects in 1995.

Figure 23. Egg loss rates for each kelp type category for 1995.

Figure 24. Egg loss rates against depth and air exposure for 1995.

Figure 25. Egg loss rates against average bird abundance at 1995 transects.

Figure 26. Egg loss rates against average glaucous winged gull abundance at 1995 transects.

Figure 27. Egg loss rates against fish predation index at 1995 transects.

Figure 28. Egg loss rates for wave-exposed and wave-protected transects for 1990-1991 combined.

Figure 29. Egg loss rates at previously oiled and unoiled transects for 1990-1991 combined.

Figure 30. Egg loss rates for each substrate type sampled in 1990-1991 combined.

Figure 31. Egg loss rates from each year, 1990 and 1991.

Figure 32. Egg loss rates in each kelp type category for 1990-1991 combined.

Figure 33. Egg loss rates against depth and air exposure for 1990 and 1991 combined.

Figure 34. Egg loss rates for wave-exposed and wave-protected transects for 1994-1995 combined.

Figure 35. Egg loss rates from each year, 1994 and 1995.

Figure 36. Egg loss rates in each kelp type category for 1994 and 1995 combined.

Figure 37. Egg loss rates against depth and air exposure for 1994 and 1995 combined.

Figure 38. Egg loss rates for wave-exposed and wave-protected transects on Montague Island.

Figure 39. Egg loss rates from Montague Island for each year against depth.

Figure 40. Egg loss rates from Montague Island for each year against air exposure.

Figure 41. Egg loss rates from Montague Island in each kelp type category.

Figure 42. Egg loss rates from Montague Island against depth and air exposure.

Figure 43. Air exposure against depth.

Figure 44. Average  $R^2$  values for analysis of covariance models.

Figure 45. Average  $R^2$  values for analysis of variance models.

Figure 46. Average  $R^2$  values for analysis of variance models from 1994 and 1995 only.

Figure 47. Regression of the square root of air exposure and depth for 1995.

Figure 48. Percentage of eggs lost from time of spawning to time of survey in 1995.

Figure 49. Percentage of eggs lost from time of spawning to time of hatching in 1995.

Figure 50. Changes in egg abundance between sampling visits against depth in 1995.

Figure 51. Changes in egg abundance between sampling visits against wave energy.

Figure 52. Changes in egg abundance between sampling visits against wave energies less than  $600 \text{ j}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ .

Figure 53. Average wave energy per day and average change in egg abundance between sampling visits against date sampled for 1995 transects.



## List of Tables

Table 1. Summary of habitat variables available for each year of the egg loss study.

Table 2. Summary of 1990 egg loss regressions from each transect by depth.

Table 3. Results of analysis of covariance of 1990  $\ln(\text{egg abundance})$  data.

Table 4. Results of factorial analysis of 1990 egg loss rates.

Table 5. Results of factorial analysis of 1990 egg loss rates with air exposure in the place of depth.

Table 6. Summary of 1991 egg loss regressions from each transect by depth.

Table 7. Results of analysis of covariance of 1991  $\ln(\text{egg abundance})$  data.

Table 8. Results of factorial analysis of 1991 egg loss rates.

Table 9. Results of factorial analysis of 1991 egg loss rates with air exposure in the place of depth.

Table 10. Summary of 1994 egg loss regressions from each transect by depth.

Table 11. Results of analysis of covariance of 1994  $\ln(\text{egg abundance})$  data, without the wave exposure variable.

Table 12. Results of analysis of covariance of 1994  $\ln(\text{egg abundance})$  data, without the substrate type variable.

Table 13. Results of factorial analysis of 1994 egg loss rates.

Table 14. Results of factorial analysis of 1994 egg loss rates, excluding the kelp type variable from the analysis.

Table 15. Summary of 1995 egg loss regressions by depth.

Table 16. Results of analysis of covariance of 1995  $\ln(\text{egg abundance})$  data.

Table 17. Results of factorial analysis of 1995 egg loss rates.

Table 18. Results of factorial analysis of 1995 egg loss rates, excluding the average bird abundance variable.

Table 19. Results of analysis of covariance of the combined 1990 and 1991 ln(egg abundance) data.

Table 20. Results of factorial analysis of combined 1990 and 1991 egg loss rates.

Table 21. Results of factorial analysis of combined 1990 and 1991 egg loss rates, with the kelp type\*substrate type interaction removed.

Table 22. Average egg loss rates for 1990 and 1991 combined for each significant habitat variables from factorial analysis.

Table 23. Results of analysis of covariance of the combined 1994 and 1995 ln(egg abundance) data.

Table 24. Results of factorial analysis of combined 1994 and 1995 egg loss rates, from the rocky substrate only.

Table 25. Results of factorial analysis of combined 1994 and 1995 egg loss rates from rocky and boulder substrates.

Table 26. Average egg loss rates for significant habitat variables from the factorial analysis of 1994 and 1995 egg loss rates.

Table 27. Average egg loss rates for each depth for the combined years, 1994 and 1995.

Table 28. Results of analysis of covariance of Montague Island ln(egg abundance) data.

Table 29. Results of factorial analysis of Montague Island egg loss rates.

Table 30. Results of factorial analysis of Montague Island egg loss rates, with air exposure in the place of depth.

Table 31. Average egg loss rates for significant habitat variables from factorial analysis of Montague Island data.

Table 32. Average egg loss rates for each depth category for Montague Island data.

Table 33. Analysis of variance of egg loss rates from subtidal depths using kelp type as the only explanatory variable.

Table 34. Comparison of residual sums of squares for models including depth and models including air exposure.

Table 35. Summary of  $R^2$  values for analyses of covariance of  $\ln(\text{egg abundance})$  data.

Table 36. Summary of  $R^2$  values for the models of egg loss rates resulting from factorial analyses of each data set.

Table 37. Summary of  $R^2$  values for each data set for models of egg loss rates containing only depth as an explanatory variable.

Table 38. Summary of  $R^2$  values for each data set for models of egg loss rates containing only air exposure as an explanatory variable.

Table 39. Summary of  $R^2$  values for each data set for models of egg loss rates containing transect and depth as explanatory variables.

Table 40. Parameter estimates of depth and air exposure models for each data set.

Table 41. Results of analysis of covariance to determine the effect of wave energy on egg abundance.

Table 42. Results of analysis of covariance to determine the effect of high or low wave energy on egg abundance.

## Introduction

The reasons for the failure of the Prince William Sound herring (*Clupea pallasii*) fishery in 1993-1996 are not well understood at the present time; however, a combination of physical and biological processes may be involved. Physical processes (Royer 1986) may be important for fish stocks, through effects on growth and mortality at all stages of life. Herring recruitment in particular show strong relationships with the environment (e.g. Zebdi 1991, Wespestad 1991).

Physical variables related to habitat type (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, in that bird species (glaucous winged gulls, surfbirds), invertebrates (crabs, seastars), marine mammals, and fishes (sculpins, salmonids, greenling) are found in the nearshore zone and known to be predators of herring eggs and juveniles. Finally, the *Exxon Valdez* oil spill of 1989 may have affected adult and juvenile health, egg viability, and genetic composition of Prince William Sound herring.

The Alaska Department of Fish and Game (ADF&G) has been analyzing factors affecting the survival of Pacific herring eggs in Prince William Sound since the occurrence of the *Exxon Valdez* Oil Spill. Mapping and enumeration of spawn deposition using aerial and dive surveys dates back to 1972 (Funk 1993). Estimates of the amount of spawn deposited are used to calculate the total spawning biomass of Pacific herring. Because the spawn deposition surveys typically occur 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 on herring in Prince William Sound and British Columbia (Biggs-Brown and Baker 1993, Schweigert, pers. comm.) suggests that egg loss is variable across years and across sites and higher than previously thought (Wilcock and Brown 1994). Biggs-Brown and Baker (1993) determined a range of correction factors from 10 to 15% for 1990-91 Prince William Sound data.

Biometrics and modeling assistance for the egg loss study was contracted to the School of Fisheries and Ocean Sciences (SFOS), University of Alaska Fairbanks (UAF) in late 1994, under the Herring Natal Habitats project #95166 of the Sound Ecosystem Assessment (SEA) program. The goal of this project is to build a sound-wide embryo survival model including factors such as habitat type, egg density, predation, and meteorological conditions.

This document summarizes the findings of the Pacific herring egg loss modeling study. Chapter 1 of this report develops a model of herring egg loss based on physical and biological variables. In Chapter 2 the egg loss model is used to predict the initial number of eggs at selected spawn deposition transects in 1995. Finally, Chapter 3 documents the effort to directly measure the effects of wave energy on egg loss in 1995.

## **Chapter 1. Factors affecting Pacific herring egg loss in Prince William Sound.**

### **1.1. Introduction**

Previous studies have found that many factors can contribute to Pacific herring egg loss. Large proportions of egg loss in the intertidal zone have been attributed to bird predation (Cleaver and Franett 1946; Outram 1958; Steinfeld 1971; Haegele and Schweigert 1989; Haegele and Schweigert 1991). Subtidally, marine mammal (Haegele and Schweigert 1989) and invertebrate predation (Haegele and Schweigert 1989; Haegele 1993) have been implicated as sources of herring egg loss. Wave action is also considered a major cause of egg loss (Hart and Tester 1934; Hay and Miller 1982). Both physical (wave action) and biological (predation) processes were included in Prince William Sound egg loss modeling.

#### **Prior analysis**

Studies of egg loss for herring in Prince William Sound were conducted in 1990, 1991, 1994 and 1995. The focus of the 1990 and 1991 studies was to examine the effects of oil on egg loss, and did not include collection of data relating egg loss to habitat, environmental conditions, or predation. In 1990 and 1991, the major auxiliary variable used in analyses was depth, although vegetation type was used to estimate calibration factors for different divers. The 1994 study collected some information regarding habitat factors, but the primary research effort occurred in 1995.

Methods and results from the 1990 and 1991 studies are found in Biggs-Brown and Baker (1993). Analyses of covariance were conducted with egg abundance as the dependent variable, transect and depth as factors, and days as the covariate, along with several interaction terms; all main effects and interactions were statistically significant. The egg loss model explained about 70% of the variability in the data, with most of the variability explained by transect-related parameters. The authors speculated that oil itself was probably not involved in the differences in egg loss, because very little was present at that time. Because transects in previously-oiled areas were in more exposed locations, the authors suggested that the significant effect of oil actually indicated that wave or tidal action was the most important factor determining egg loss in Prince William Sound.

### **Current analysis**

In our study, we revisit the analyses of Biggs-Brown and Baker (1993) and attempt to explain the variability among transects by habitat differences. Because transects represent specific locations, the use of transects as a factor does not provide understanding of the possible mechanisms which affect egg loss rates. In this study, both physical and biological components were analyzed to determine their individual contribution to egg loss. The physical variables included depth, time of air exposure over incubation, spawning substrate, and egg loss due to wave action. Biological variables included: predation by fish, predation by birds, and the effect of vegetation type upon which eggs are deposited. The objective of this report is to use the egg loss data to determine which habitat variables (both physical and biological) affect Pacific herring egg loss in

Prince William Sound, and to develop a model for predicting egg loss based on those variables.

## **1.2. Materials and Methods.**

### **Habitat variables**

Data sets (1990, 1991, 1994 and 1995) were acquired from Alaska Department of Fish and Game, in Cordova Alaska. Habitat variables of interest were evaluated as to importance in affecting egg loss; consequently, transects from all years were classified by wave exposure, oiled or unoiled condition, substrate type, vegetation type, depth, and time of air exposure over incubation. Additional variables in 1994 were average bird abundance, average abundance of glaucous winged gulls and cumulative loose eggs observed at each transect. In 1995 average bird abundance, average glaucous winged gull abundance, and an index of fish predation were additional variables used.

### **Wave exposure**

Since no data were collected in 1990-91 or 1994-95 that directly measured the force of wave action at each transect, a dichotomous categorical classification was developed (wave-exposed/protected). This variable was used to classify transects as exposed to waves or protected from waves based on the observations of biologists in the field. In most cases the difference between the two categories was whether the transect was within an embayment or on a headland.



### **Oiled/Unoiled**

This variable was based on the trajectory of oil released from the *Exxon Valdez* spill in 1989: oiled transects were in the path of spilled oil, while unoiled transects were not. Since all unoiled transects occurred in the north sound and all oiled transects occurred in the south sound, the presence of oil is confounded with a north/south location factor. In 1994 and 1995, low abundance of spawning herring in Prince William Sound resulted in the majority of spawning occurring in the southern half of the sound on Montague Island. Since egg loss transects were only installed on Montague Island, oiled/unoiled variable was eliminated as a factor in both 1994 and 1995.

### **Substrate type**

The substrates observed at egg loss transects during the study were classified as rocky, boulder, gravel, sand and mud. In 1991 and 1995 all transects were on rocky substrates, and in other years most transects were located on rocky substrates.

### **Kelp type**

This variable had two categories based on the dominant vegetation in each of the sampling quadrats: 1) any type of large brown kelp was dominant in the quadrat, or 2) some other type of vegetation was dominant. This variable was developed to account for differences in egg adherence due to the slick surface of large brown kelp fronds observed by divers.

### **Depth**

Since quadrats for sampling egg loss were at fixed depths each year, depth was used as a habitat variable. However, the depths used in 1994 and 1995 were different than those used in 1990 and 1991, so this variable was not directly comparable among all years.

### **Air exposure**

A computer tide program was used to calculate the cumulative time of air exposure in hours over the entire incubation period for each depth. This variable was calculated because air exposure may be a principal factor relative to egg loss mechanisms such as desiccation or bird predation.

### **Bird abundance**

Abundance of birds in 1994 and 1995 was measured by US Forest Service, Copper River Delta Institute personnel as a part of the Avian Predation on Spawn project (EVOS #96320-Q) which estimated the total number of herring eggs consumed by birds over the incubation period. The methods for collecting this information were not the same both years, so the results may not be comparable.

### **Loose eggs**

The cumulative number of loose eggs counted at each transect was an additional set of information collected. Divers counted and recorded the number of unattached and floating eggs they observed at each quadrat. However, this information was collected only in 1994.

## **Fish Predation**

In 1995 the effect of fish predation on egg loss was examined using gillnet sampling. An index of fish predation was developed for 1995 transects using catch per unit effort for fish species weighted by egg consumption. The resulting index was used in factorial analysis of habitat variables.

Since the original egg loss study had not been designed to examine these habitat variables, an unbalanced design resulted. This imbalance predetermines the analyses that were performed, as not all factors can be compared with all others. For example, in 1994 all transects that were wave-exposed occurred on rocky and boulder substrates, therefore the effect of exposure could not be compared for all substrates. In 1995 an attempt was made to define habitat variables of interest prior to the sampling season and then balance the sampling design around those variables. A summary of the habitat variables available for each year can be found in Table 1, and the locations and habitat classifications for each transect can be found in Figure 1. Egg loss models were developed for each year individually, as well as for combinations of the years. In each case graphical analysis served as a guide for development of egg loss models.

## **Preliminary Analysis**

The first step in analyzing the egg loss data from Prince William Sound was to repeat the analyses performed by Baker and Biggs on the 1990 and 1991 data using analyses of covariance techniques (Baker and Biggs, 1993). This analysis was performed using the SAS statistical package, and assured that analyses are complementary. For the

analyses involving the habitat variables and the 1994 and 1995 data, SYSTAT was used. All databases have been transferred from Rbase and maintained in Excel spreadsheets.

### Graphical Analysis

Analysis of egg loss was carried out using two dependent variables; log transformed egg abundance data, and the egg loss rates ( $Z$ ) developed from linear regressions. In graphical analysis of  $\ln(\text{egg abundance})$  data, transformed egg counts were plotted against days since spawn for each transect, showing the egg loss rate at each depth.

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

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

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

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

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

Graphical analyses of egg loss rates ( $Z$ ) was then performed for each of the habitat variables. Each egg loss rate represents the slope of the linear regression at one depth at one transect of  $\ln(\text{egg abundance})$  against days since spawn. Since a positive egg loss rate ( $Z$ ) implies negative egg loss, graphical analyses and summaries were conducted

using the negative of the instantaneous egg loss rate (-Z). Thus, more negative egg loss rates correspond to higher egg loss, an intuitively satisfying result. Both depth and air exposure were used as independent variables in the graphical analyses to determine which variable is more useful in predicting egg loss rates.

### **Analyses of Covariance**

In these analyses,  $\ln(\text{egg abundance})$  was used as a dependent variable with days since spawn as the covariate in an analysis of covariance. The other predictors used in the analysis of covariance were the habitat variables, so that

$$\ln N(t) = \ln N_0 - Zt + \alpha_i + \beta_j + \dots + \epsilon.$$

### **Factorial Analyses**

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

$$Z = \mu + \alpha_i + \beta_j + \gamma_k + (\alpha\beta)_{ij} + \dots + \epsilon.$$

Independent variables included the habitat variables, predation variables and year. Factorial analyses of these variables were performed, sequentially removing insignificant factors. In most cases the resulting models explained a significant portion of the variability in egg loss rates.

Factorial analyses were also performed on egg loss rates, using air exposure as a covariate in the place of depth, and the habitat variables as factors, with the equation

$$Z = \mu + \alpha A_E + \beta_j + \gamma_k + \dots + \epsilon.$$

Air exposure was used in the place of depth to determine which term was the most parsimonious in explaining variability in egg loss rates.

Models with air exposure in the place of depth were then compared to models containing only the depth variable using an F-test of the sums of squares to determine if there were significant differences between the two models. Models with air exposure were compared to models with depth across all data sets used in the factorial analyses.

The results of all statistical analyses were then compared to determine the best model for herring egg loss. The  $R^2$  values for each model from factorial analysis were compared to three simple models: a model containing only the depth term, a model containing only the air exposure term, and a model containing both transect and depth. The  $R^2$  values for these four types of models were compared over all data sets examined, as well as averaged across all data sets. A model was then recommended based on its  $R^2$  value and the consistency of its significance in factorial analyses.

Because of the unbalanced nature of the study design, various subsets of the data were modeled using these analysis of variance techniques. For example, the rocky substrate type, represented by the most transects, was analyzed independently and as part of the entire data set. This eliminated noise associated with the substrate variable, while using the largest available data set.

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 two years 1990 and 1991 and two years 1994 and 1995 were each combined for analysis. Then data from

Montague Island transects (representing previously oiled locations) only were combined over all four years for analysis.

A special analysis to separate the effects of the kelp type variable and the depth variable was performed on egg loss rates from subtidal depths only. Subtidal egg loss rates were compared between the two kelp types using analysis of variance, to determine the significance of the kelp type variable.

### **1.3. Results**

#### **1.3.1. 1990 Analyses.**

Egg loss sampling during 1990 took place at nine transects in both previously oiled (southern PWS) and unoiled (northern PWS) areas (Figure 1). Egg loss quadrats were placed at six depths relative to mean low water: -30 ft, -15 ft, -5 ft, 0 ft, 1 ft, and 5 ft, although most transects were not sampled at either of the two deepest depths (Table 2).

#### **Graphical Analysis**

Egg loss rates in 1990 ranged from 0.244 to -0.025 with an average of 0.078 and a standard error of 0.011 (Table 2, Figure 2), with about 62.5% of the egg loss regressions significant at the 0.05 level. Egg loss rates at wave-exposed transects appear to increase more sharply with depth than at protected transects in 1990 (Figure 3). This difference is not as distinct when egg loss rates were plotted against air exposure. The wave-exposed category was represented by only one transect in 1990, while the protected category included eight transects.

Egg loss rates in 1990 differed at oiled and unoiled transects (Figure 4). When plotted against both depth and air exposure, egg loss rates were substantially higher at oiled transects than at unoiled transects.

The most noticeable pattern in data in the substrate categories is the decrease in egg loss rates with increasing depth in the rocky substrate (Figure 5). The rocky substrate includes data from five transects while both the gravel and boulder substrates have fewer data points, being represented by three and one transects respectively.

One of the problems with analyzing the kelp type variable is the absence of large brown kelp at the upper depths of herring spawn deposition. Patterns in egg loss rates between the two kelp type categories may be the result of the confounding effects of the variable with depth (Figure 6). The large brown kelp dominant category does not include depths above mean low water, while the large brown kelp non-dominant category has very few data points below mean low water.

Depth appeared to strongly influence egg abundance, with higher egg loss rates at the higher depths (Figure 7). This pattern is evident when egg loss rates are plotted against air exposure as well.

### **Analysis of Covariance**

Analysis of covariance techniques were used to evaluate the  $\ln(\text{egg abundance})$  data, with days since spawn as the covariate. Habitat variables used included depth, wave exposure, oiled/unoiled, kelp type and substrate type, as well as a number of interaction terms. Most terms in the ANCOVA were significant (Table 3). The habitat term explaining the most variability in the data set was the interaction between kelp type and



oiled/unoiled condition. The analysis of covariance itself explained only 43.6% of the variability in  $\ln(\text{egg abundance})$ .

### **Factorial Analyses**

Egg loss rates obtained from each transect at each depth in 1990 were dependent variables in analysis of variance models to determine habitat variables affecting egg loss. A number of different data sets were modeled for egg loss rates in 1990, because of the unbalanced sampling design in this year. The data was grouped by substrate in three ways: all substrates, rocky and boulder substrates combined, and rocky substrates only. Because of the different depths sampled at some transects, models including only some of the depths were analyzed to maximize the interaction terms available for each model. Data sets with the -30 foot depth removed were modeled for all substrates as well as for rocky substrate only. Similarly data sets with both the -30 and +5 foot depths were modeled in both substrate groupings. Factorial analysis of data sets including air exposure over the incubation period in the place of depth was also performed in each of the substrate groupings. The complete set of models analyzed for the 1990 data are reported in Appendix A.

The best model of 1990 egg loss rates contained data from all depths from transects on the rocky substrate. Factorial analysis resulted in a model explaining approximately 85.4% of the variability (Table 4), containing three terms; presence or absence of oil, wave exposure and depth.

Factorial analysis of the same data with air exposure in the place of depth leads to a model explaining 80.3% of the variability in egg loss rates (Table 5). The model also contains three terms; wave exposure, oiled/unoiled condition and kelp type.

The presence of the kelp type variable probably reflects the strength of depth in explaining egg loss rates. No large brown kelp dominated quadrats were located above mean low water, so the variables are confounded. Average egg loss rates in large brown kelp dominated quadrats was 0.030 (SE=0.018), while at quadrats dominated by other kelp types, egg loss rates averaged 0.123 (SE=0.023). The expected result was that large brown kelp would lead to higher egg loss, and since this was not observed, the observed effect may be that of depth. The average egg loss rate at oiled transects in 1990 was 0.125 (SE=0.022) while the average in unoiled transects was only 0.019 (SE=0.015). At wave-exposed transects, the average egg loss rate was 0.091 (SE=0.027), slightly higher than at wave-protected transects, 0.070 (SE=0.022).

### **1.3.2. 1991 Analysis**

The 1991 data set included  $\ln(\text{egg abundance})$  estimates over time from six transects (Figure 1). Quadrats were placed at the same depths in 1991 as in 1990, with the exception of the -30 ft depth which was excluded in 1991. The only substrate sampled in 1991 was the rocky type substrate.

### **Graphical Analyses**

Egg loss rates in 1991 ranged from 0.263 to -0.059 with an average of 0.042, and a standard error of 0.013 (Table 6, Figure 8). About 58% of the egg loss regressions were

significant. Differences in egg loss rates between the wave-exposed and wave-protected categories were apparent when they were plotted against both depth and air exposure (Figure 9). Egg loss appeared to be slightly higher at wave-protected transects than at wave-exposed transects. As in the previous year, egg loss rates appeared to be higher at oiled transects than at unoiled transects in 1991 (Figure 10). This pattern was especially apparent when egg loss rates are plotted against air exposure.

When egg loss rates were plotted against depth in the two kelp type categories, no large differences were observed (Figure 11). No large brown kelp dominated quadrats were ever exposed to air during incubation, since no quadrats above mean low water were dominated by large brown kelp.

The remaining variable in 1991 is depth. There appeared to be a general trend of higher egg loss rates at higher depths, which is consistent with the 1990 results (Figure 12).

#### **Analysis of Covariance**

Analysis of covariance was performed on the 1991  $\ln(\text{egg abundance})$  data using days as the covariate. The habitat variables available for this analysis included depth, wave exposure, oiled/unoiled and a number of interaction terms. Most of the terms were insignificant except the wave exposure\*depth, wave exposure\*(days since spawn), and the depth\*(days since spawn) interaction, as well as the depth and (days since spawn) terms (Table 7). The analysis of covariance explained 41.1% of the variability in  $\ln(\text{egg abundance})$  with the wave exposure\*depth interaction term the most significant of the habitat variables.

### **Factorial Analyses**

As in 1990, multiple models of the 1991 egg loss rates were examined. Three models of the 1991 data were analyzed and compared: a model of all the 1991 data, a model of all the 1991 data with air exposure in the place of depth, and a subset of the 1991 data excluding the +5 foot depth. The best model in 1991 explained 65.3% of the variability in egg loss rates and contained two significant habitat variables, depth and wave exposure (Table 8).

A similar model resulted from replacing depth with air exposure. The significant variables in this model were: air exposure and wave exposure. The model explains 62.8% of the total variability in egg loss rates in 1991 (Table 9).

At wave-protected transects the average egg loss rate ( $Z$ ) was 0.074 (SE=0.015), while at wave-exposed transects the average was -0.018 (SE=0.010). Egg loss rates were inversely related to depth and air exposure: higher egg loss rates occurred at shallower depths, and at longer times of air exposure (Figure 12).

#### **1.3.3. 1994 Analyses**

Egg loss sampling in 1994 was carried out at 10 transects located between Rocky Bay and Port Chalmers on Montague Island (Figure 1). Four transects located on boulder substrate and three transects on rocky substrate were classified as wave-exposed, while the remaining three transects were classified as wave-protected. Of the remaining transects, one was located on mud substrate and the other two on a sandy substrate. Quadrats sampled over the incubation period were placed at three different depths at each transect, ranging from -10 feet to +3 feet (Table 1). All of the transects had quadrats at the lowest

depth; however, the other two depths varied depending on the location of spawn. This resulted in an unbalanced design for most variables within transects as well as on a transect by transect basis. Since the same depths were not replicated at each transect and the substrate variable was confounded with the wave exposure variable, several different subsets of the egg loss data were examined, resulting in a number of different egg loss models.

### **Graphical Analyses**

The average egg loss rate ( $Z$ ) was 0.096 with a standard error of 0.012 in 1994. The range of egg loss rates was from 0.242 to -0.112, and about 90% of the egg loss regressions were statistically significant (Table 10, Figure 13).

Graphical analysis of data in the wave-exposed and the wave-protected categories revealed that egg loss rates did not vary much between the two conditions in 1994 when plotted against both depth and air exposure (Figure 14).

Egg loss rates in each of the substrate types were also plotted against both depth and air exposure (Figure 15). In these plots it is evident that egg loss did not differ much between rocky and boulder substrates. However, the sand and mud substrates did seem to exhibit differences in egg loss rates. These two substrates were represented by far fewer data points which may explain the observed patterns.

Graphical analysis of kelp type revealed that, except at the lower depths, there were not many data points for the large brown kelp dominated category (Figure 16). So even though the two categories seem to exhibit a high degree of difference in egg loss, it is unclear if this is caused by kelp effects, depth effects, or sample size effects.

Egg loss rates at each depth were also examined, as well as egg loss rates against air exposure (Figure 17). As in previous years, egg loss rates appeared to be inversely related to both depth and air exposure.

Egg loss rates were then plotted against the covariate, cumulative loose eggs (Figure 18), and the two bird covariates, average glaucous winged gull abundance and average bird abundance (Figure 19 and Figure 20). Egg loss rates seem to increase with all covariates: at higher bird and gull abundance egg loss rates are higher, and at transects with higher loose egg counts, egg loss rates are higher.

### **Analyses of Covariance**

Two analyses of covariance were performed on the raw data from 1994, with  $\ln(\text{egg abundance})$  as the dependent variable and (days since spawn) as the covariate. Two factors included in the ANCOVA were kelp type and depth relative to mean low water. Because of the unbalanced design, substrate and wave exposure were confounded, so one ANCOVA was run with substrate as a factor without wave exposure, and one ANCOVA excluding substrate with the wave exposure variable.

The results of the analyses with the substrate variable included yield a model explaining 40.6% of the variability in  $\ln(\text{egg abundance})$  data (Table 11). All of the factors, interaction terms and the covariate were significant in the analysis, with the covariate explaining the most variation in the data. When the wave exposure variable was included instead of substrate a model explaining 37.7% of the variability resulted (Table 12). Again, the covariate, days since spawn, accounted for the most variability in the data set, and most of the terms included in the model were significant.

## Factorial Analyses

Because sampling at some depths was not repeated at more than one transect, a number of different categorizing strategies were used to obtain replication for the depth variable. The data were modeled for each of the strategies to determine the best method for handling the lack of replication for the depth variable. To maximize the number of replicates at each depth, one technique was to divide the depths into three fairly arbitrary categories:  $d > 1$  ft,  $1 \text{ ft} > d > -3$  ft and  $d < -3$  ft. The next technique used for categorizing depths was to group them with their closest linear category from the 1990 and 1991 depths. Another was to place them in corresponding 1990 and 1991 categories based on the amount of air exposure received throughout the incubation period. The best technique based on the results of modeling was to group the two depths with only one egg loss rate apiece with their closest possible depth. All the models were run for data combined over all substrates and for data in the rocky and boulder substrates only; these models are reported in Appendix A.

The best model for the 1994 data explained 87.7% of the variability in egg loss rates (Table 13). The model contains egg loss rates combined over all substrates, and the two depths with single observations combined with their closest depth. The model contains two significant interaction terms, depth\*bird abundance and wave exposure\*kelp type. The habitat variables wave exposure, depth, kelp type, and average gull abundance were also significant. Depth explains the most variation in egg loss rates for this model.

The significance of kelp type in the model is probably a byproduct of the extremely high significance of depth. Since large brown kelp dominated at depths below 0 ft, there is

a slight confounding between the two variables. This makes it unclear which effect is being observed, the effect of depth or the effect of kelp type.

With the exclusion of kelp type from the factorial analysis, the best model for the 1994 data explained 73.6% of the variability in egg loss rates and contained only two terms, depth and the depth\*average bird abundance interaction, with depth explaining the majority of the variation (Table 14). The 1994 data plotted by depth show that egg loss rates decrease with increased depth (Figure 17), and that increasing bird abundance also lead to higher egg loss rates (Figure 20).

#### **1.3.4. 1995 Analyses**

In 1995 eight egg loss transects were monitored over the incubation period. The transects were again located between Rocky Bay and Port Chalmers on Montague Island, since the major concentration of spawning herring occurred between these two inlets (Figure 1). Six of the eight transects were placed in rocky areas, and of these two were wave-protected and four were wave-exposed. The two other transects were located on gravel, did not include all the depths, and did not have many data points, so they were not used in the analyses. At each transect, quadrat frames were placed at six standard depths relative to mean low water, +5 ft, +3 ft, +1 ft, 0 ft, -1 ft, and -5 ft (Table 1).

#### **Graphical Analyses**

Ln(egg abundance) changes over time at each depth at each egg loss transect were used to compute the egg loss rate (Z) using linear regression (Figure 21). About 66% of the



egg loss regressions were significant (Table 15). The average egg loss rate in 1995 was 0.096 with a standard error of 0.011. Egg loss rates ranged from 0.231 to -0.007.

There appear to be no distinct differences in 1995 egg loss rates between the two wave exposure categories (Figure 22). Similar patterns in egg loss rates with both increasing depth and increased air exposure occurred at both wave-exposed and wave-protected transects.

Egg loss rates in 1995 seem to be lower where large brown kelp is the dominant vegetation (Figure 23). The majority of the data points are at quadrats and depths where large brown kelps are not dominant, so the true pattern of egg loss in these categories may not be clear from the graphical analysis.

Egg loss rates for all levels of both depth and air exposure sampled in 1995 are also shown (Figure 24). Increased depth relative to mean low water corresponds to a decrease in egg loss rate, as in previous years. This is the clearest pattern from the graphical analysis of 1995 egg loss data.

In all three covariates evaluated in 1995 the same pattern is seen. Increased bird abundance is associated with a decrease in egg loss rates in 1995 (Figure 25), and the same pattern occurs with increased glaucous winged gulls (Figure 26). Increased abundance of fish is also correlated with a slight decrease in egg loss rates (Figure 27). These results seem highly counterintuitive (the presence of known predators reducing egg loss rates), and suggest that predator abundance is related to some other variable that affects egg loss.

### **Analysis of Covariance**

An analysis of covariance was performed on the 1995 egg loss data, as with previous years' data. The dependent variable was  $\ln(\text{egg abundance})$  with days since spawn as a covariate. Categorical variables available in 1995 included depth, wave exposure and kelp type. Two interaction terms between factors were available for this analysis, depth\*wave exposure, and kelp type\*wave exposure, as well as a number of covariate interactions. Most factors and interaction terms were significant with the exception of the kelp type variable, the wave exposure\*days since spawn, and the kelp type\*days since spawn interactions (Table 16). The covariate term, days since spawn, was highly significant, explaining the most variability in the data. The analysis itself explained 58% of the variability in  $\ln(\text{egg abundance})$  data for 1995.

### **Factorial Analyses**

The habitat variables available for modeling egg loss rates in 1995 were depth, wave exposure, and kelp type. Covariates included were the average number of glaucous winged gulls and average number of total birds of all species at each transect, as well as average catch per unit effort of fish at each transect weighted by consumption. A separate analysis using air exposure in the place of depth was also performed.

The best model of egg loss rates in 1995 included just two variables, depth and average bird abundance (Table 17). This model explained 78.4% of the variation in egg loss rates. Graphical analysis of the relationship between depth and egg loss rate shows that the rate of egg loss seems to be higher at higher depths (Figure 24). This is a similar result to that of previous years. However, it appears that an inverse relationship exists between

egg loss rates and bird abundance; egg loss rates are higher at lower bird abundance (Figure 25). This is not the expected result, and is the opposite relationship of that found in 1994. Therefore, the observed relationship between bird abundance and egg loss rates is probably a reflection of some other variable.

Exclusion of the bird covariates from the factorial analysis leads to a model explaining 53.9% of the variability in egg loss rates, and containing only the depth term (Table 18).

#### **1.3.5. 1990 and 1991 combined analysis**

The same methods were used to analyze the combined 1990 and 1991 data as were applied to the individual years. An analysis of covariance was performed on the  $\ln(\text{egg abundance})$  data using all available habitat variables. To model egg loss rates, the slope,  $Z$  of linear regressions fitted to the  $\ln(\text{egg abundance})$  data at each depth for each transect in 1990 and 1991 was used as the dependent variable for factorial analyses.

#### **Graphical Analyses**

Combined 1990 and 1991 egg loss data were broken down by habitat variables for graphical analysis using the same techniques as for individual years. Variability associated with the substrate variable was accounted for by choosing only transects occurring within the rocky and boulder substrates (except where the substrate variable itself is examined).

A plot of the negative of the instantaneous egg loss rates ( $-Z$ ) against air exposure and depth in each of the wave exposure categories shows that egg loss was probably

higher in wave-protected areas than wave-exposed areas (Figure 28). It also appears that egg loss rates are higher at higher depths. The exposed category is represented by three transects, the protected category by eight.

Graphical analysis of egg loss in oiled/unoiled breakdown shows a distinct difference in egg loss between the two categories (Figure 29). Egg loss rates appear to be higher in previously oiled areas than in unoiled areas. The unoiled category includes data from six transects, the oiled data from five, and as in the previous figures egg loss rate appears to decrease with depth.

Egg loss rates for the combined years 1990 and 1991 plotted by substrate type show that there are few data points from substrates other than rocky (Figure 30). The rocky substrate occurred at eleven transects, the boulder at one transect, and the gravel at three transects. Within the rocky substrate, egg loss rates decrease as depth increases, while data from the gravel substrate show the opposite effect. This may be a result of the small number of transects within the gravel type substrate.

A plot of egg loss rates from each year against both depth and air exposure shows egg loss may have been higher in 1990 than in 1991 (Figure 31). This suggests that interannual variability may be important when considering egg loss rates.

A problem arises when comparing egg loss rates in the two kelp type categories. Large brown kelp seems to be more likely to dominate at subtidal depths, so there are few data points for this classification above mean low water (Figure 32). This makes it hard to distinguish the patterns in egg loss resulting from this variable, since it is difficult to determine which effects are due to depth and which to kelp type.

The final habitat variable, depth, shows the familiar pattern of increasing egg loss at higher depths (Figure 33). The effect of depth on egg loss rates seems to be the most consistent from this and previous analyses.

### **Analysis of Covariance**

An analysis of covariance was performed on the combined 1990-1991 ln(egg abundance) data with days since spawn as the covariate. This analysis also included all the habitat variables available for both years as well as a number of interaction terms. The results of the ANCOVA explained 42.1% of the variation in ln(egg abundance) data, with the wave exposure term accounting for the most variability of all the terms included in the model (Table 19). The majority of interaction terms in the model were significant, as well as all main effects except depth.

### **Factorial Analyses**

A number of factorial analyses were carried out on the combined 1990 and 1991 data using instantaneous egg loss rate ( $Z$ ) as the dependent variable. These analyses attempted to measure the effects of the various habitat variables seen in the graphical analyses and any interaction effects between the variables. The habitat variables: year, substrate, oiled/unoiled, wave exposure, and depth were available for both years as independent variables.

Due to the unbalanced nature of the sample design, a number of different subsets of the combined 1990-1991 data were modeled in order to maximize the interaction terms available. The major division of data was in the substrate variable. Subsets of data from the rocky substrate only, data from rocky and boulder substrates, and data pooled over all

substrates were each analyzed. To maximize the number of interaction terms, the -30 foot depth and the +5 foot depth were eliminated individually as well as simultaneously from some analyses. Appendix B includes results of all data sets modeled for the combined 1990-1991 data

The data set resulting in the best model was from all depths pooled over rocky and boulder substrates. When data were pooled over these substrates, a variety of two-way interactions could be analyzed for the remaining factors, and after sequential removal of insignificant terms a model containing the interaction terms oiled/unooled\*year, kelp type\*year and kelp type\*substrate type, and the habitat variables wave exposure, oiled/unooled, year and depth results (Table 20). This model explains about 77.7% of the variability in egg loss rates for the combined years 1990 and 1991.

The presence of the substrate type\*kelp type variable probably reflects the small number of transects in each substrate, as well as the confounding problem of kelp type and depth. Removal of this term leads to a model containing only the year\*oiled/unooled interaction term, and the habitat variables: year, oiled/unooled, wave exposure and depth (Table 21). This model explains 73.4% of the variability in egg loss rates for 1990 and 1991.

Depth and the interaction term accounted for the most variability in egg loss rates, suggesting that these two were the most important factors affecting egg loss in 1990 and 1991. The significance of the interaction term implies that the condition oiled/unooled (location) had different effects on egg loss in the individual years. From the individual analyses performed on each year's data, it is evident that oiled/unooled condition was very

important in determining egg loss in 1990, but insignificant in determining egg loss in 1991.

The average negative instantaneous egg loss rates (-Z) and corresponding standard errors are summarized for each significant habitat factor (Table 22). These were calculated from Table 2 and Table 6 for all levels of the depth, wave exposure, year and oiled/unooled categories. The average egg loss rate decreases with increasing depth, and the average egg loss rate is higher for oiled transects than unooled transects when both years are combined. However, the year\*oiled/unooled interaction term shows that average egg loss rates were higher in oiled areas only in 1990, in 1991 egg loss rates were higher in unooled areas. Egg loss was higher in 1990 than in 1991, with average egg loss rates of 0.086 and 0.042 respectively. The average egg loss rate is also higher for protected transects than for exposed transects, a counterintuitive result since transects that were exposed to higher wave forces over the incubation periods would be expected to experience higher egg loss.

#### **1.3.6. 1994 and 1995 combined analyses**

The combination of 1994 and 1995 data includes data from transects on Montague Island only. To maximize the number of data points available, and to reduce variability associated with the substrate variable, data from rocky and boulder transects combined, and rocky transects only were used exclusively for the 1994 and 1995 analysis.

## **Graphical Analyses**

Graphical analyses were performed on the rocky and boulder data from the combined years 1994 and 1995, in order to identify important habitat variables. Egg loss rates seem to be slightly higher in wave-protected areas than in wave-exposed areas (Figure 34). Egg loss rates plotted against air exposure and depth both show egg loss was higher in 1994 than in 1995 (Figure 35).

The breakdown of egg loss rates into the two kelp type categories yields two very different pictures (Figure 36). Egg loss seems to be lower at quadrats dominated by large brown kelp when the data is plotted against depth. When egg loss rates are plotted against air exposure, the opposite trend results, egg loss is greater at stations dominated by large brown kelp. The difference may be a function of the small sample size associated with the large brown kelp dominated category, as well as the fact that large brown kelp dominates only at subtidal depths.

Depth has been an extremely important variable in the previous analysis, and that pattern continues in the combined 1994 and 1995 data set. Egg loss rates increase at higher depths, and with increasing times of air exposure over incubation (Figure 37).

## **Analysis of Covariance**

An analysis of covariance was performed on the combined  $\ln(\text{egg abundance})$  data from 1994 and 1995 as for the previous data sets. The covariate term was days since spawn, and all available habitat variables and interaction terms were included. Days since spawn explained the most variability in  $\ln(\text{egg abundance})$  data from these two years, with the total model explaining 53.8% of the variability (Table 23). All other



terms except the depth\*days interaction, kelp type, wave exposure and depth were insignificant in the model.

### **Factorial Analyses**

When egg loss rates from the combined years, 1994 and 1995, are subjected to a factorial analysis, a model explaining 52.4% of the variability in egg loss rates results (Table 24). This model is of rocky data only, and includes only the depth term. The model is consistent with the previous analyses of egg loss rates, with egg loss rates decreasing with increasing depth.

The second best model of egg loss rates for the combined years 1994 and 1995 comes from rocky and boulder substrates combined. This subset of data represents the majority of transects in the two years, 13 of 16. Factorial analysis of habitat variables led to a model explaining 51.3% of the variability in egg loss rates (Table 25). In this model, depth is represented by air exposure. The air exposure term proves to be the most significant, explaining most of the variability by itself. The other significant terms in the model are year ( $p=0.008$ ) and wave exposure which is marginally significant ( $p=0.048$ ).

Average egg loss rates for significant habitat variables in both models were calculated for the combined 1994 and 1995 rocky and boulder data (Table 26). Egg loss rates were higher at wave-protected transects ( $-Z=-0.108$ ,  $SE=0.018$ ) than at wave-exposed transects ( $-Z=-0.098$ ,  $SE=0.009$ ). In 1995 egg loss rates were lower ( $-Z=-0.096$ ,  $SE=0.011$ ) than in 1994 ( $-Z=-0.105$ ,  $SE=0.010$ ). Average egg loss rates associated with each depth sampled are also summarized for rocky data only, and the results show that as depth increases, egg loss rates generally decrease (Table 27).

### **1.3.7. Combined Montague Island analyses**

Because of the significance of the oiled/unoiled variable in the 1990, and combined 1990 and 1991 analyses, combining data from all four years was done only for Montague Island transects. By using this subset of data, egg loss rates from the two locations (previously oiled and unoiled) were not combined. The Montague Island analysis used all rocky and boulder transects from all four years of the egg loss study. In both 1990 and 1991 there were three rocky or boulder transects on Montague Island. In 1994 and 1995 all transects were located on Montague Island, the majority of which occurred on rocky and boulder substrates.

#### **Graphical Analyses**

Graphical analyses of the combined data for Montague Island were performed on rocky and boulder data using the same methods as for previous analyses. Egg loss rates at wave-protected transects seem to be higher than those at wave-exposed transects on Montague Island (Figure 38). Although this is a counterintuitive result, it has been consistent throughout most analyses.

Egg loss rates for each year are plotted against both depth (Figure 39) and air exposure (Figure 40). It is evident from these graphs that interannual variation is a factor that must be considered when modeling egg loss, since egg loss rates differed among years.

A plot of egg loss rates against depth and air exposure reveals that egg loss may be higher where large brown kelp is not dominant (Figure 41). However, since this

category occurs mainly at the higher depths it is unclear which effect is being seen, the effect of kelp type or the effect of depth.

The final habitat variable used in the analysis of transects occurring on Montague Island was depth. Egg loss rates seem to decrease with increasing depth and decreasing air exposure, which is consistent with all previous results (Figure 42).

### **Analysis of Covariance**

The first step in the statistical analysis of the combined Montague Island egg loss data was to perform an analysis of covariance on data from rocky and boulder transects only, with  $\ln(\text{egg abundance})$  and days since spawn as the dependent and covariate terms respectively. All possible habitat variables and interactions were included in the analysis, resulting in a model explaining 48.1% of the variability in  $\ln(\text{egg abundance})$  (Table 28). All the individual habitat variables were significant in the analysis, except kelp type and substrate type. Days since spawn explained the most variability in  $\ln(\text{egg abundance})$ , followed by the depth variable. Only about half of the interaction terms were significant, with the majority of the significant terms being covariate interactions.

### **Factorial Analyses**

Factorial analysis of the combined Montague Island data from only the rocky substrate resulted in a model explaining 71.5% of the variability in egg loss rates (Table 29). It contained three significant terms: depth, wave exposure, and year, with depth explaining the majority of the variation in egg loss rates.

A model of egg loss rates with air exposure in place of depth from data collected at rocky transects only explained 67.2% of the variability in egg loss rates (Table 30).

Year explained the most variation in egg loss rates in this model. Other significant variables were wave exposure and the covariate term, air exposure.

The average egg loss rate for the Montague Island combined data is higher in areas protected from waves ( $-Z=-0.116$   $SE=0.015$ ) than in exposed areas ( $-Z=-0.071$   $SE=0.012$ ) (Table 31). The year with the highest egg loss on Montague Island was 1990 ( $-Z=-0.154$ ,  $SE=0.029$ ), and the following year had the lowest average egg loss ( $-Z=-0.003$ ,  $SE=0.015$ ). As depth increased, egg loss rates decreased, a consistent pattern within all the egg loss data (Table 32).

#### **1.3.8. Kelp type analysis**

From the previous graphical analyses as well as the factorial analyses, it is apparent that the kelp type variable is confounded with the depth variable. Since large brown kelp is dominant only at subtidal depths, the effect of kelp type cannot be accurately assessed by examining the entire data set. For this reason an additional analysis was performed to directly compare egg loss rates between the large brown kelp dominated and nondominated categories.

To directly compare kelp types, all egg loss rates below 1 ft relative to mean low water were selected, and an analysis of variance using only the kelp type variable was performed (Table 33). The results show that there is not a significant difference in egg loss rates at depths dominated by large brown kelp and at stations dominated by other vegetation types. Based on this result it appears that in previous analyses where kelp type

was significant, the variable responsible for the significance may have actually been depth.

### **1.3.9. Air exposure versus depth**

Based on the factorial analyses of egg loss models, depth is probably the most important variable affecting egg loss. The depth variable was included in the best model of egg loss rates for every data set examined. Time of air exposure was calculated for each depth and used as covariate in the factorial analyses, but the resulting models were not as significant as the models including depth. In most cases where depth was included in the best model of egg loss rates, the second best model included the air exposure term instead of depth. To analyze whether there are 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 the best model for each data set examined, an F-test was performed to determine if the models with depth were significantly different than models with air exposure (Table 34). 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 1990 and 1994.

A significant difference in 1994 was probably the result of the combination of depth categories used. This meant that the depth categories used in the modeling did not represent the true relationship between depth and air exposure, resulting in a significant difference between the depth and air exposure models. In 1990 the lack of permanently

secured quadrats may have influenced the results for air exposure. Since the same patch of eggs were not necessarily measured on every visit, depths may not have been consistent.

The benefit of using air exposure instead of depth is that it eliminates the need to estimate egg loss for each depth category, thus reducing the number of parameters estimated without significantly increasing variation. The air exposure increases exponentially as depth relative to mean low water decreases (Figure 43).

#### **1.3.10. Model comparisons**

##### **Analyses of Covariance**

The analysis of covariance models using habitat variables were compared to analysis of covariance models using only transect and depth as explanatory variables for each of the seven divisions of  $\ln(\text{egg abundance})$  data (Table 35). The transect-depth model is equivalent to the model used by Biggs-Brown and Baker (1993) in the analysis of the 1990 and 1991 data. The transect-depth models were consistently better at explaining variability in the data than the models containing only habitat variables (Figure 44). The average  $R^2$  value for the transect-depth models is 0.518 (SE=0.039) while for habitat variable models the average  $R^2$  value is 0.468 (SE=0.026). This is not surprising since the transect-depth models had many more parameters.

##### **Factorial Analyses**

To compare  $R^2$  values from the different modeling techniques, the best habitat models were averaged across each egg loss rate data set modeled. This average was

compared to average  $R^2$  values across the same data sets from the three simpler models, models containing the depth term only, models containing the air exposure term only, and models containing transect and depth (Figure 45).

The best models from factorial analyses of egg loss rates had  $R^2$  values ranging from 0.524 for 1995 data to 0.854 for 1990 data (Table 36). The models from factorial analyses include different combinations of the habitat variables, and the average  $R^2$  for these habitat models is 0.679 (SE=0.044).

Models using only depth as an explanatory variable for egg loss rates have an average  $R^2$  of 0.344 (SE=0.057) (Table 37). This is a relatively low average  $R^2$  when compared to the habitat variable models. The low average  $R^2$  may not entirely reflect the strength of depth as an explanatory variable. In 1990 and 1991 differences in egg loss rates between oiled and unoiled areas, and between the two years were more important, therefore the  $R^2$  values for models including only depth are low. In 1994 and 1995 the  $R^2$  values for models including only depth are high, and for both 1995 and the combined 1994 and 1995 data, models containing only depth resulted from the factorial analyses of all habitat variables (Table 36). When average  $R^2$  values are compared for the four types of models for 1994, 1995 and both years combined, models containing only depth and only air exposure are much closer to the other two types of models (Figure 46).

Models containing only air exposure also have a fairly low average  $R^2$  value of 0.257 with a standard error of 0.056 (Table 38). As in the case for models containing only depth, this low value also reflects the differences between the two sets of years (1990-1991 and 1994-1995).

Models containing only depth and transect explained the most variability of all the models (Table 39). The average  $R^2$  value for these models over all the egg loss rate data sets examined was 0.769 (SE=0.049).

#### 1.4. Discussion

Some major differences between the first two years of the study, 1990 and 1991, and the last two years, 1994 and 1995, are evident from the egg loss models. In the later years depth seems to be the most important environmental variable driving egg loss in Prince William Sound, while in the early years a combination of variables including depth were significant. There were some differences between the two sets of years which may be related to this result. Spawning biomass was higher in the early years than the later years, which may have affected egg loss. The 1990 and 1991 data is from a wide range of locations in Prince William Sound, while the 1994 and 1995 data is from Montague Island only. Thus, egg loss may be influenced by depth within each location, but sound-wide patterns in egg loss may be strongly influenced by the different conditions experienced in each area. This seems to be true from examination of the egg loss model for Montague Island transects only. This data set included all years, but was limited to a fairly small range of locations, and indeed depth proved to be the most significant factor in the model.

It is apparent that depth is probably the most important variable affecting egg loss. It was included in all factorial analyses of egg loss, and was the predominant variable in



the models of 1994 and 1995 data. 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 consistently higher at protected transects than at exposed transects. The only year where egg loss was higher at exposed transects was 1990, and in this year the wave-exposed category was represented by only one transect. Lower egg loss in exposed areas is highly counter-intuitive and may reflect the presence of an undiscovered process driving egg loss in protected areas. Examination of data collected by wave sensors placed at three egg loss transects in 1995 indicate there may be a threshold wave energy level (Chapter 3). 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. The analysis of egg loss rates to address the problem of kelp type indicated that kelp type was highly insignificant in predicting the rate of egg loss.

Oiled/unoiled condition (location) was 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 observed egg loss between the two areas. In

1991 the differences in egg loss rates between oiled and unoiled locations was not significant, suggesting the physical and biological regimes in the two areas were more similar in 1991 than in 1990. 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, when increased bird abundance resulted in higher egg loss rates. Predator exclusion experiments were conducted at egg loss transects in 1994 and 1995, the results of which are summarized in Appendix C. These experiments showed there was no significant effect of birds on egg loss, but this may have been caused by the failure of the exclusion cages to exclude all predators. These results suggest that predation is a relatively unimportant process driving egg loss in Prince William Sound.

However, the "Avian Predation on Spawn" study carried out by the US Forest Service (C.R.D.I.) estimated that birds removed 19.24% of the total herring spawn in an area of Montague Island, quite a large percentage. The reason for the conflicting results may lie in the choice of predator indices used in egg loss modeling. For modeling, the average abundance of predators was used as a covariate; however, this failed to account for the total abundance of spawn at the egg loss transect. Thus, the consumption of eggs by a lesser number of predators at a transect with low egg density would result in a higher egg loss rate than the consumption by many predators at a transect with large numbers of eggs. This would explain the inverse relationship between predators and egg loss rates

found in 1995 for both fish and birds, and still allow predation to be an important process regulating egg loss.

Model parameters were estimated for each data set using both depth categories and air exposure (Table 40). The model of egg loss recommended by this study is based on the time of air exposure over the incubation period. The basic assumption for this approach is that the rate of egg loss is linearly related to air exposure. Our results do not reveal any violation of this linear assumption. Using the time of air exposure from each depth where spawn is estimated during spawn deposition surveys it is possible to estimate the rate of egg loss at that depth and thus the number of eggs initially spawned for each observation. This eliminates the need for a blanket estimate of an egg loss correction factor, such as the 10% value used for previous biomass estimates. Instead, the biomass of spawning herring can be directly estimated from the spawn deposition data itself.

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 the oiled/unoled term in 1990. An air exposure based model will account for a significant proportion of egg loss in most years, without having to include transect based variation.

## **Chapter 2. Calculations of egg loss at selected 1995 transects.**

### **2.1. Introduction**

One of reasons for studying egg loss for Prince William Sound herring is that the population biomass is annually estimated using the number of eggs spawned. The number of eggs spawned is estimated for Prince William Sound by dive surveys at randomly located transects throughout the spawning beds. Since the survey cannot be conducted until some time after spawning, egg loss must be accounted for. As mentioned previously a correction factor of 10% has been used in the past, and from the 1990 and 1991 egg loss data Biggs-Brown and Baker (1993) determined a range of correction factors from 10 to 15%. They also estimated that the total loss of eggs from the beginning of spawning until hatching ranged from 50% to 91%.

One of the objectives of the 1995 egg loss sampling was to estimate the correction factor and the total loss of eggs using the egg loss model developed for Prince William Sound. Rather than compute these for the egg loss transect itself, a spawn deposition transect was used. Egg loss transects do not reflect the gradient of the spawning bed, or the distribution of eggs at each depth; they are just snapshots of egg loss occurring at each depth where quadrats were installed. They do not tell us how many eggs were deposited in the area at that depth, nor the total number of eggs lost for the area. To accomplish this a spawn deposition transect must be used.

## 2.2. Materials and Methods

To accurately represent the depth distribution and total abundance of spawn, a spawn deposition transect was placed at the same location as each egg loss transect in 1995. Divers counted eggs along a transect extending perpendicular from the beach, continuing past the depth at which no more spawned eggs were observed. The data collected were estimates of the number of eggs in 0.1 m<sup>2</sup> quadrats at 5 meter intervals along the transect.

The best model of egg loss developed for Prince William Sound from Chapter 1 of this report was then used to calculate the total number of eggs initially deposited at these transects, as well as the number of eggs retained until hatching at the transect. In 1995 the best model of egg loss included only the depth term, which was replaced by air exposure since this variable estimates fewer parameters.

From examination of air exposure at each depth from 1995 egg loss transects, it is apparent that the square root of the time of air exposure is a linear function of depth, (Figure 47). Thus, for depths above -3.5 feet, air exposure in 1995 was calculated using the relationship,

$$AE=(6.013697+1.696911*D)^2 \quad (1)$$

where AE is air exposure over incubation in hours and D is depth in feet. All depths below -3.5 feet were not exposed to air during incubation, thus AE is equal to zero.

The egg loss rate for each depth where estimates of egg abundance were available from spawn deposition surveys was calculated using the equation

$$Z=0.052357+0.000601*AE. \quad (2)$$

from the linear relationship in Figure 24. The number of eggs observed at the time of the spawn deposition survey is

$$N_t=N_0e^{-Zt}, \quad (3)$$

where  $t$  is the time in days since spawning occurred. Thus, the initial number of eggs deposited,  $N_0$ , is

$$N_0=N_t e^{Zt} \quad (4)$$

where  $Z$  is calculated from (2).

### 2.3. Results.

In 1995 the beginning of spawning ranged from May 27 to May 29, with spawning at most transects beginning on May 28. The average time from beginning of spawning to spawn deposition survey was 4.9 days, with a range from 4 to 7 days. The average time of the incubation period in 1995 was 21.1 days, with a range of 21 to 22 days.

Based on the model, the average percent eggs lost from the time of their spawning to the time at which the spawn deposition survey took place was 6.69% per day. This value increased from 4.61% per day at subtidal depths to 21.61% per day at higher depths (Figure 48). The model calculates the average egg loss from the time of spawning to the time of the survey at 33% (SE=1.0%). This value ranges from 18.9% at deeper depths to 89.6% at the highest depths.

The percentage of eggs lost over the entire incubation period ranged from 67.40% at subtidal depths to an asymptote at 100% at the higher depths (Figure 49). The average percentage of eggs lost over the incubation period was 76.06%.

#### **2.4. Discussion.**

The average percentage of eggs lost from the time of spawning to the time of the survey in 1995 was calculated at 33%. This value is much higher than the assumed value of 10%, and higher than the range of values from 10 to 15% found by the previous method (Biggs-Brown and Baker 1993). In the previous evaluation Biggs-Brown and Baker (1993) excluded the highest depth station from their estimate of the percentage of eggs lost from spawn to survey. When that depth is included, their range of eggs lost from spawn to survey increases to 21-38%.

The range of the total percentage of eggs lost over incubation according to the 1995 model (67.4-100%) is slightly higher than the range found by Biggs-Brown and Baker (1993) of 50.4% to 91.2%. Other ranges of total egg loss from Pacific herring spawning beds are from 56-99% for Barkeley Sound, British Columbia (Outram 1959) and from 46-92% for Georgia Strait, British Columbia (Haegele and Schweigert 1991). The results of our model are quite similar to other studies of Pacific herring egg loss, and all studies have found that extremely high egg loss occurs at the highest depths.

It is important to note that the relationship between air exposure and depth changes with both the length of the incubation period and year, since tides will be

different from year to year depending on when spawning and hatching occur. For this reason it is important to calculate a new relationship between time of air exposure and depth in each year, specific to the timing and duration of the herring egg incubation period in each year.



## **Chapter 3. Wave energy analyses.**

### **3.1. Introduction.**

The force of wave action has been observed to dislodge Pacific herring eggs in British Columbia creating large windrows of unattached eggs (Hart and Tester 1934; Hay and Miller 1982). Wave action was also believed to cause a substantial proportion of egg loss in Prince William Sound (Biggs-Brown and Baker 1993). In 1995 sampling was undertaken to measure the effect of wave action on egg abundance at three egg loss transects. Two primary objectives of this portion of the egg loss study were (1) to correlate egg loss between sampling visits with wave energy measurements at the transects, and (2) to provide justification for the wave exposure variable used in the egg loss model (Chapter 1).

### **3.2. Materials and Methods.**

A SEAGAUGE wave and tide recorder (SBE 26-OX) was installed at each of three egg loss sites by an oceanographer from the Prince William Sound Science Center. The recorders provided a continuous measure of wave pressure which was then converted into wave energy ( $\text{joules} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ ) by a summary program. The installation sites included two wave-exposed transects, #9 (Graveyard Point) and #6 (Montague Point), as well as one wave-protected transect #2 (inside Rocky Bay).

To assess the effect of wave force on egg loss, changes in egg abundance between sampling visits were correlated to the average wave energy\*day<sup>-1</sup> during the same period at each transect using analysis of covariance techniques. Wave energy was the covariate predicting changes in egg abundance between visits.

The mean wave energy at the two wave-exposed transects was also compared to the mean wave energy at the wave-protected transect using a paired t-test. This analysis was designed to test the integrity of the wave exposure dummy variable included in the egg loss model. For the wave exposure variable to be considered valid, there must be significant differences in wave energy between the two classifications, wave-exposed and wave-protected. Because of the extremes of wave energy recorded during the incubation period, each observation of wave energy\*day<sup>-1</sup> was ranked and compared between the two classifications using nonparametric methods. This helped to minimize the variance of the observations while preserving the integrity of each observation.

### **3.3. Results**

To directly assess the effect of wave energy on egg loss, wave energy was used as a covariate predicting changes in egg abundance during the time interval between transect visits. Based on the graphical analysis of the data, depth was not included as a categorical predictor, since changes in egg abundance between transect visits seem to exhibit no relationship with depth (Figure 50). It was originally thought that more herring eggs would

be lost due to wave action at +5 feet on the beach where eggs would be exposed to breaking waves than at -5 feet where the eggs are submerged.

Changes in egg abundance between sampling visits plotted against average wave energy during the same time period reveals that, as average wave energy\*day<sup>-1</sup> increases, egg loss increases (changes in egg abundance become predominantly negative) (Figure 51). However, the relationship is heavily influenced by the largest average wave energy recorded, 8229 joules\*m<sup>-2</sup>\*day<sup>-1</sup>. The large wave energy value was recorded at transect #6 (Montague Point) only, and marked the occurrence of a large storm event. Large losses of eggs were associated with this wave energy value.

Excluding the largest value, the range of wave energies recorded is from 2 to 561 joules\*m<sup>-2</sup>\*day<sup>-1</sup>. A plot of these smaller wave energies against the corresponding changes in egg abundance reveals no relationship (Figure 52). At these levels of wave energy both egg losses and egg gains were observed, and no real pattern can be discerned.

When wave energy and changes in egg abundance are plotted for each transect against sample date, no clear pattern can be seen in the data, except in the case of the large storm event at transect #6 (Figure 53). Changes in egg abundance and wave energies at transect #6 span a considerably larger range than were recorded at other transects.

The analysis of covariance performed on the wave energy data resulted in a good model explaining 34.8% of the variability in the data (Table 41). The covariate, wave energy, was highly significant in predicting changes in egg abundance. Another analysis of variance was performed using high or low energy level as factors to predict the same changes in egg abundance between sampling visits. The high energy level included the

points associated with the large storm event recorded at Montague Point, while the low energy level encompassed the remaining points. Energy level was again highly significant in the resulting analysis of variance, explaining 35.1% of the variability in egg abundance (Table 42). Changes at high and low energy levels were significantly different with higher egg loss at the high energy level. The mean loss at the high energy level was 283,873 eggs (SE=33,300), at low energy levels the mean egg loss was 4,083 (SE=4,797).

To test the validity of the wave exposure habitat variable used in egg loss modeling, average wave energy\*day<sup>-1</sup> from the wave energy recorders was compared between the two categories; wave-exposed and wave-protected. The average wave energy\*day<sup>-1</sup> for the exposed transects was 1333.5 joules\*m<sup>-2</sup> (SE=689.4). The average wave energy\*day<sup>-1</sup> for the wave-protected transect was 71.1 joules\*m<sup>-2</sup> (SE=35.6). A t-test of average wave energy\*day<sup>-1</sup> shows that there is no significant difference between the two categories, wave-exposed and wave-protected (p=0.19). This may be a function of the wide range of wave energy\*day<sup>-1</sup> measured at each transect resulting in large standard errors calculated for each category. Wave energy values at the protected transect ranged from 1 to 491 j\*m<sup>-2</sup>, and at the exposed transects the range was from 2 to 19,001 j\*m<sup>-2</sup>.

Therefore, a nonparametric test of the wave exposure variable using ranks of wave energy\*day<sup>-1</sup> was evaluated. This reduced the variance estimate in each category, while maintaining the relative values of each wave energy measurement. A Mann-Whitney test performed on the ranks of wave energies showed there is a highly significant difference (p<0.000) between wave energy\*day<sup>-1</sup> rankings in the two wave exposure categories. Thus,

the wave exposure variable used in the model seems to have been justified as being a valid division of transects into two levels of wave action.

### 3.4. Discussion.

The differences in egg loss between the lower and higher wave energy levels are striking and may imply the existence of a threshold energy level beyond which significant egg loss occurs. The lower energy levels did not have any clear effect on egg loss, which is explainable if the wave energies were not larger than the threshold. The large wave energy recorded at Montague Point associated with egg loss would therefore be above the wave energy threshold. The problem with the data is a lack of observations from intermediate wave energy levels. There is a large gap between lower energy levels,  $<600 \text{ j}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ , and the higher energy level ( $8229 \text{ j}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ ). Although the two levels are significantly different from one another, the existence of a threshold energy level for egg loss cannot be confirmed because of the limited range of wave energy values recorded during the 1995 herring egg incubation period.

Storm events did have a large effect on wave energy levels measured at transect #6, and in turn these resulted in large egg losses, averaging 283,873 eggs per quadrat. Using the egg loss model, an estimated 393,771 eggs per quadrat were initially spawned; therefore, 72.1% of the eggs at the transect were removed by the large storm. Hart and Tester (1934) and Hay and Miller (1982) estimated the removal of eggs at 26% and 40% by storms and resulting wave action. The periodic occurrence of storm events may drastically

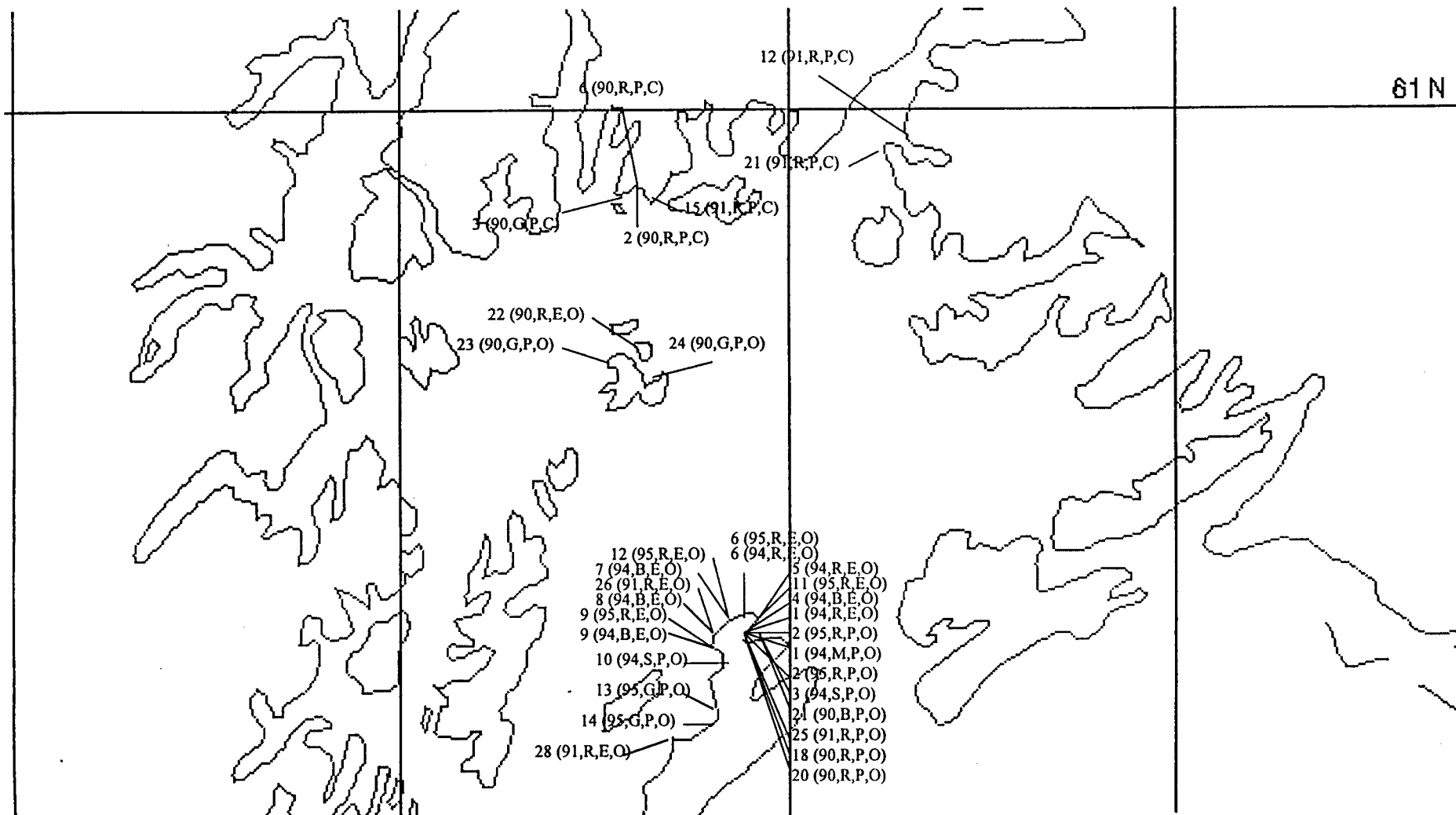
influence the number of eggs lost during incubation. Since wave energy was observed to be highly variable, egg loss due to storm events is also highly variable between years, as well as short distances.

### Literature Cited

- Biggs-Brown, E.D. and T.T. Baker. 1993. Estimates of egg loss for Pacific herring in Prince William Sound, 1990-1991. NRDA Damage Assessment, Fish/Shellfish Study 11:22 p. + Tables and Figures.
- Bishop 1996, (in press)
- Cleaver, F.C., and D.M. Franett. 1946. The predation by sea birds upon the eggs of the Pacific herring (*Clupea pallasii*) at Holmes Harbor during 1945. Wash. State Dept. Fish. Biol. Rep. 46B, 18 p.
- Funk F. 1993. Forecast of the Pacific herring biomass in Prince William Sound, Alaska, 1993. ADF&G, Comm. Fish. Mgmt. Dev. Div., Regional Information Report No. 5J93-08: 32 p.
- Haegele, C.W. 1993. Seabird predation of Pacific herring, *Clupea pallasii*, spawn in British Columbia. Can. Field-Nat. 107:73-82.
- Haegele, C.W. and J.F. Schweigert. 1989. Egg loss from Pacific herring spawns in Barkeley Sound in 1988. Can. MS Rept. Fish. Aquat. Sci. 2037.
- Haegele, C.W., and J.F. Schweigert. 1991. Egg loss in herring spawns in Georgia Strait, British Columbia. Proceedings of the International Herring Symposium, Anchorage, Alaska, October 23-25, 1990. University of Alaska, Fairbanks.
- Hart, J.L. and A.L. Tester. 1934. Quantitative studies on herring spawning. Trans. Am. Fish. Soc. 64:307-313.
- Hay, D.E. and C.C. Miller. 1982. A quantitative assessment of herring spawn lost by storm action in French Creek, 1980. Can. MS Rept. Fish. Aquat. Sci. 1636.
- Outram, D.M. 1958. The magnitude of herring spawn losses due to bird predation on the west coast of Vancouver Island. Fish. Res. Bd. Canada, Pac. Biol. Sta. Prog. Rep. 111: 9-13.
- Royer, T.C. 1986. Temperature fluctuations in the northeast Pacific from 1954 to 1985 in response to El Nino/southern oscillations and longer period forcing. I.N.P.F.C. Bulletin 47:203-209.
- Steinfeld, J.D. 1971. Distribution of Pacific herring spawn in Yaquina Bay, Oregon, and observations on mortality through hatching. M.Sc. thesis, Oregon State Univ., Oregon, 75 p.

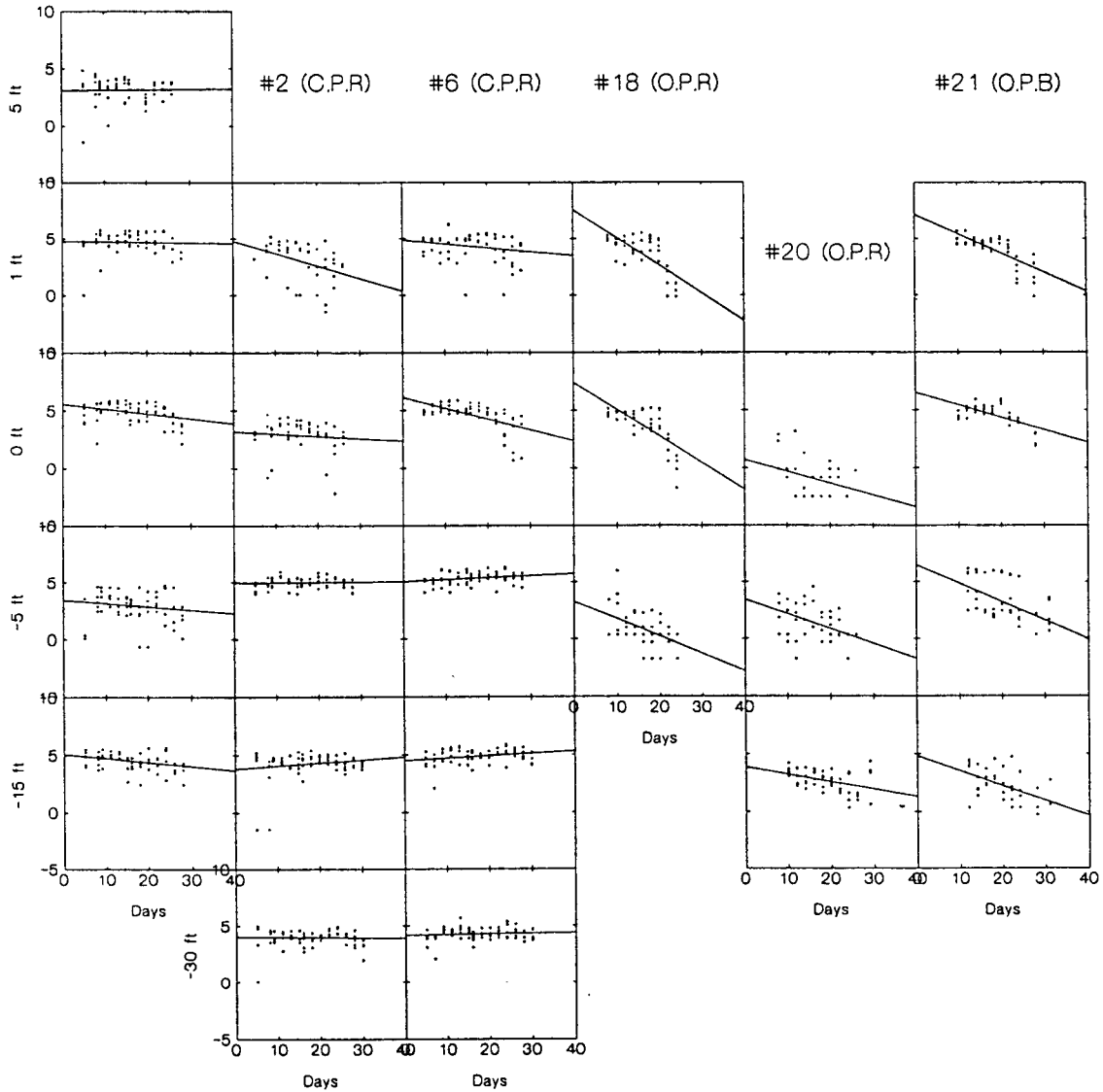
- Wespestad, V.G. 1991. Pacific herring population dynamics, early life history, and recruitment variation relative to eastern Bering Sea oceanographic factors. Ph.D. Dissertation, University of Washington, Seattle WA. 237 p.
- Wilcock, J., and E.D. Brown. 1994. Herring spawn deposition and reproductive impairment, Project ID Number 94166. FY94 detailed Project Description, Exxon Valdez Trustee Council: 27 p.
- Zebdi, A. 1991. Identification of environmental causes of recruitment variation in the herring stock of Sitka Sound, Alaska. M.S. Thesis, University of Alaska Fairbanks, Juneau, Alaska, 132 p.





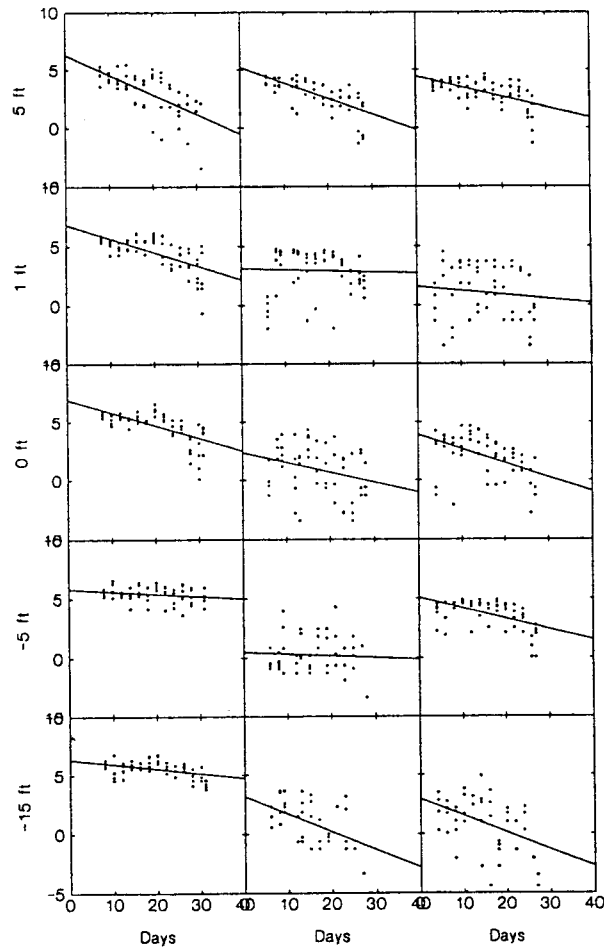
**Figure 1.** Map of Prince William Sound, Alaska showing egg loss transects. R=rocky, B=boulder, G=gravel, M=mud, S=sand substrates. E=wave exposed, P=wave protected. O=oiled, C=un-oiled.

#3 (C.P.G)



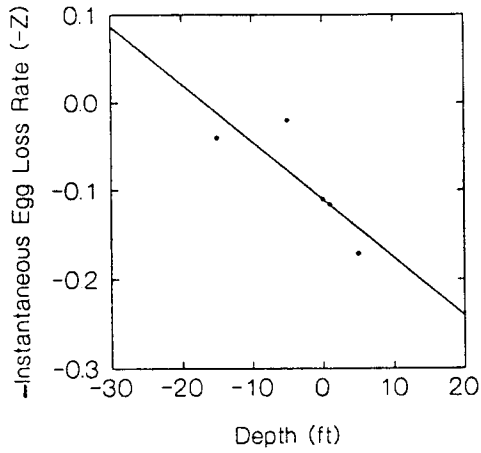
**Figure 2.** Regressions of  $\ln(\text{egg abundance})$  against days since spawn for 1990 transects. The estimate of the egg loss rate ( $Z$ ) for each depth is represented by the line in each graph. C=unoiled, O=oiled, R=rocky substrate, G=gravel substrate, B=boulder substrate, P=wave-protected, and E=wave-exposed.

#22-O.E.R    #23-O.P.G    #24-O.P.G

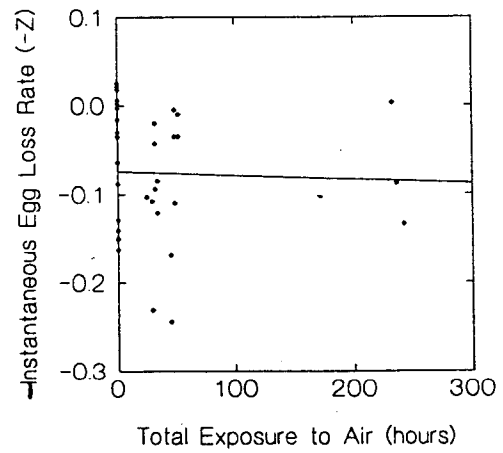
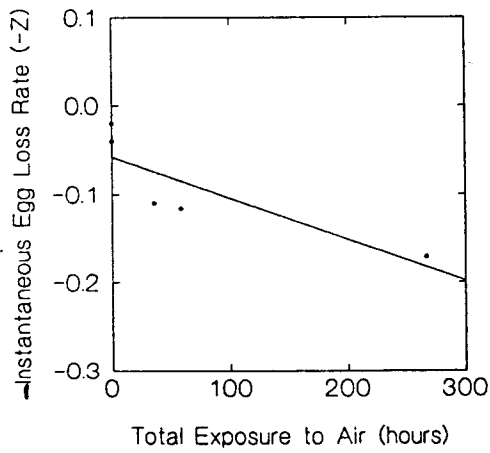
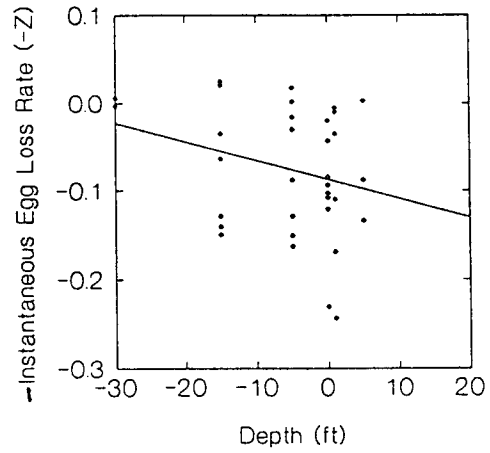


**Figure 2 (continued).** Regressions of  $\ln(\text{egg abundance})$  against days since spawn for 1990 transects. The estimate of the egg loss rate ( $Z$ ) for each depth is represented by the line in each graph. C=unoiled, O=oiled, R=rocky substrate, G=gravel substrate, B=boulder substrate, P=wave-protected, and E=wave-exposed.

Exposed Transects

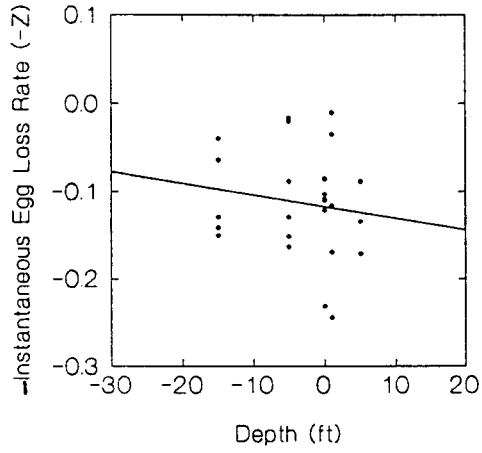


Protected Transects

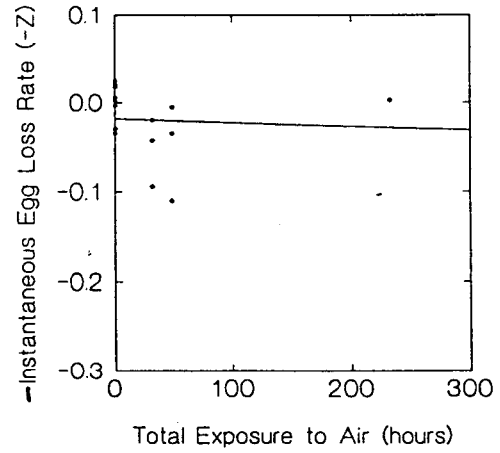
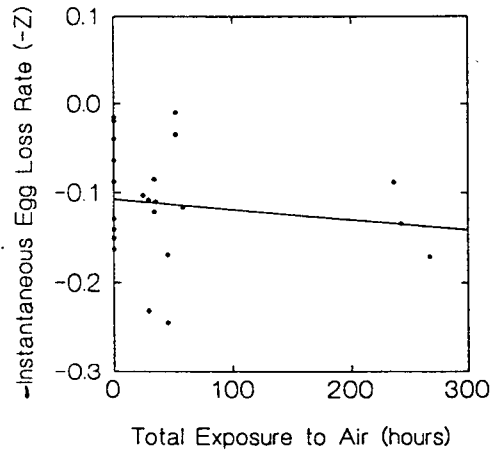
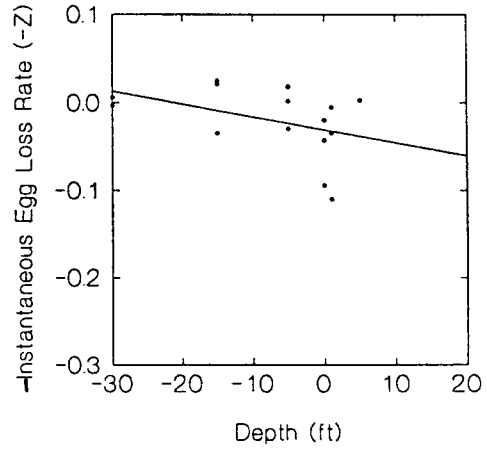


**Figure 3.** Egg loss rates for wave-exposed and wave-protected transects in 1990. Egg loss rates are plotted against both depth and air exposure.

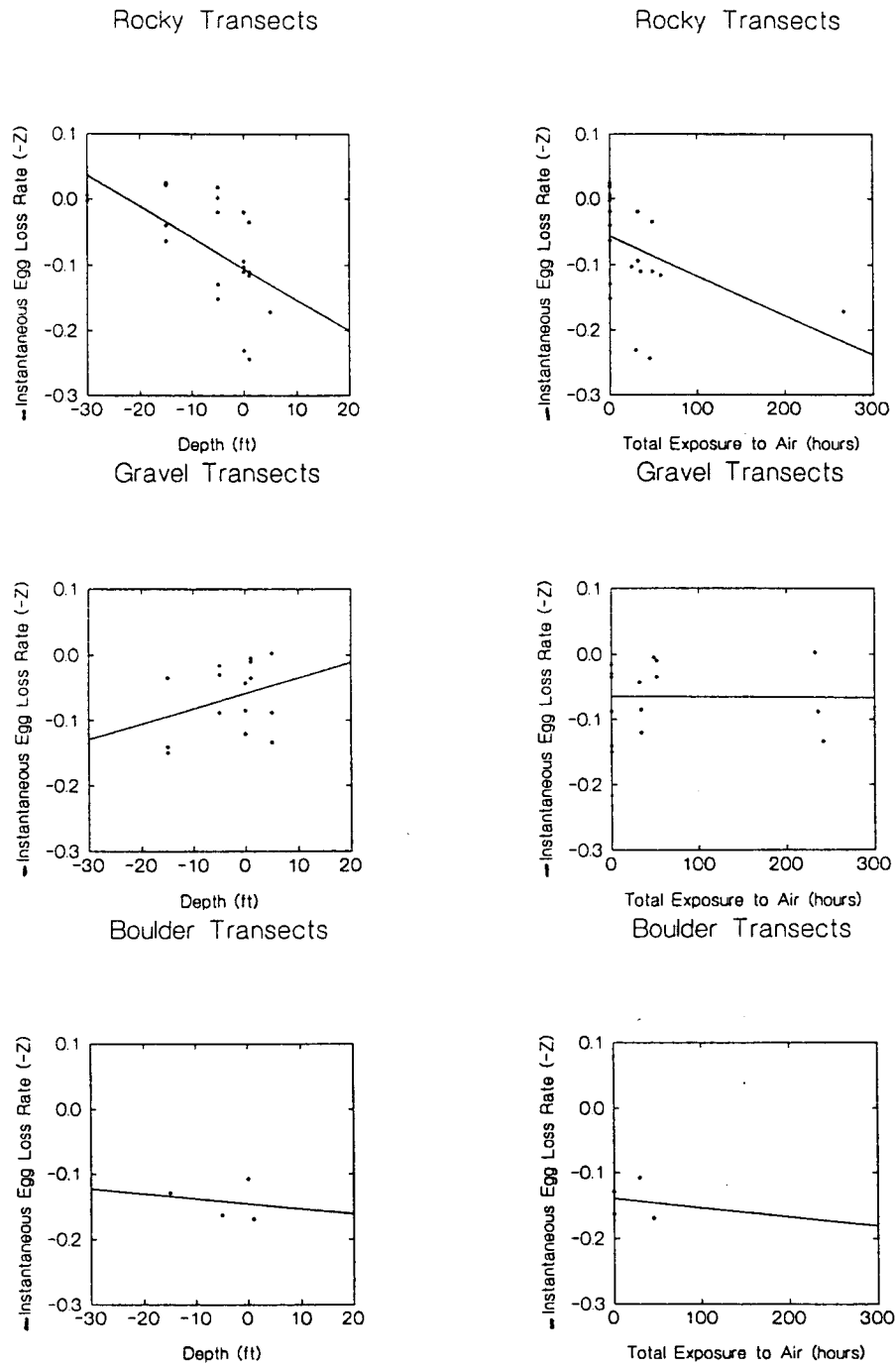
Oiled Transects



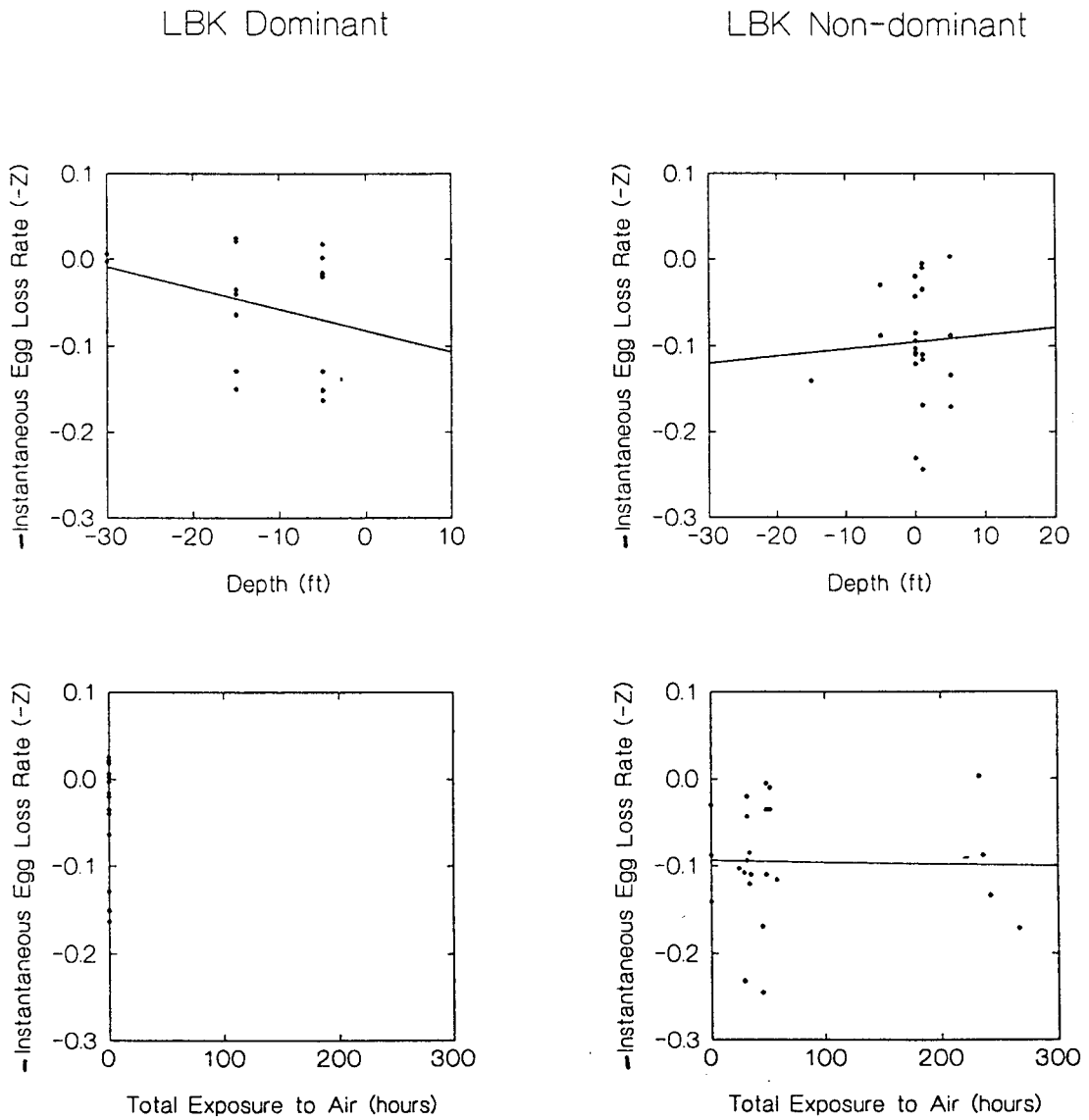
Unoled Transects



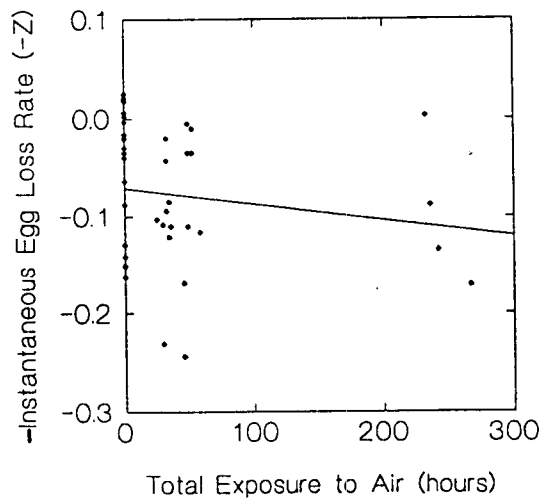
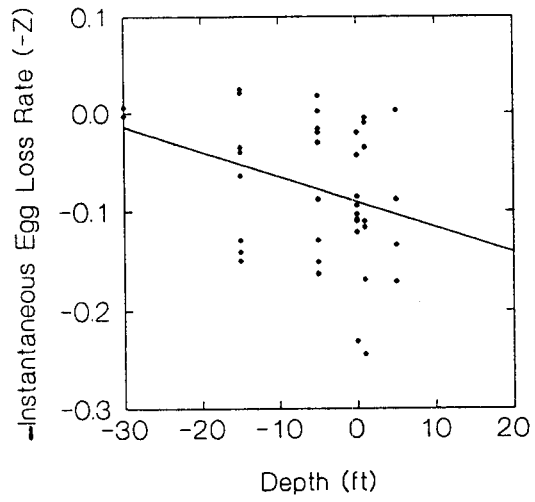
**Figure 4.** Egg loss rates for previously oiled and unoled transects in 1990. Egg loss rates are plotted against both depth and air exposure.



**Figure 5.** Egg loss rates for each substrate type sampled in 1990. Egg loss rates are plotted against both depth and air exposure.

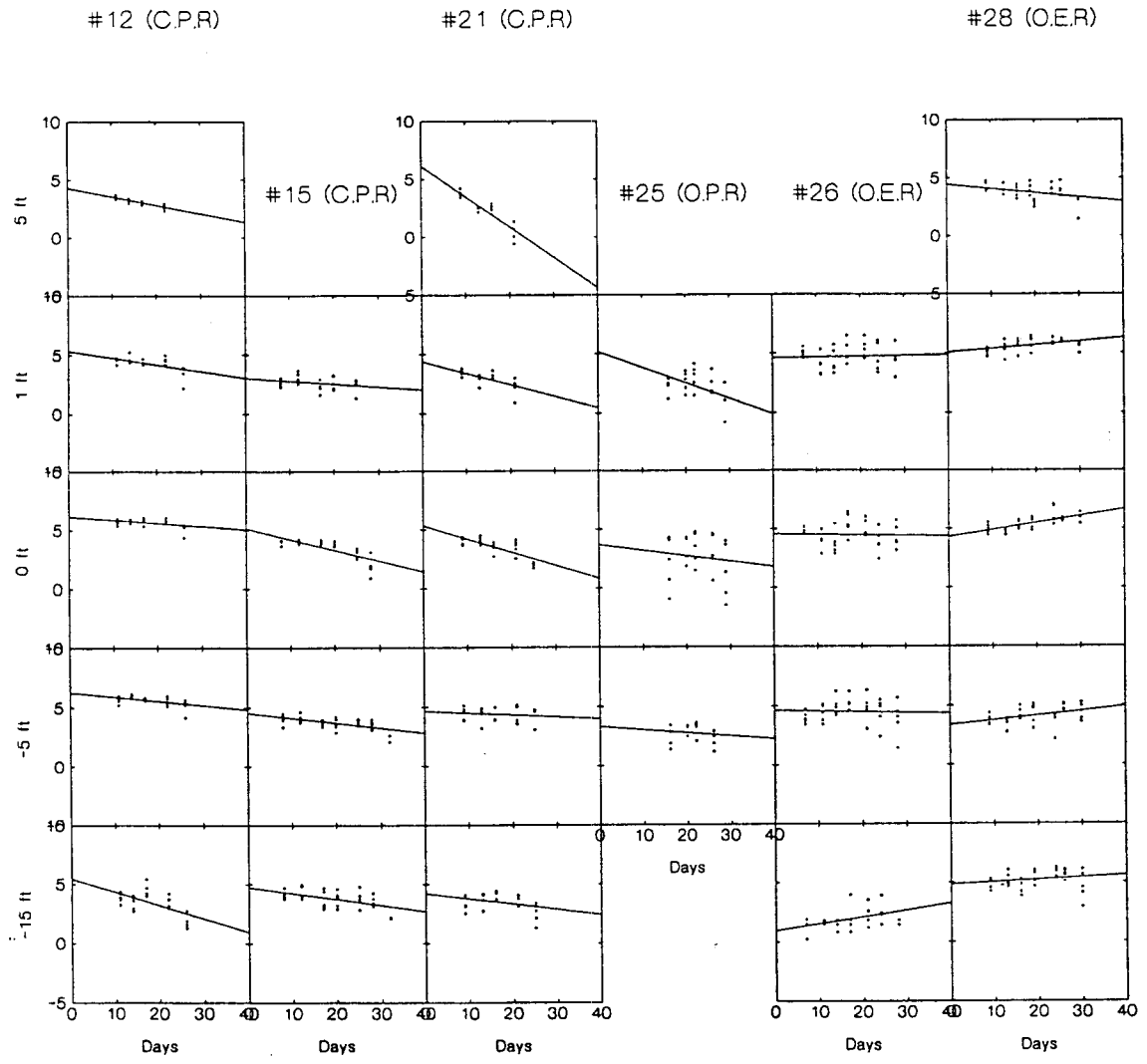


**Figure 6.** Egg loss rates in each kelp type category for 1990. LBK dominant are quadrats where large brown kelp (LBK) is the predominant kelp type, and LBK non-dominant are quadrats dominated by other kelp types. Egg loss rates are plotted against both depth and air exposure.



**Figure 7.** Egg loss rates against depth and air exposure in 1990.

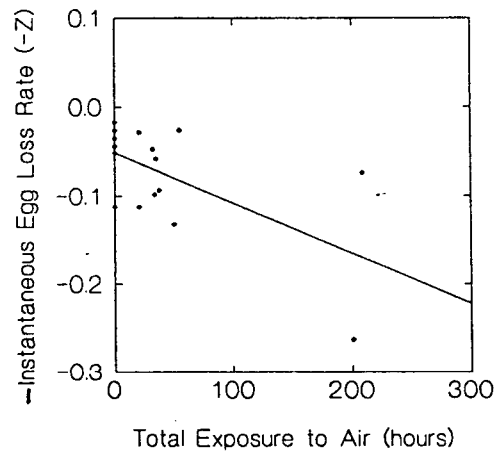
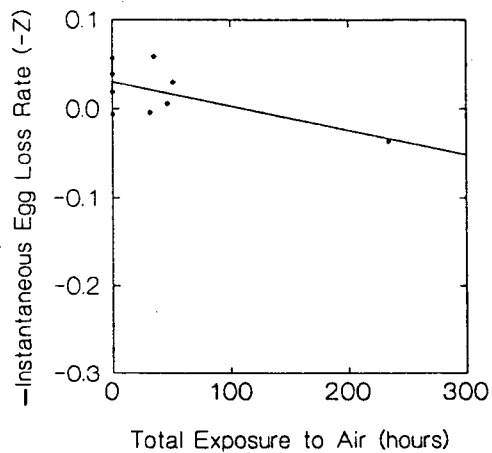
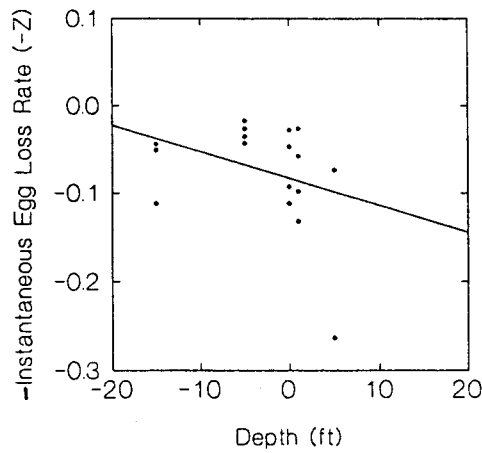
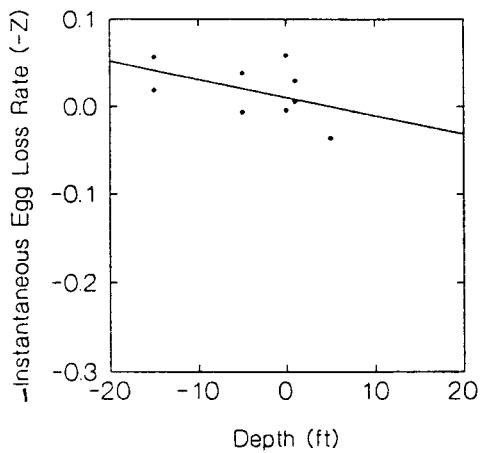




**Figure 8.** Regressions of  $\ln(\text{egg abundance})$  against days since spawn for 1991 transects. The estimate of the egg loss rate ( $Z$ ) at each depth is represented by the straight line in each graph. C=unoiled, O=oiled, R=rocky substrate, P=wave-protected, and E=wave-exposed.

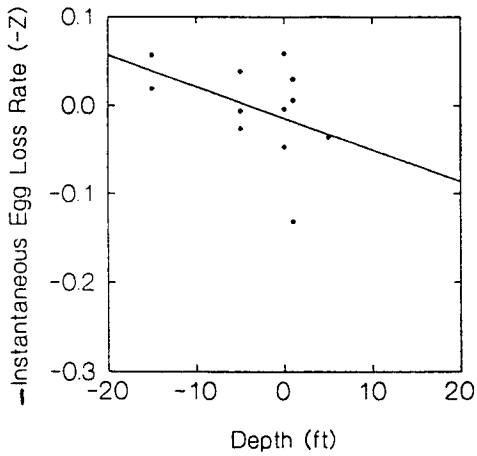
Exposed Transects

Protected Transects

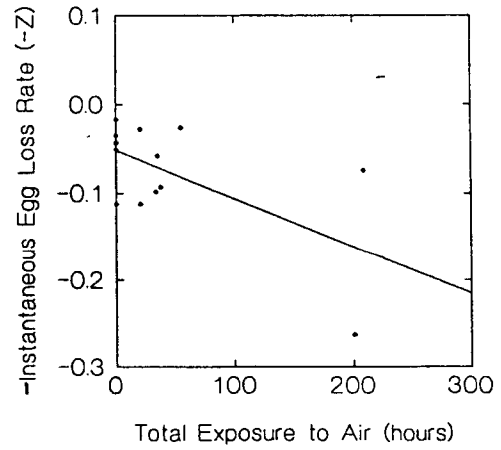
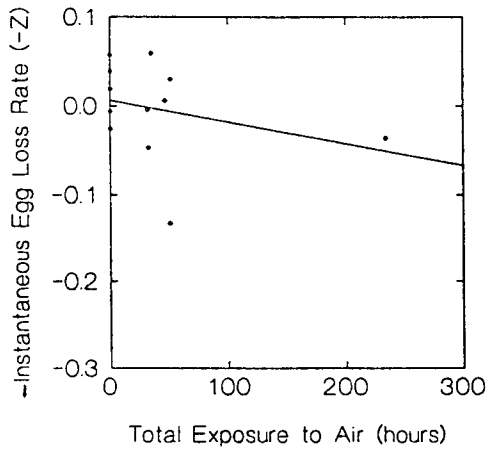
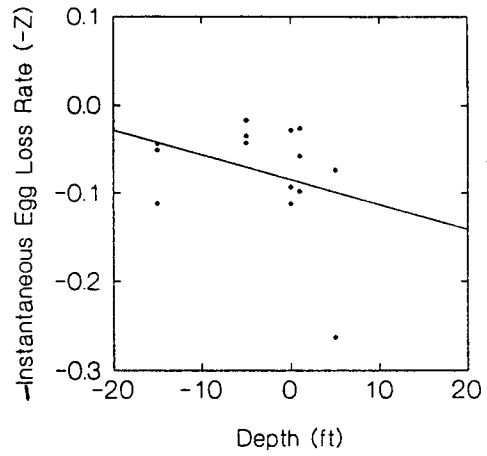


**Figure 9.** Egg loss rates for wave-exposed and wave-protected transects in 1991. Egg loss rates are plotted against both depth and air exposure.

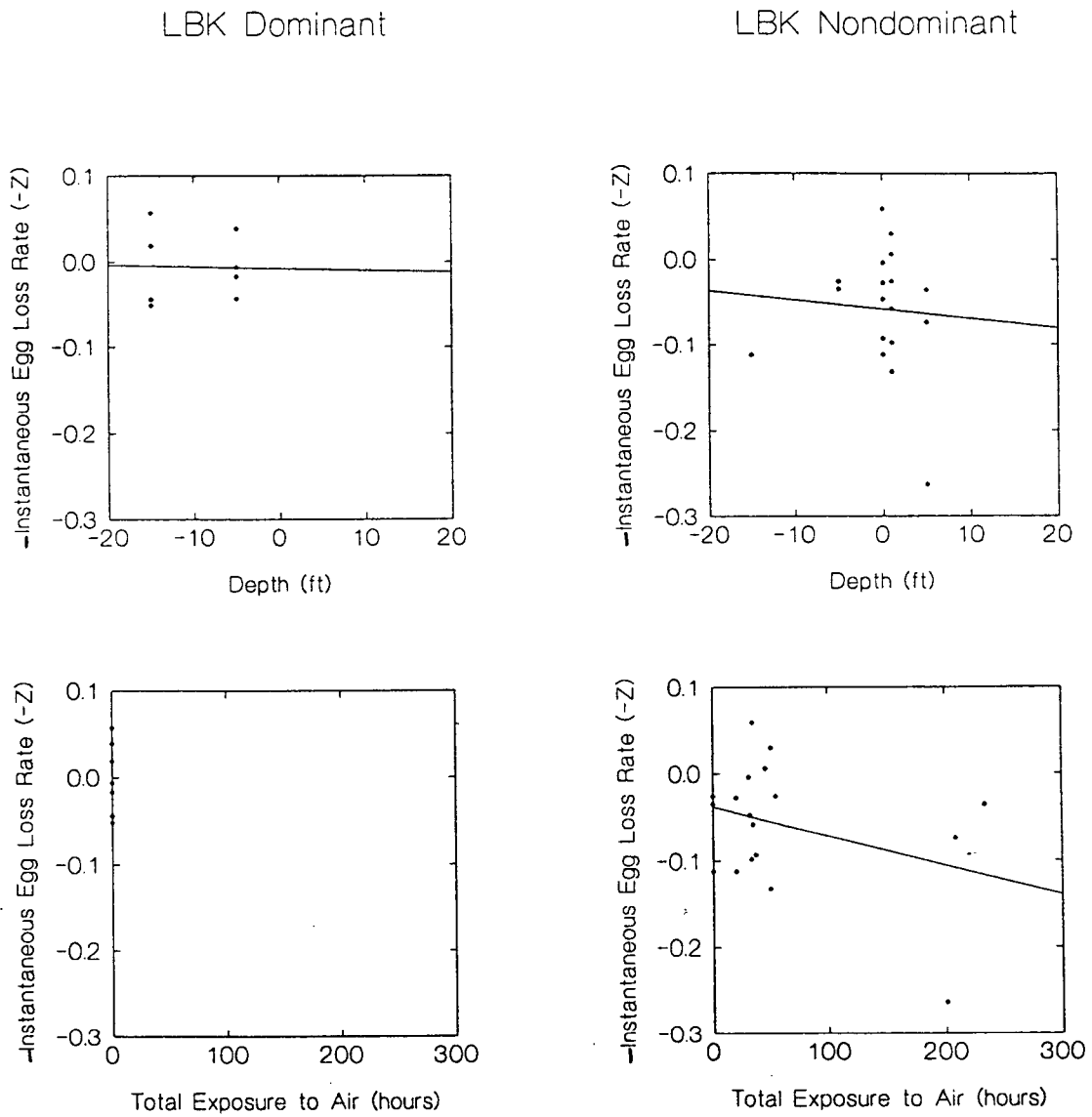
Oiled Transects



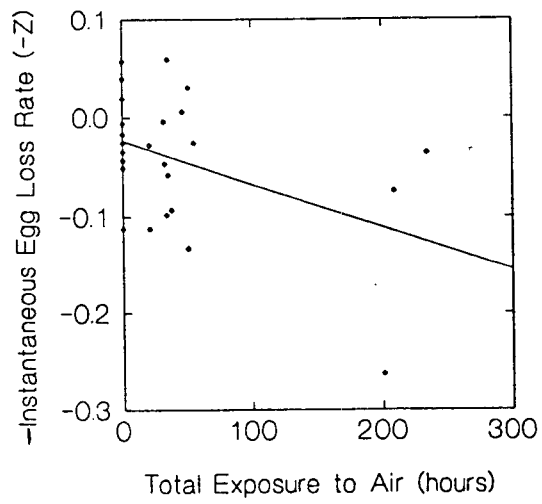
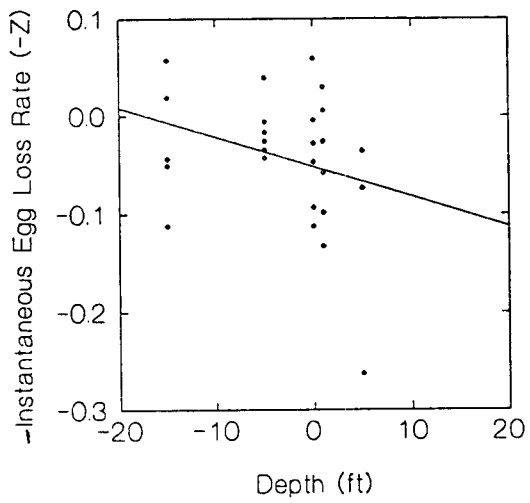
Unoled Transects



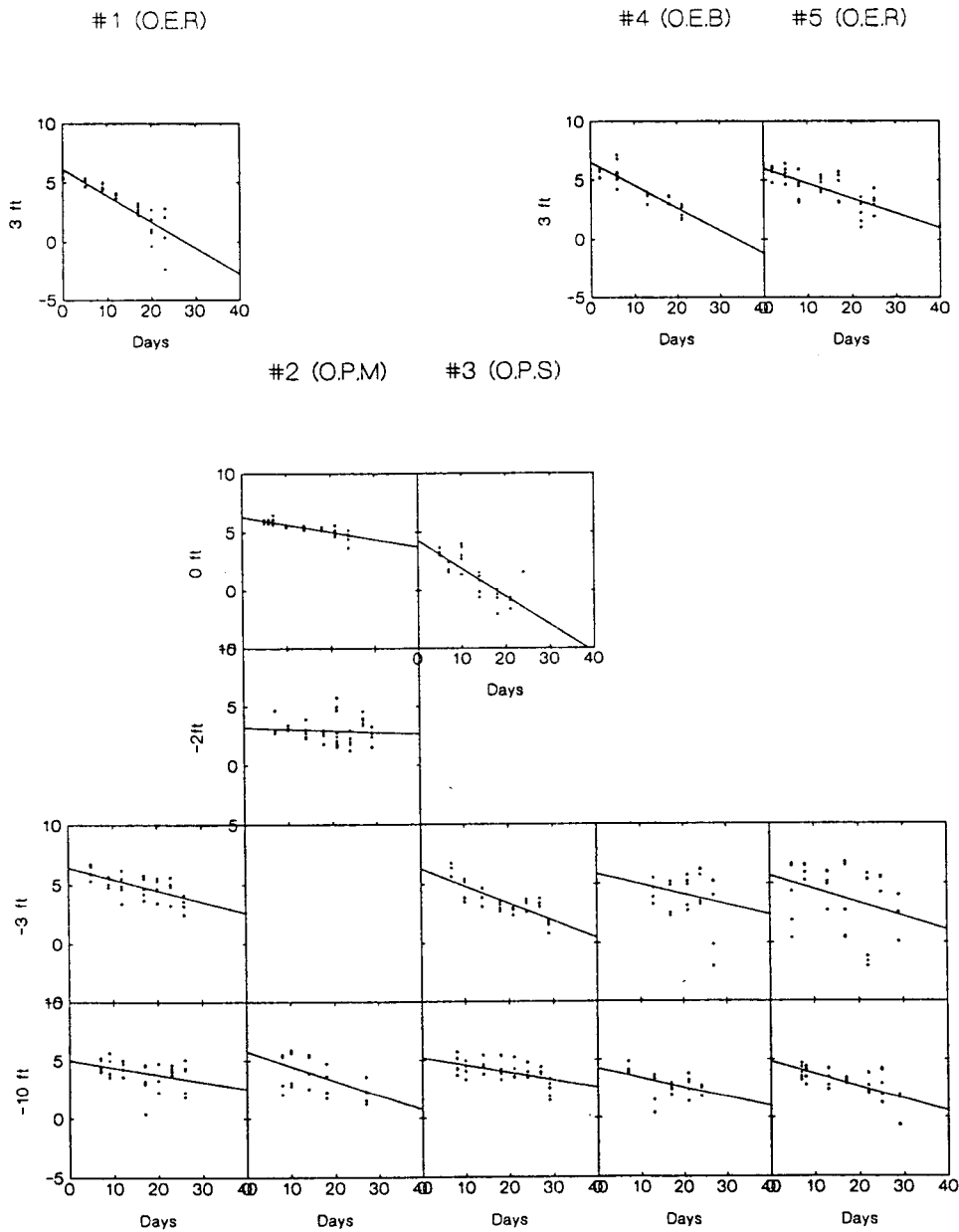
**Figure 10.** Egg loss rates for previously oiled and unoled transects in 1991. Egg loss rates are plotted against both depth and air exposure.



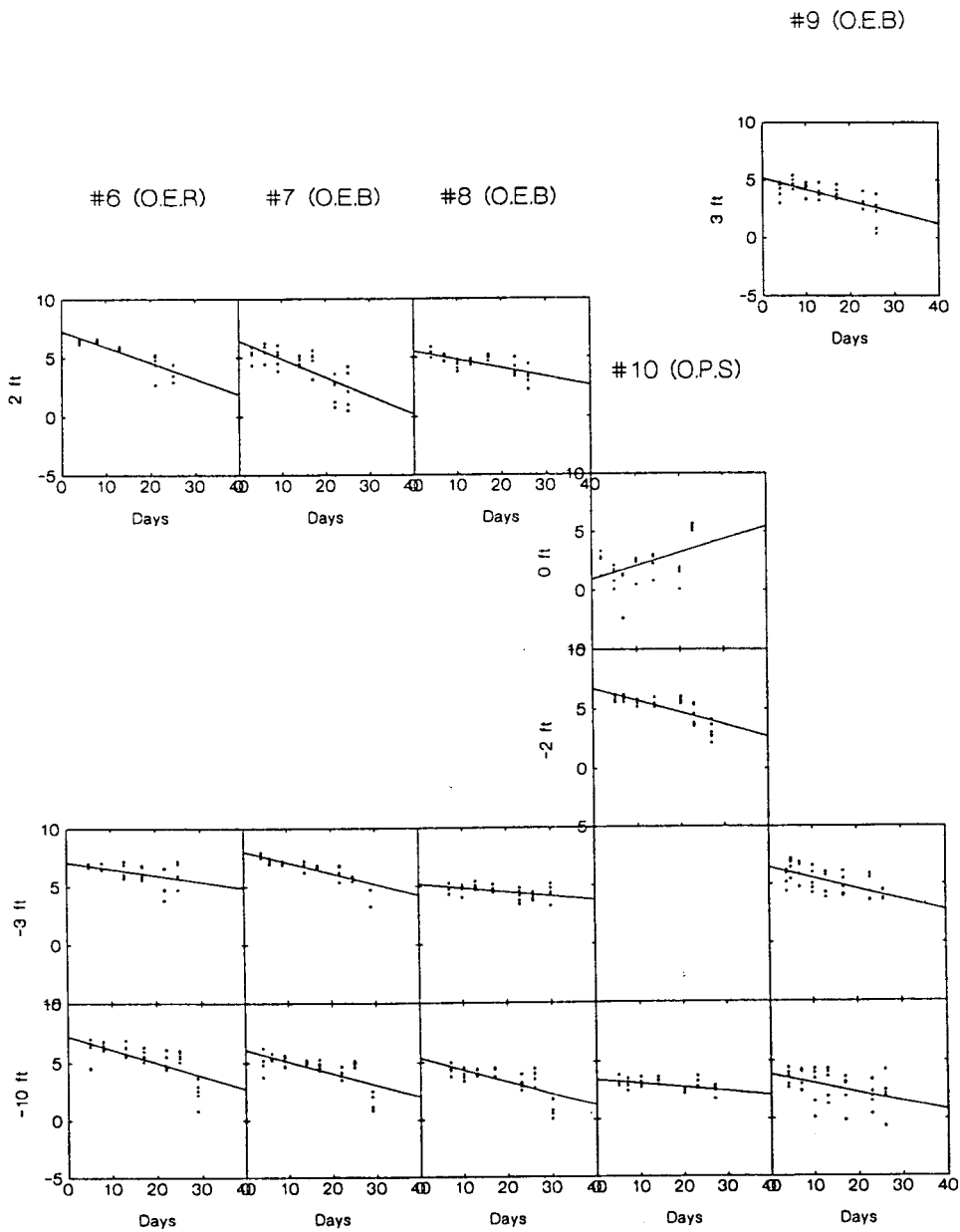
**Figure 11.** Egg loss rates in each kelp type category for 1991. LBK dominant refers to quadrats dominated by large brown kelp (LBK) and LBK non-dominant refers to quadrats dominated by other vegetation types. Egg loss rates are plotted against both depth and air exposure.



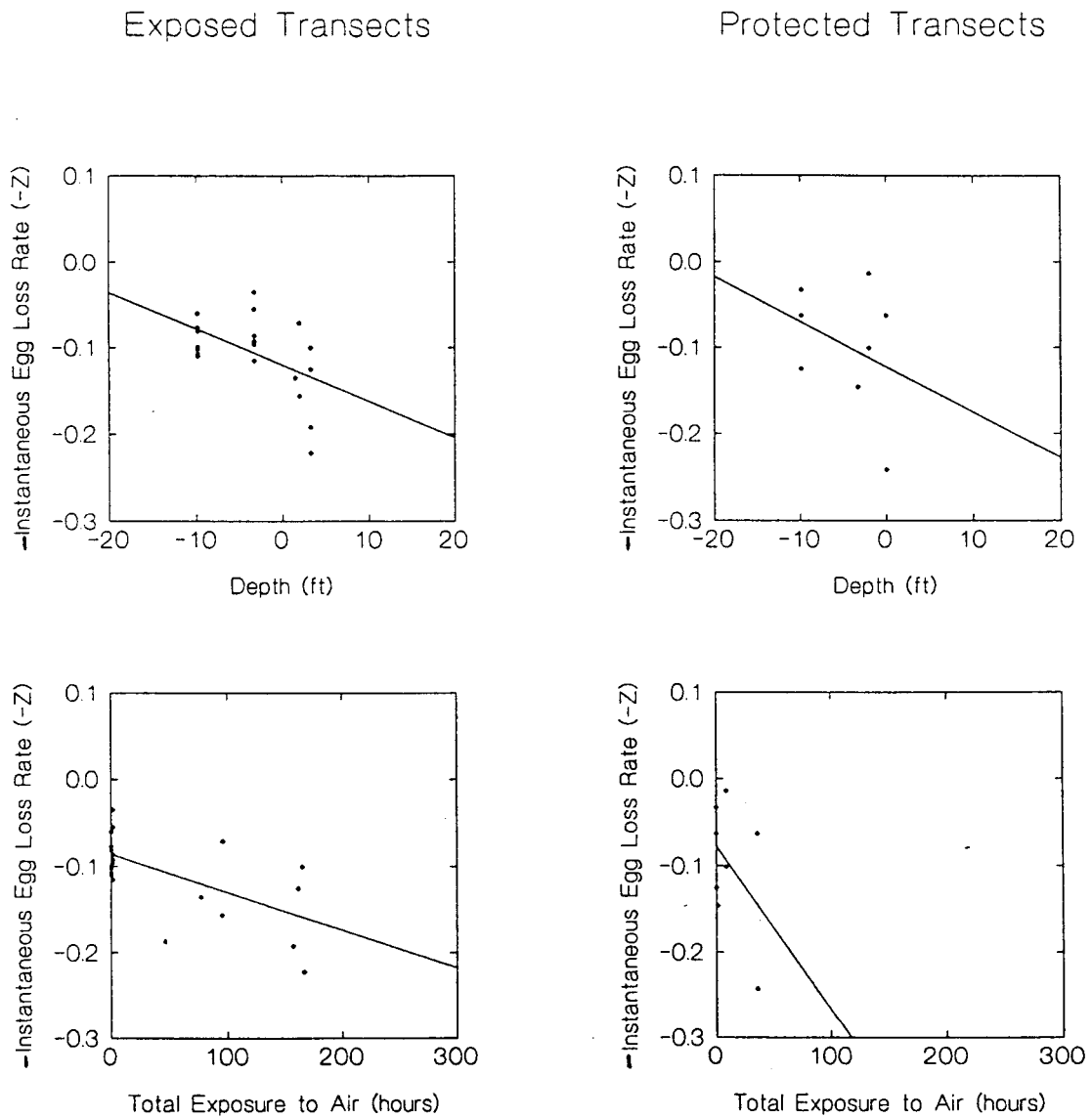
**Figure 12.** Egg loss rates against depth and air exposure in 1991.



**Figure 13.** Regressions of  $\ln(\text{egg abundance})$  against days since spawn for 1994 transects. In each graph the line represents the best estimate of the egg loss rate ( $Z$ ) at each depth. C=unoiled, O=oiled, R=rocky substrate, M=mud substrate, S=sand substrate, B=boulder substrate, P=wave-protected, and E=wave-exposed.



**Figure 13 (continued).** Regressions of  $\ln(\text{egg abundance})$  against days since spawn for 1994 transects. In each graph the line represents the best estimate of the egg loss rate ( $Z$ ) at each depth. C=unoiled, O=oiled, R=rocky substrate, M=mud substrate, S=sand substrate, B=boulder substrate, P=wave-protected, and E=wave-exposed.



**Figure 14.** Egg loss rates for wave-exposed and wave-protected transects in 1994. Egg loss rates are plotted against both depth and air exposure.



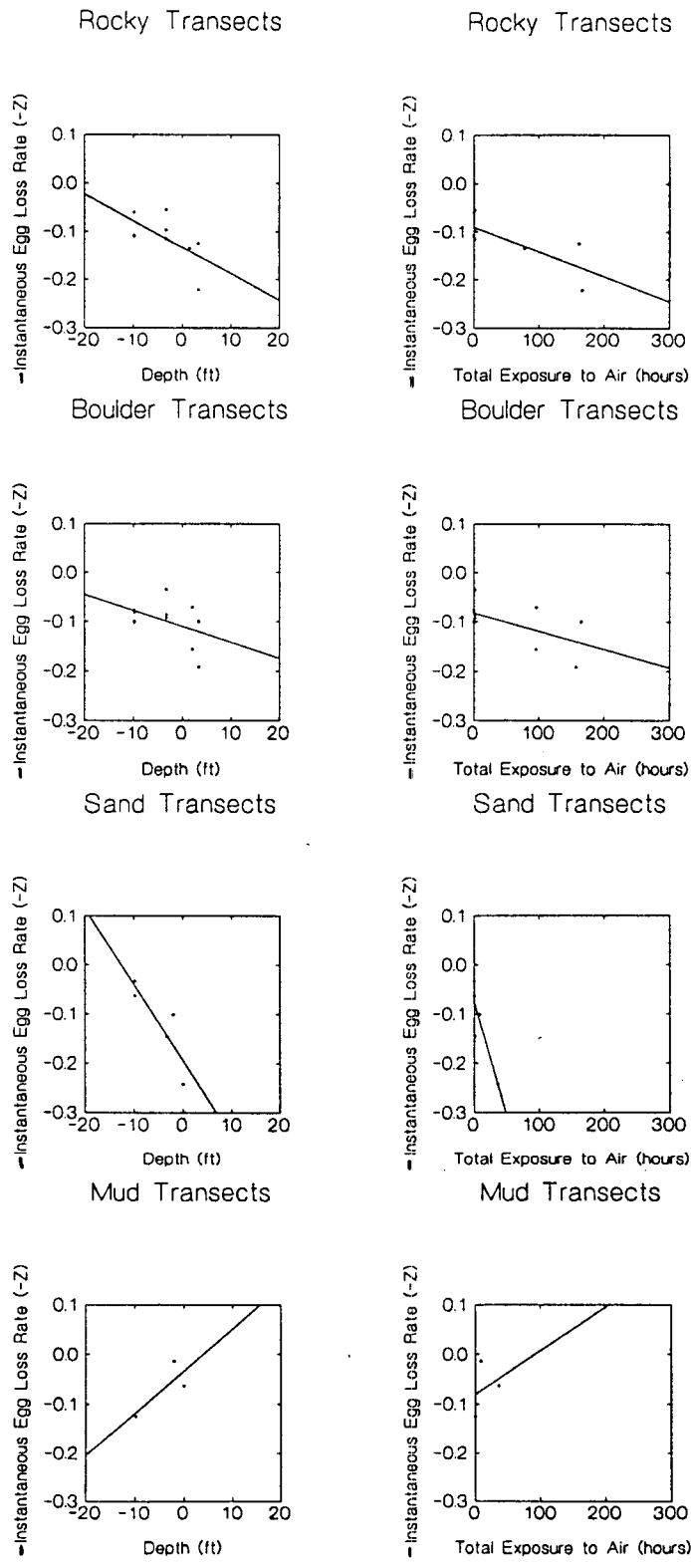
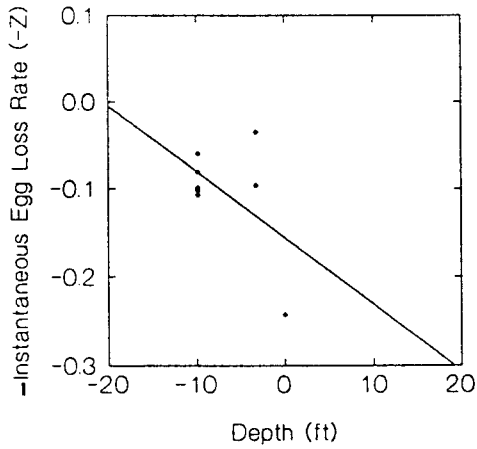
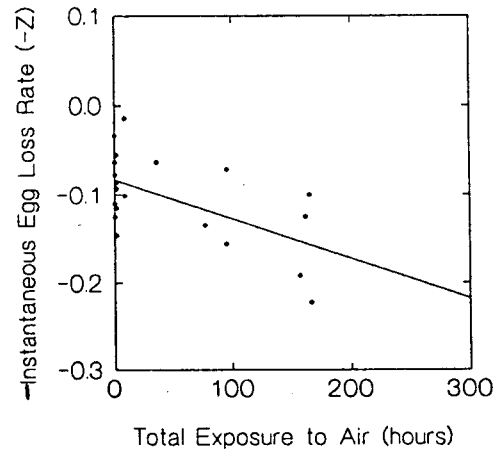
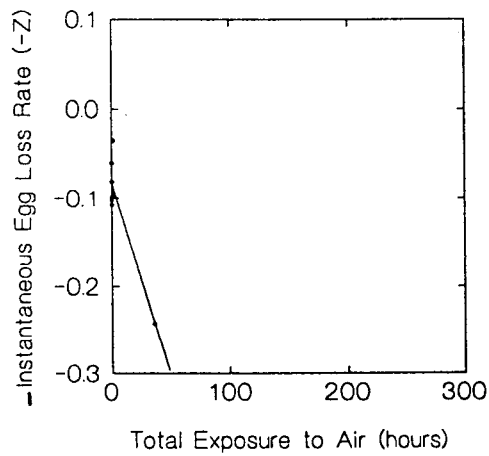
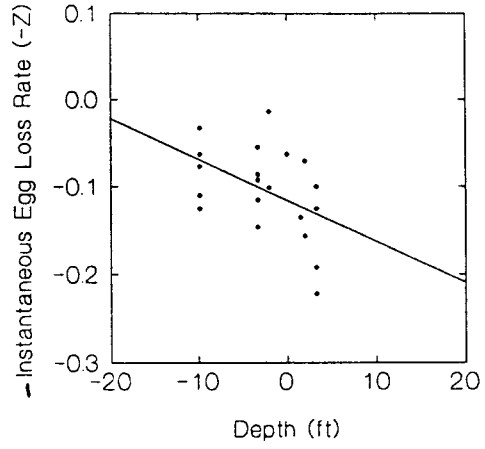


Figure 15. Egg loss rates for each substrate type sampled in 1994. Egg loss rates are plotted against both depth and air exposure.

LBK Dominant



LBK Nondominant



**Figure 16.** Egg loss rates for each kelp type category in 1994. LBK dominant refers to quadrats inhabited predominantly by large brown kelp (LBK) species, and LBK non-dominant refers to quadrats inhabited by other vegetation types. Egg loss rates are plotted against both depth and air exposure.

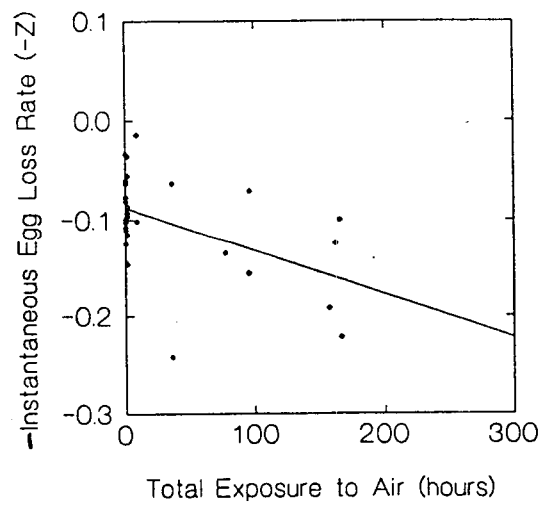
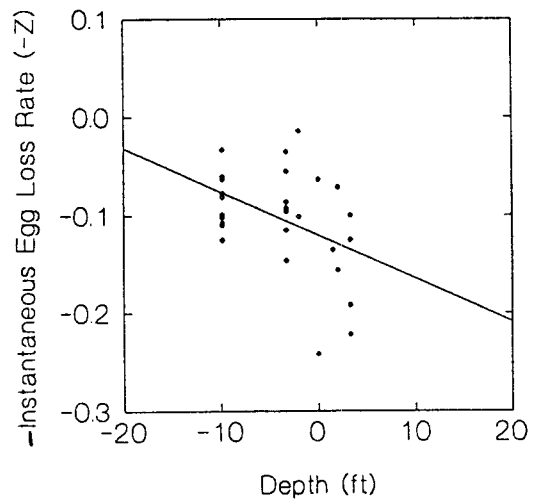
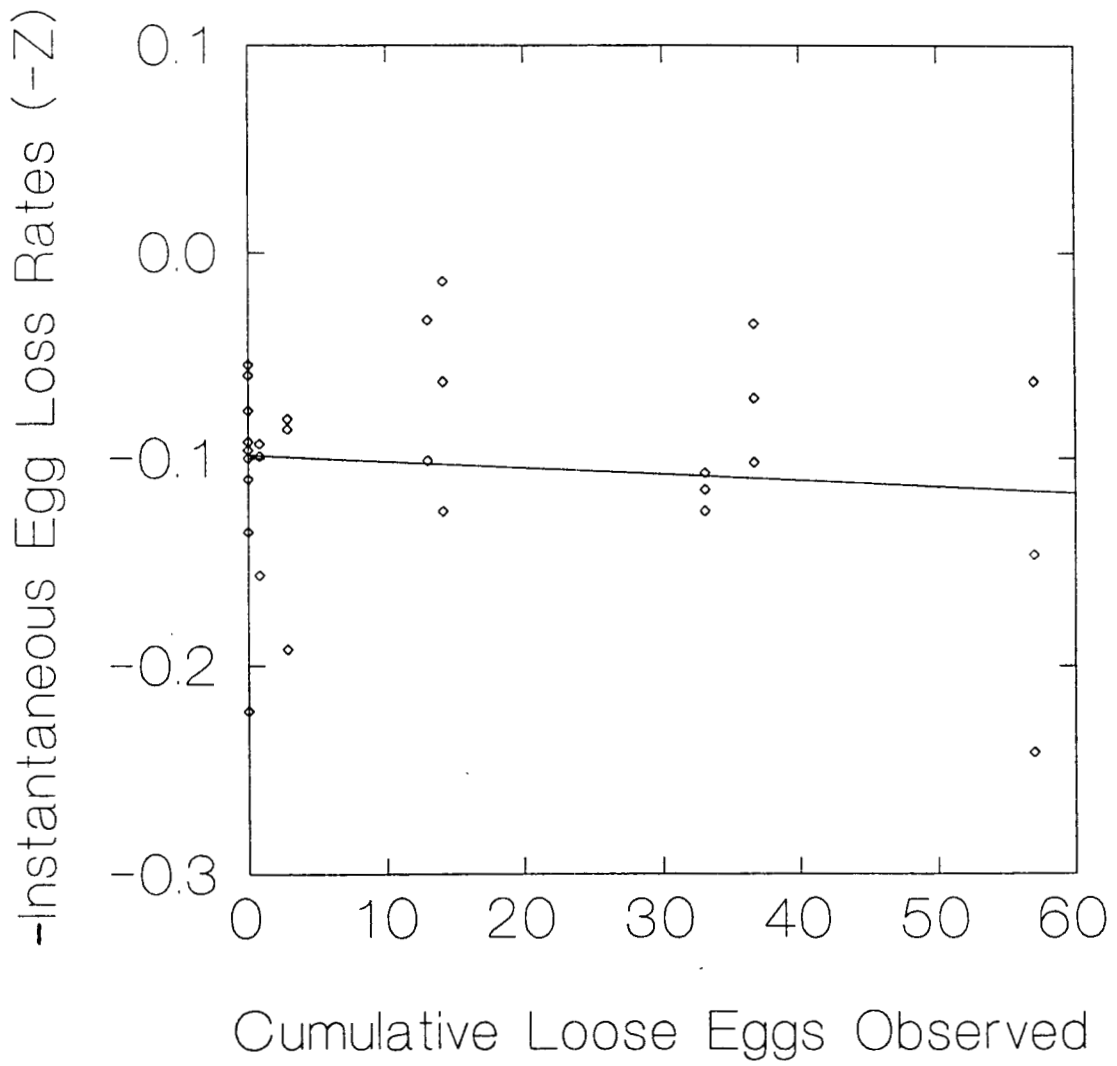
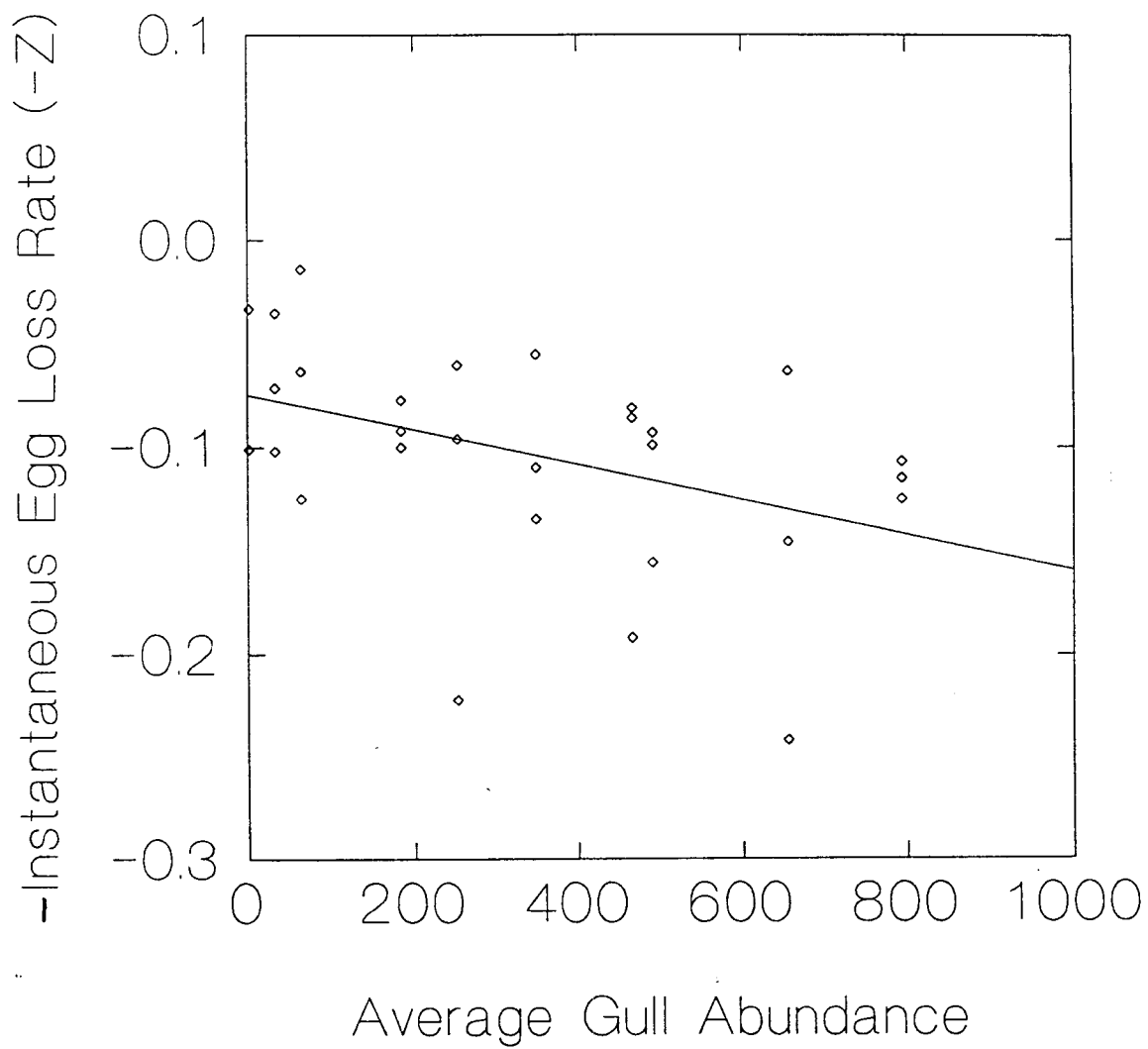
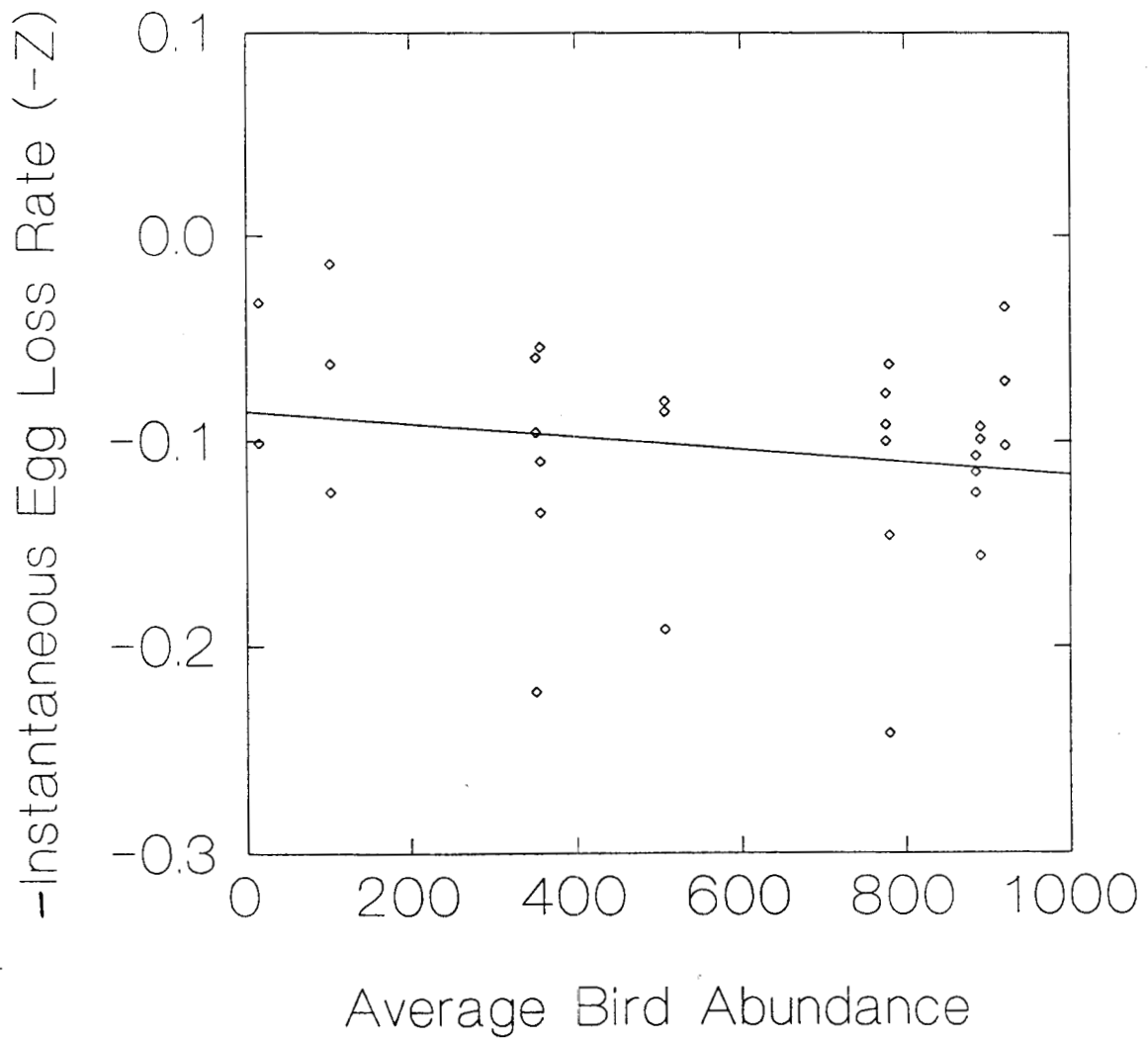


Figure 17. Egg loss rates against depth and air exposure in 1994.



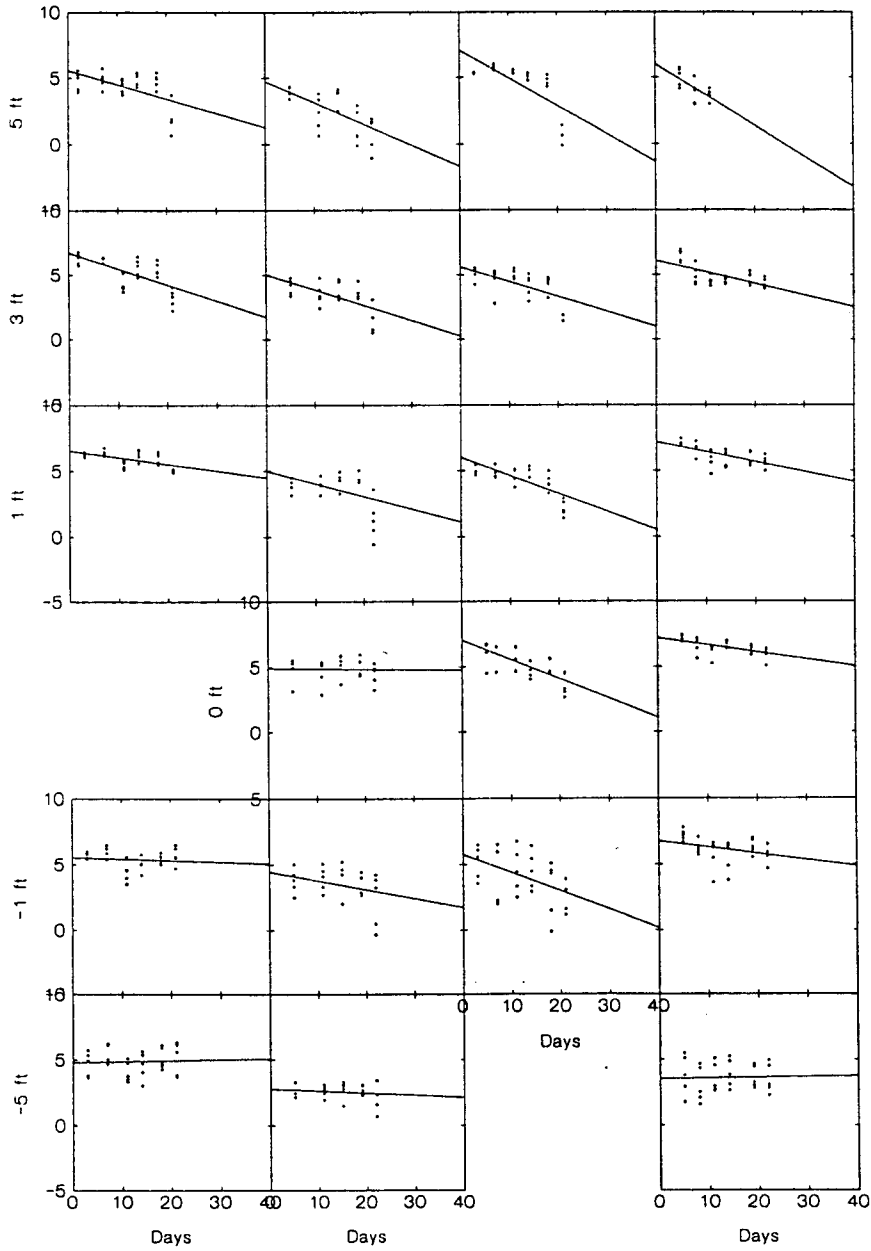


**Figure 19.** Egg loss rates against average glaucous winged gull abundance at 1994 transects.



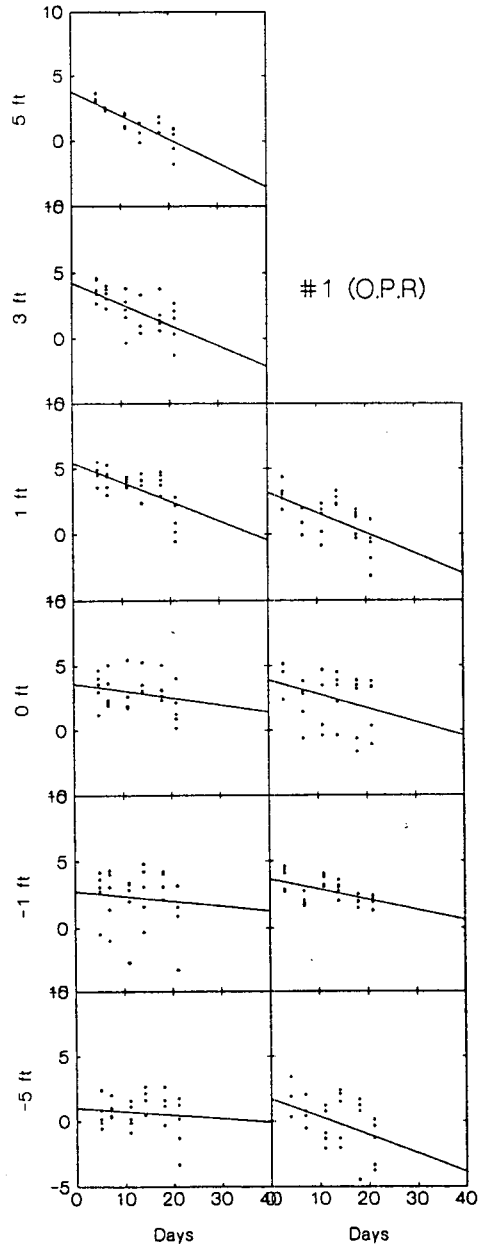
**Figure 20.** Egg loss rates against average number of birds observed at 1994 transects.

#6 (O.E.R)    #9 (O.E.R)    #11 (O.E.R)    #12 (O.E.R)



**Figure 21.** Regressions of  $\ln(\text{egg abundance})$  against days since spawn for 1995 transects. The line represents the best estimate of the egg loss rate ( $-Z$ ) at each depth. O=oiled, R=rocky substrate, E=wave-exposed, P=wave-protected.

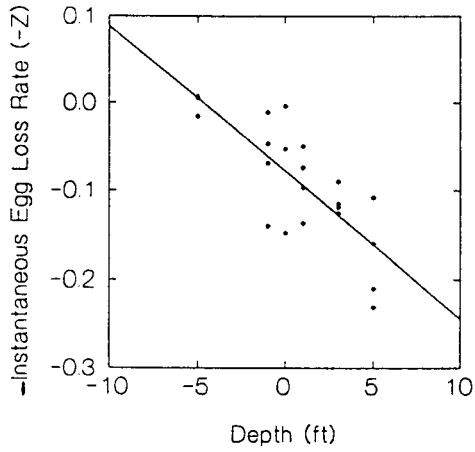
#2 (O,P,R)



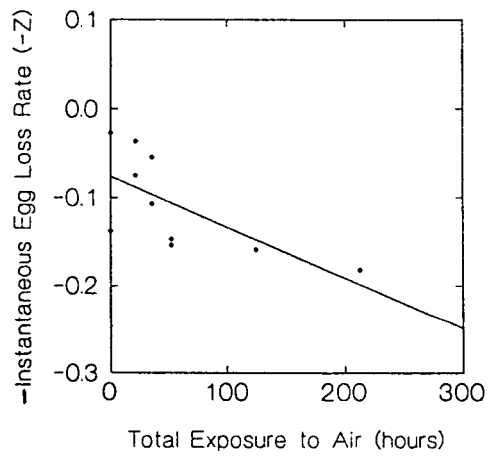
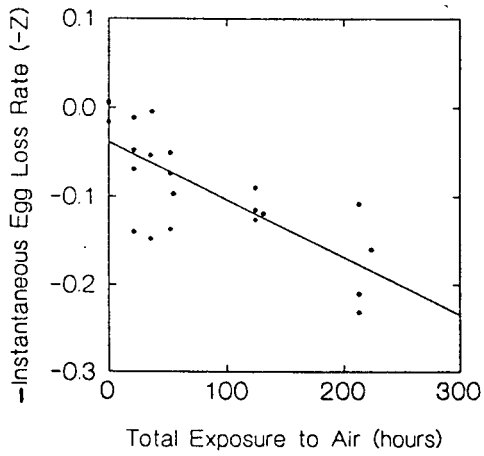
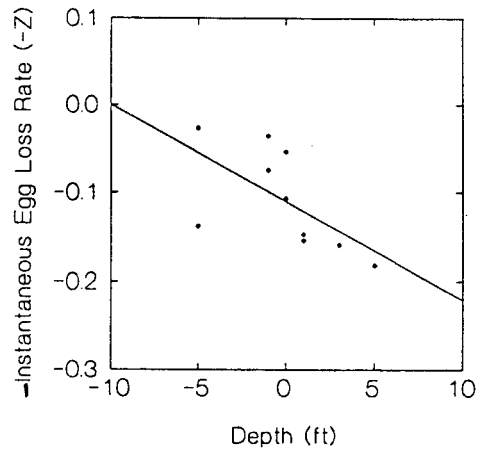
**Figure 21 (continued).** Regressions of  $\ln(\text{egg abundance})$  against days since spawn for 1995 transects. The line represents the best estimate of the egg loss rate ( $-Z$ ) at each depth. O=oiled, R=rocky substrate, E=wave-exposed, P=wave-protected.



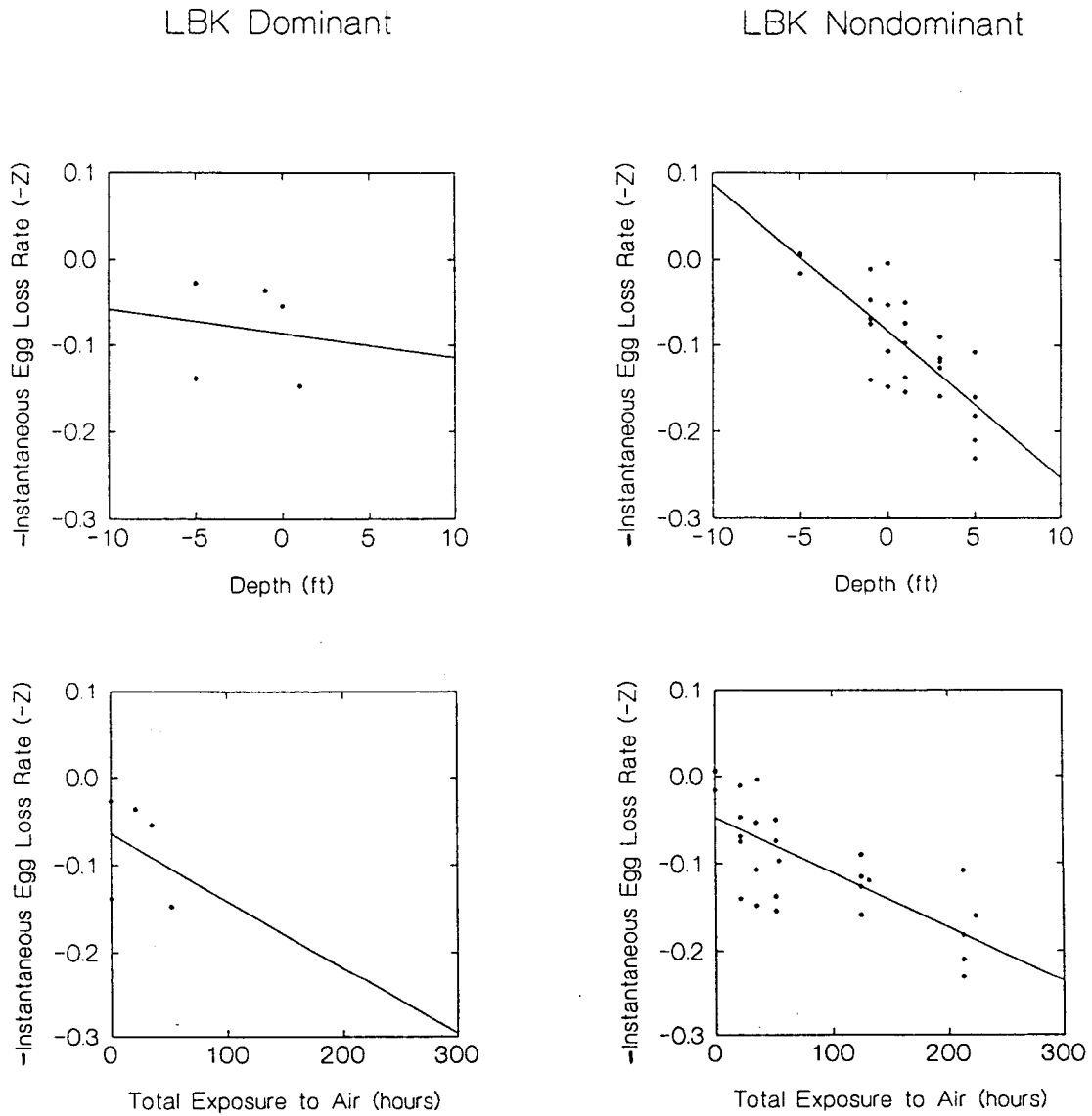
Exposed Transects



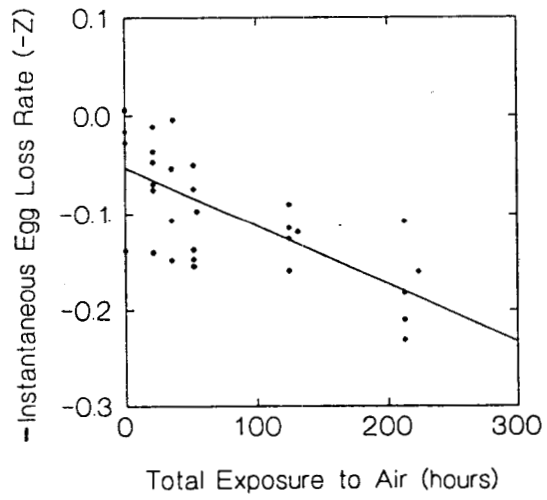
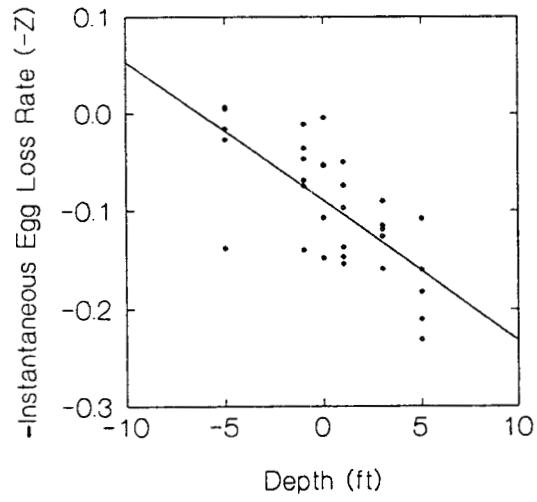
Protected Transects



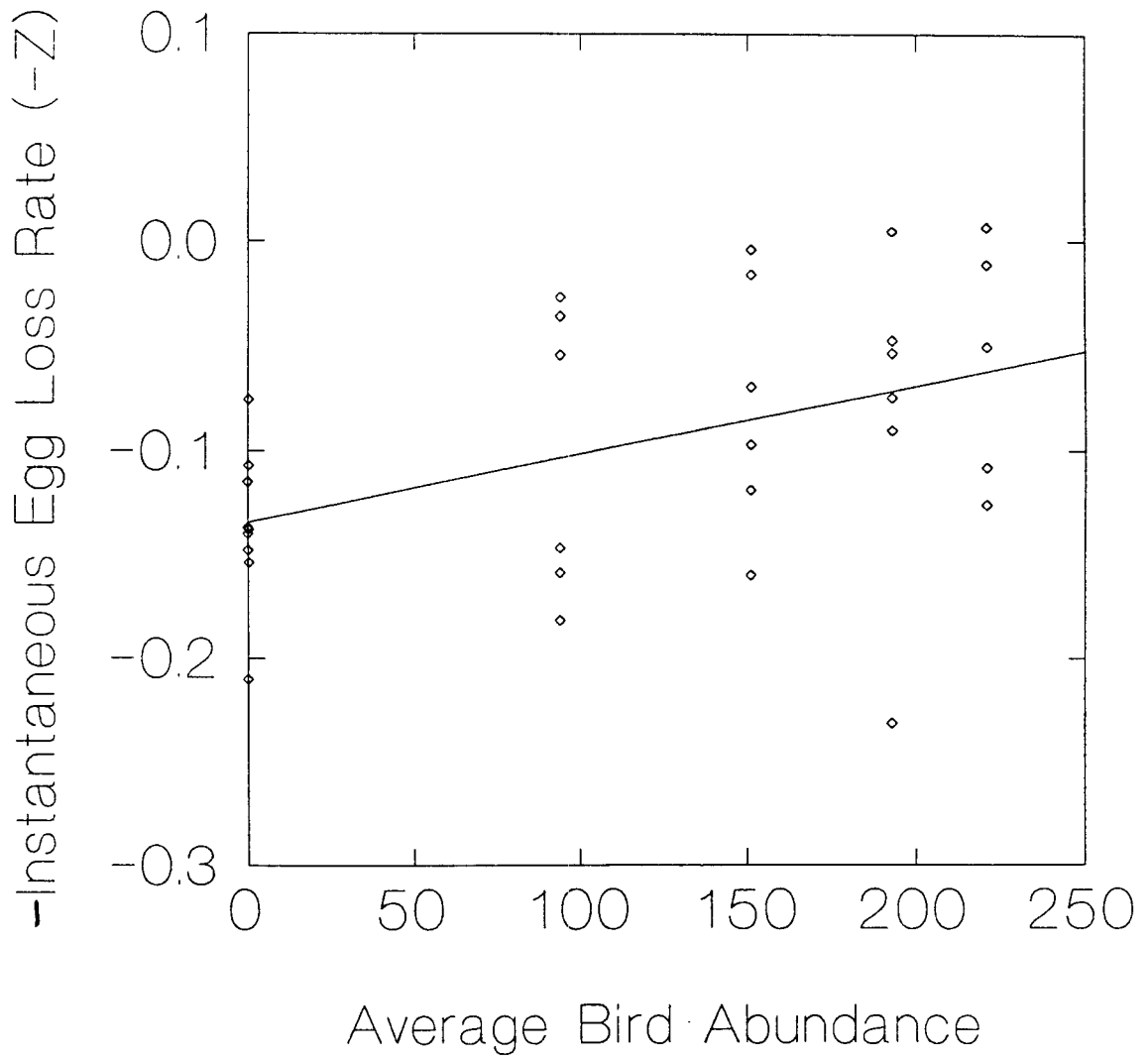
**Figure 22.** Egg loss rates for wave-exposed and wave-protected transects in 1995. Egg loss rates are plotted against both depth and air exposure.



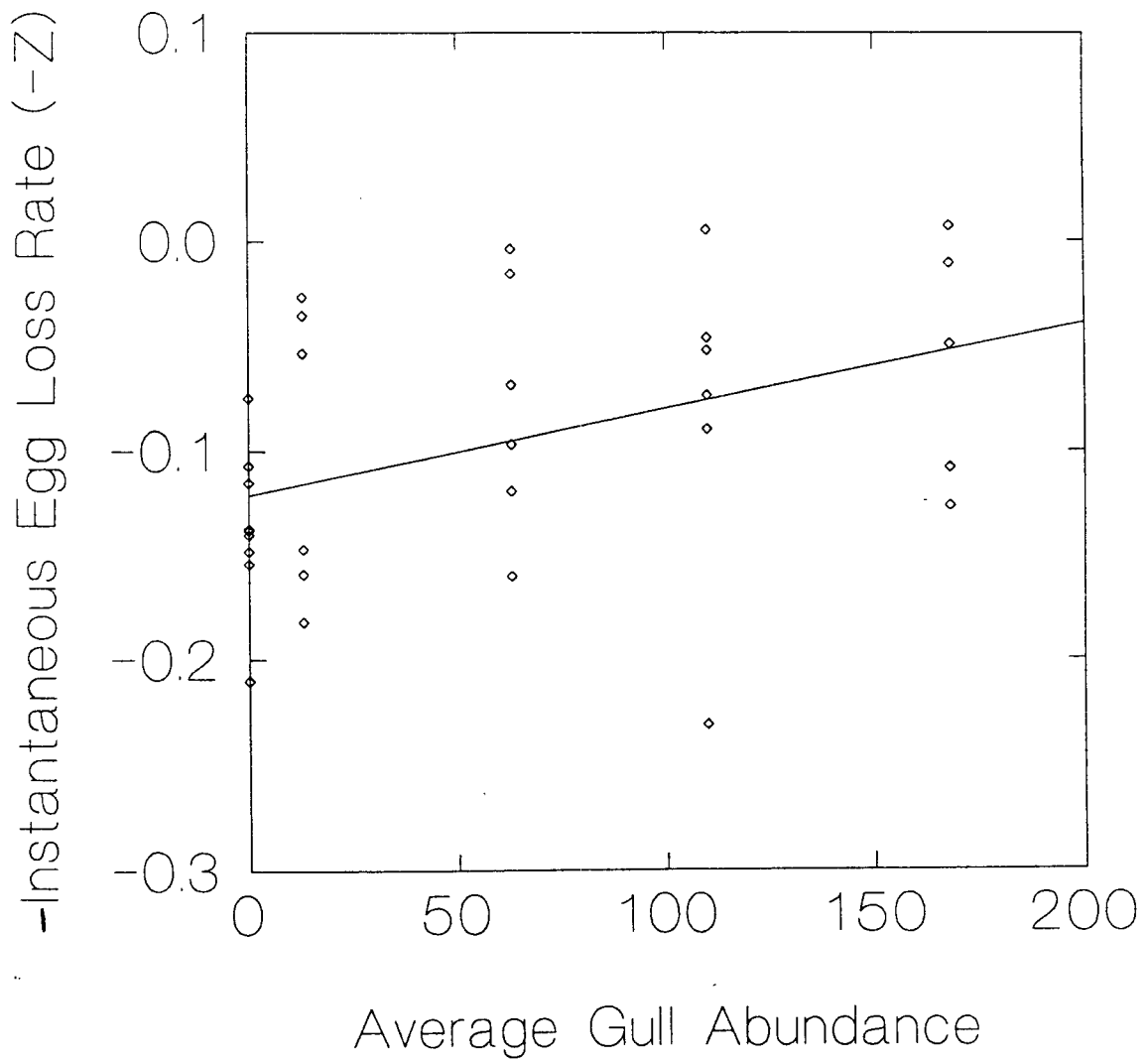
**Figure 23.** Egg loss rates for each kelp type category for 1995. LBK dominant refers to quadrats inhabited predominantly by large brown kelp (LBK), and LBK non-dominant refers to quadrats dominated by other vegetation types. Egg loss rates are plotted in each category against both depth and air exposure.



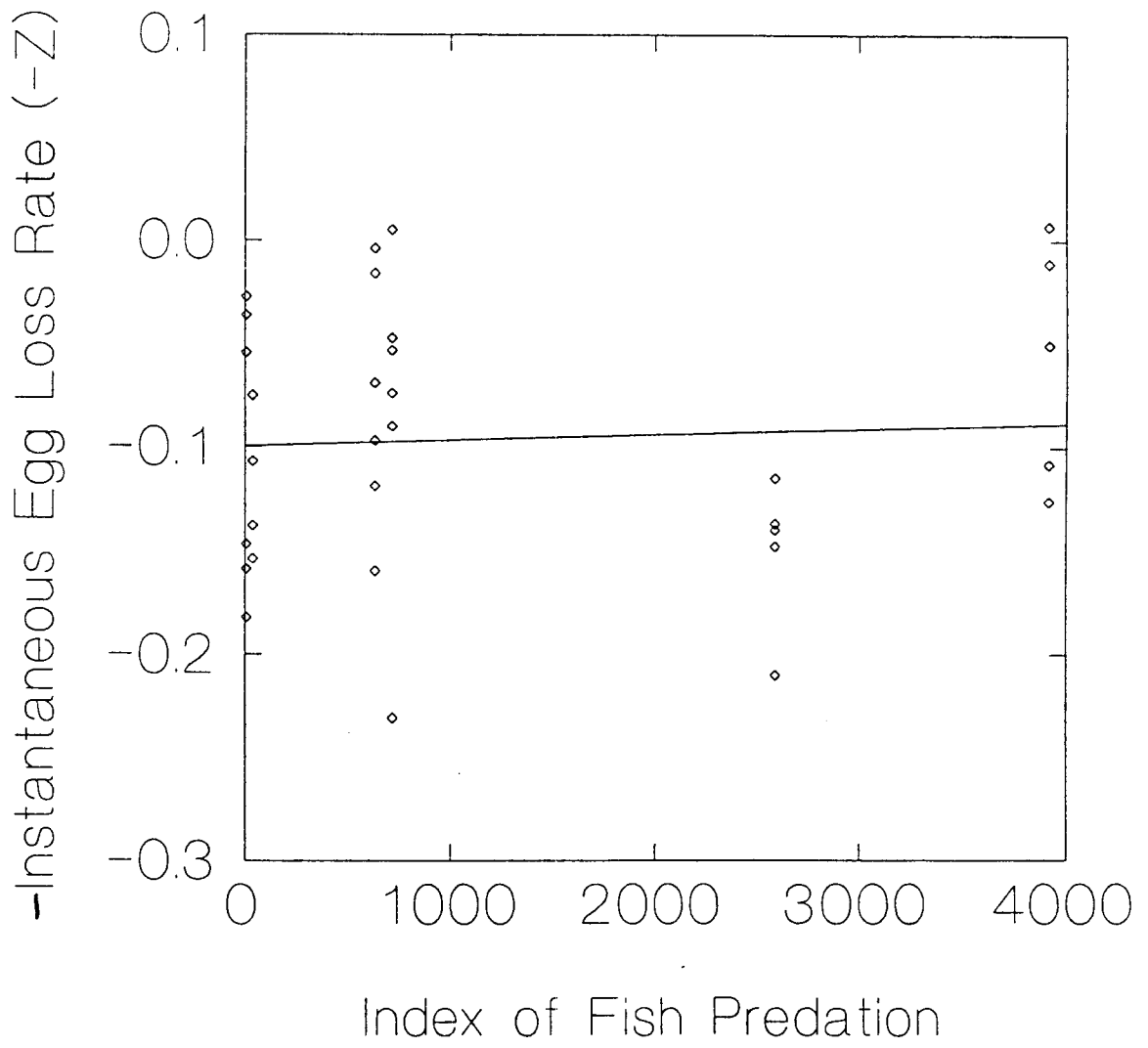
**Figure 24.** Egg loss rates against depth and air exposure for 1995.



**Figure 25.** Egg loss rates against average bird abundance at 1995 transects.

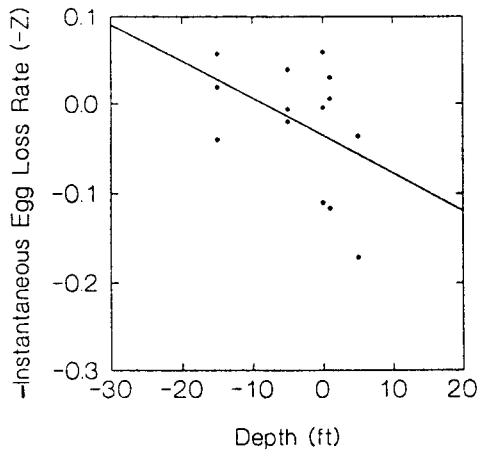


**Figure 26.** Egg loss rates against average glaucous winged gull abundance at 1995 transects.

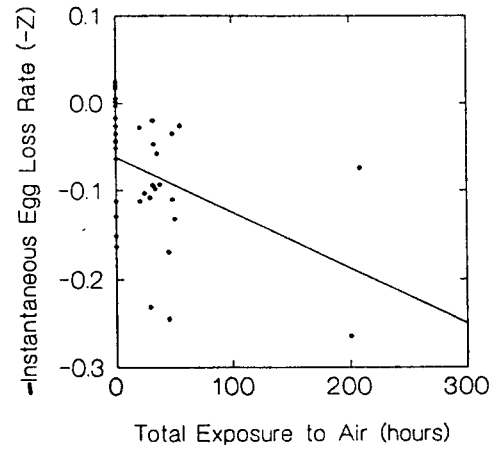
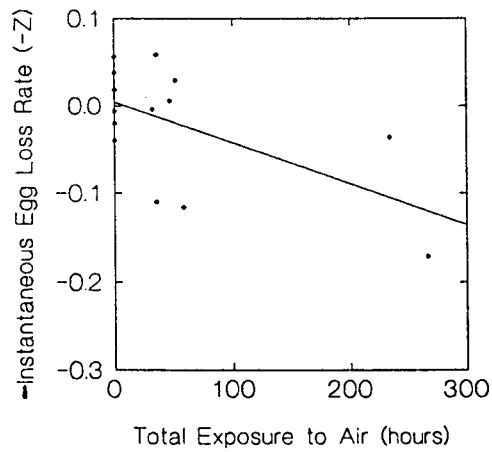
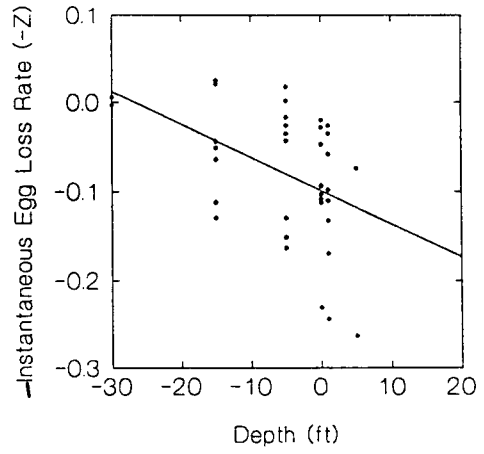


**Figure 27.** Egg loss rates against fish predation index at 1995 transects.

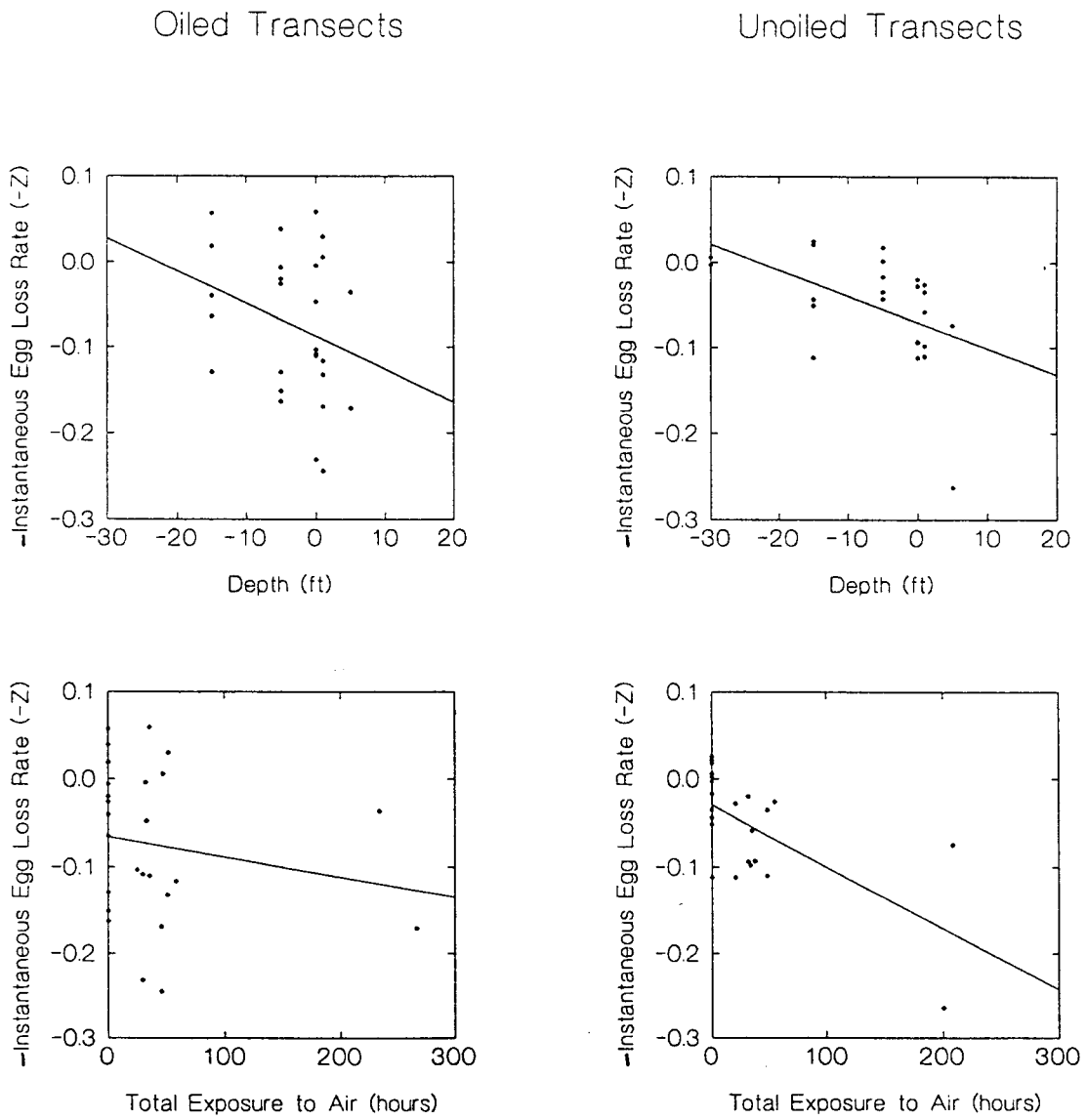
Exposed Transects



Protected Transects



**Figure 28.** Egg loss rates for wave-exposed and wave-protected transects for 1990-1991 combined. Data taken from rocky and boulder substrates only.



**Figure 29.** Egg loss rates at previously oiled and unoiled transects for 1990-1991 combined. Data taken from rocky and boulder substrates only.



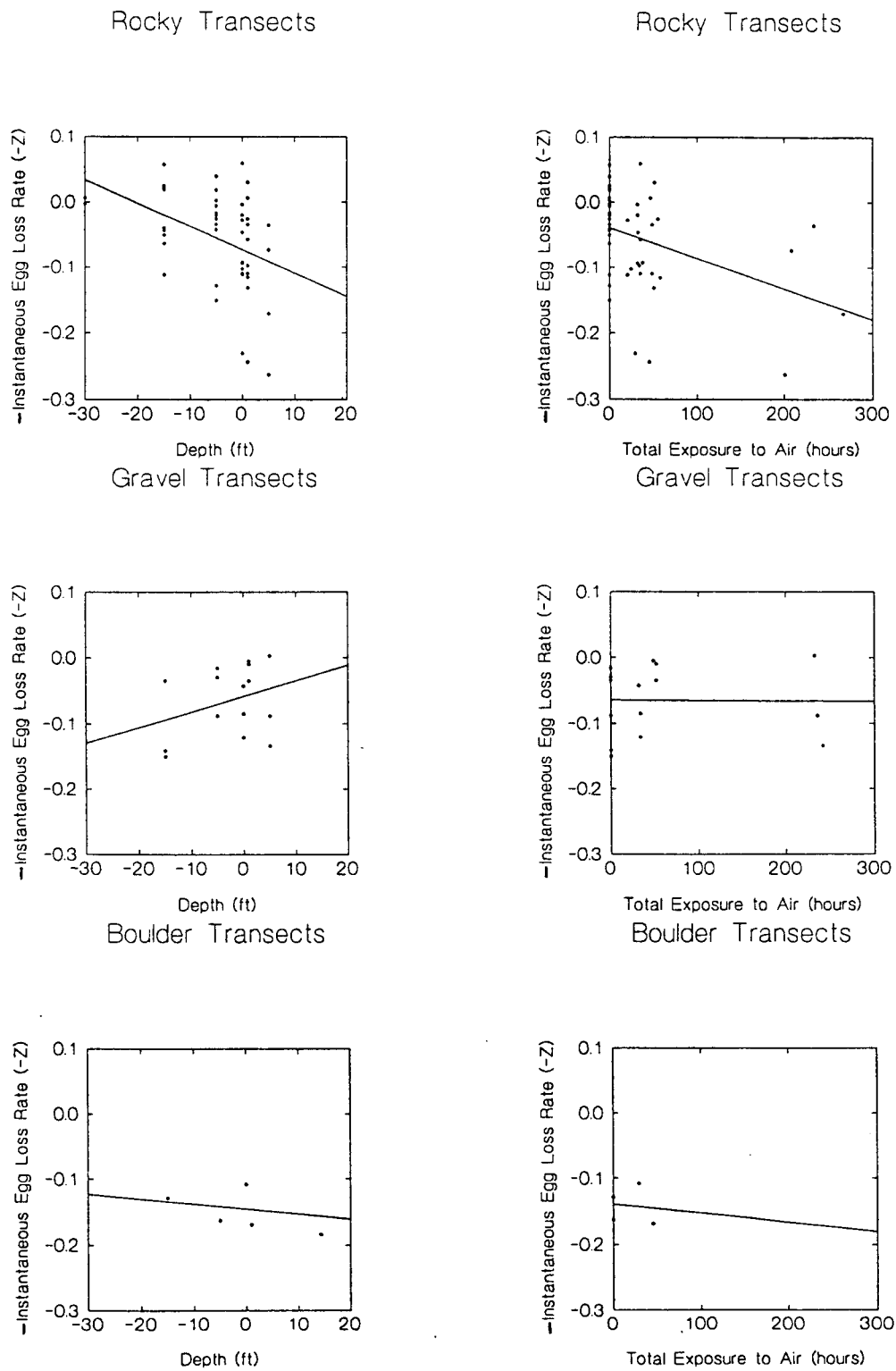
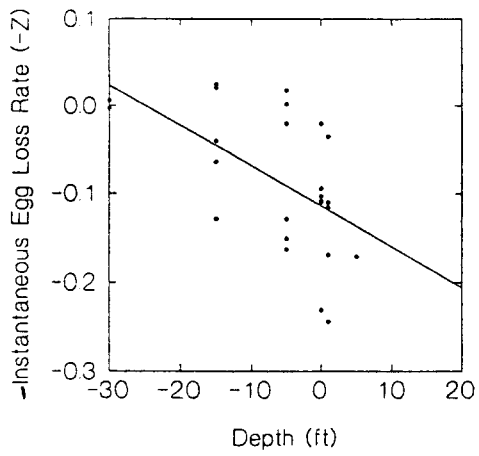
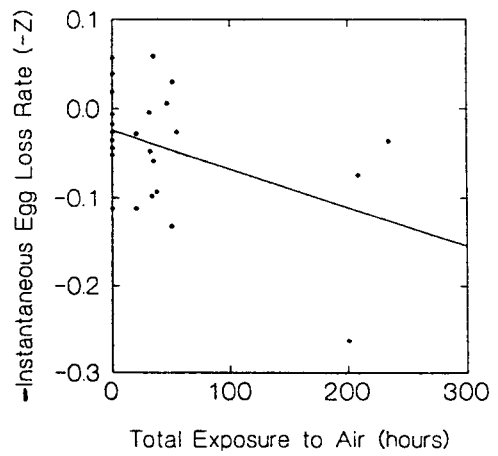
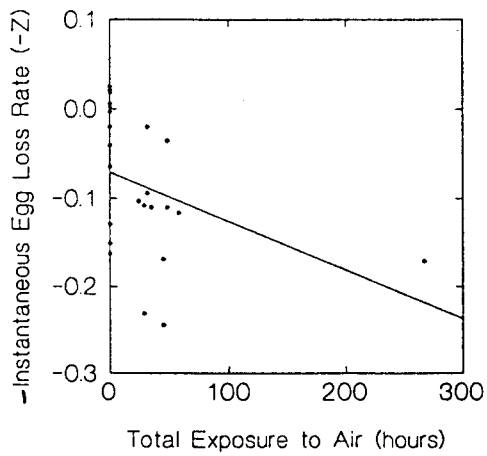
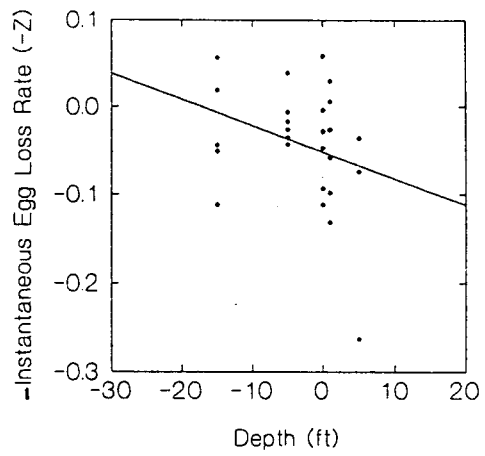


Figure 30. Egg loss rates in each substrate type sampled in 1990-1991 combined.

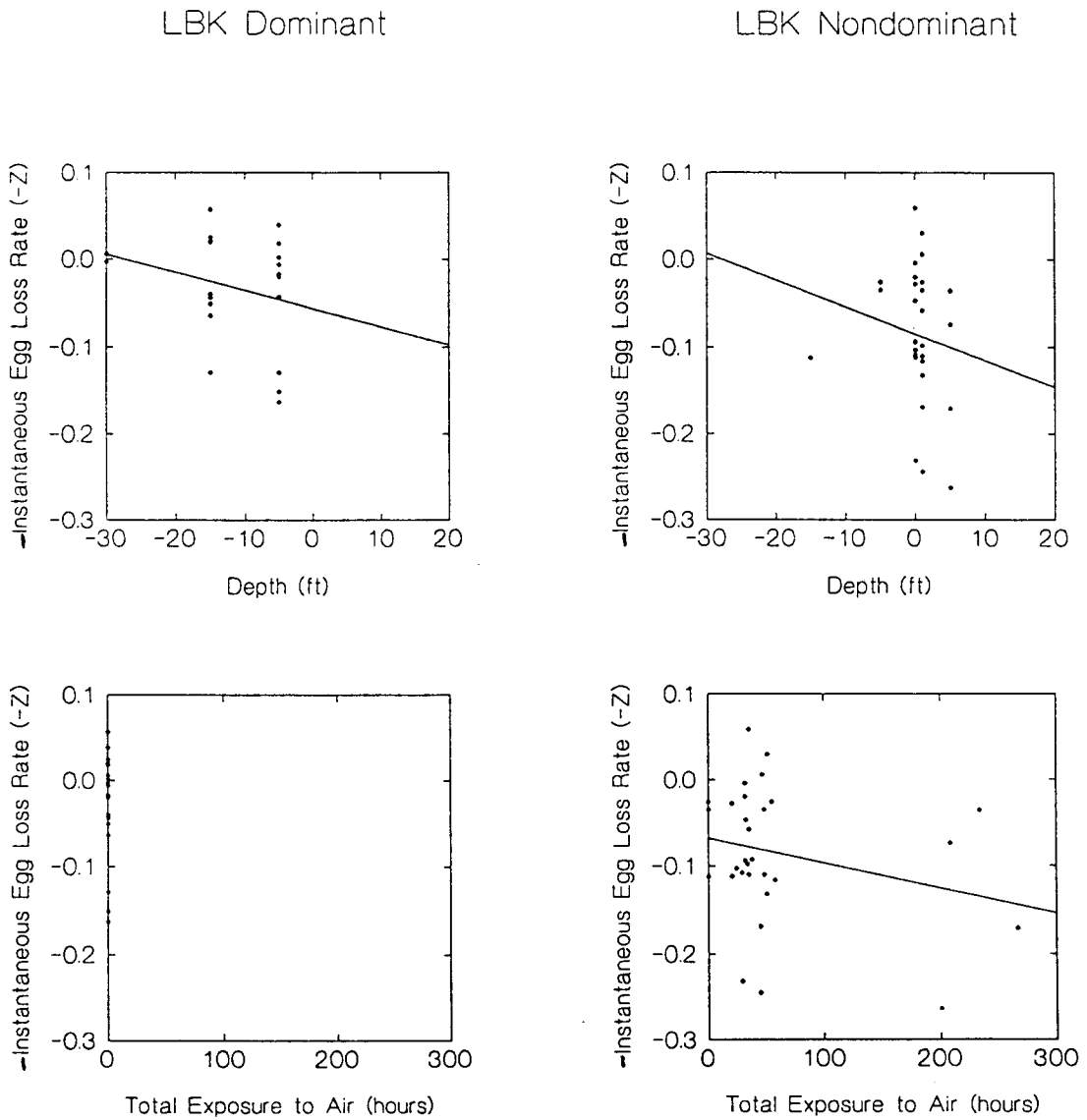
1990 Transects



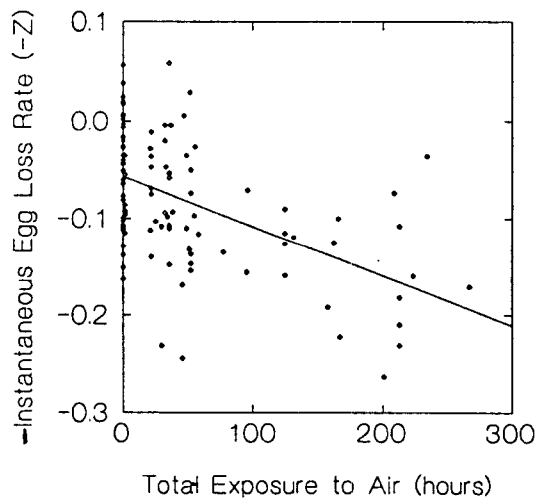
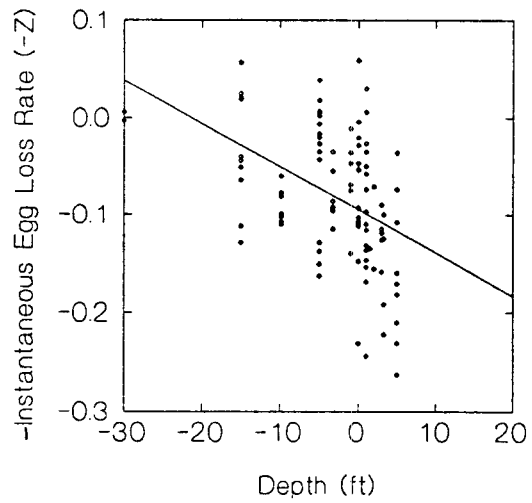
1991 Transects



**Figure 31.** Egg loss rates from each year, 1990 and 1991. Egg loss rates are plotted against both depth and air exposure. Data are from rocky and boulder substrates only.

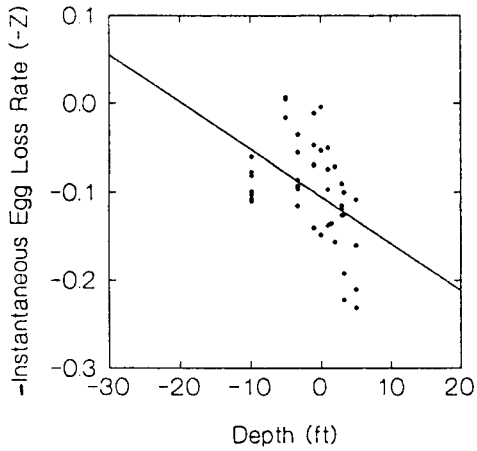


**Figure 32.** Egg loss rates in each kelp type category for 1990-1991 combined. LBK dominant refers to quadrats inhabited predominantly by large brown kelp (LBK), and LBK non-dominant refers to quadrats dominated by other vegetation types. Egg loss rates are plotted against both depth and air exposure, data are from rocky and boulder substrates only.

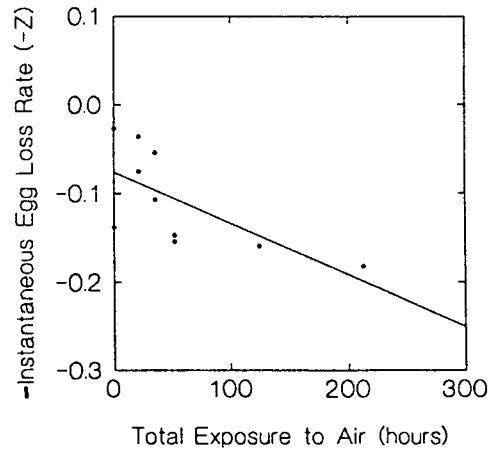
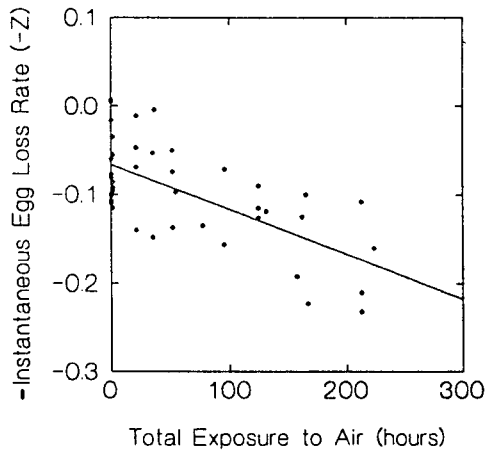
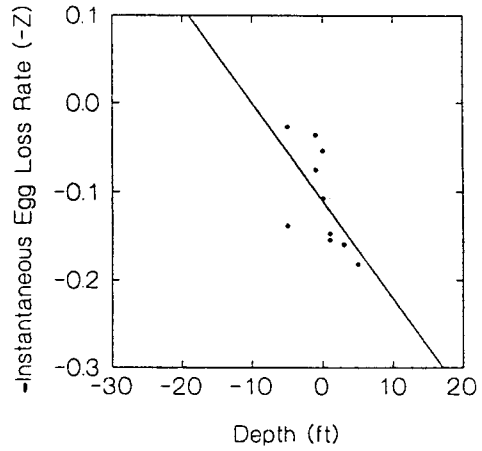


**Figure 33.** Egg loss rates against depth and air exposure for 1990 and 1991 combined. Data are from rocky and boulder substrates only.

Exposed Transects

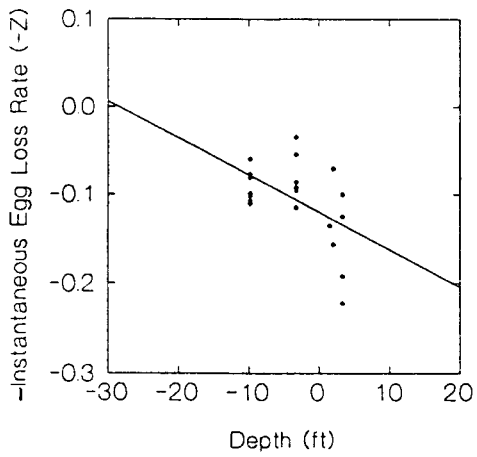


Protected Transects

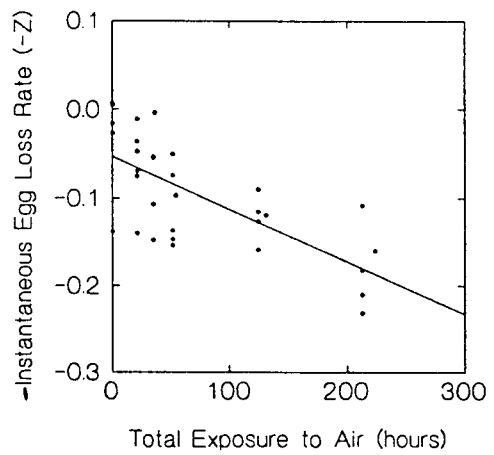
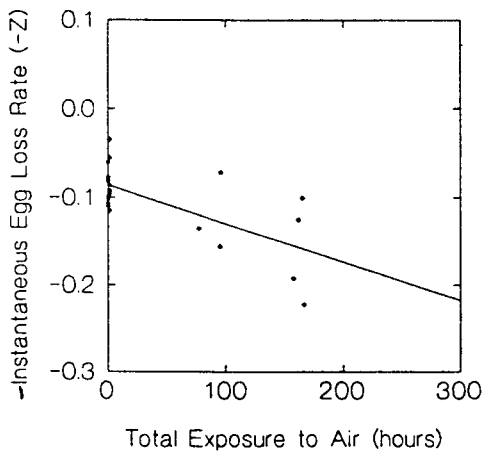
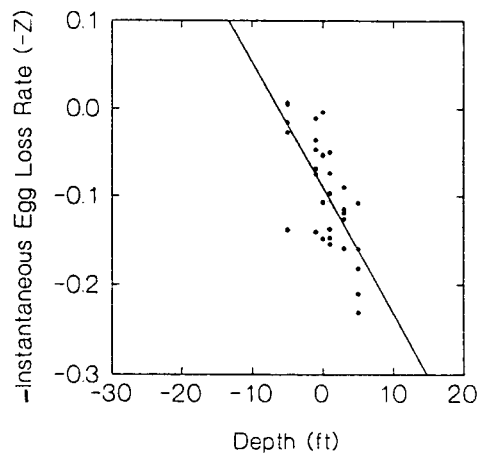


**Figure 34.** Egg loss rates for wave-exposed and wave-protected transects for 1994-1995 combined. Data taken from rocky and boulder substrates only, and are plotted against both depth and air exposure.

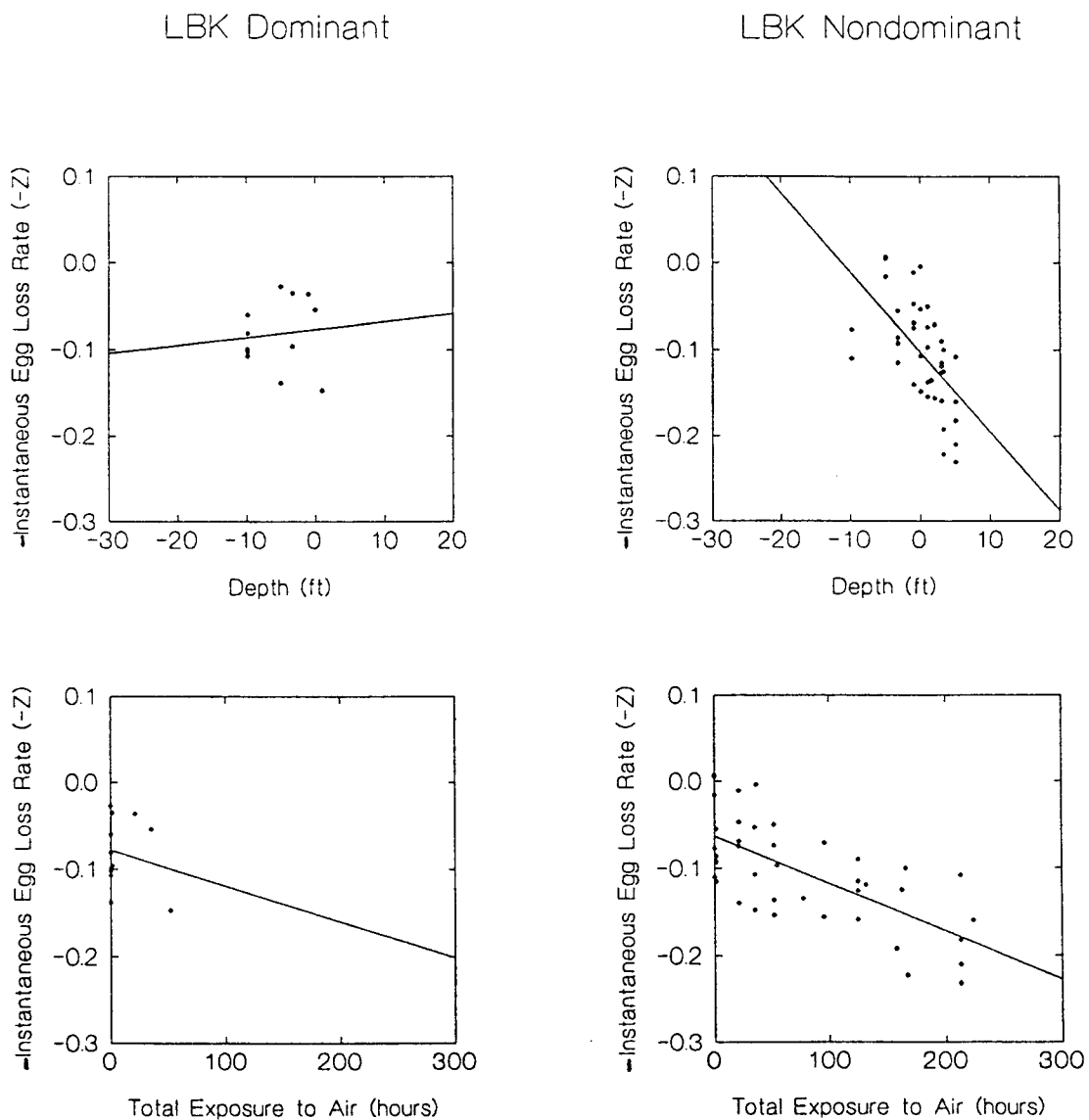
1994 Transects



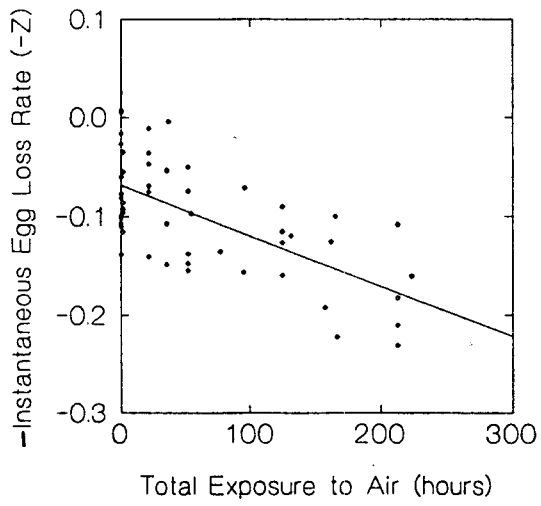
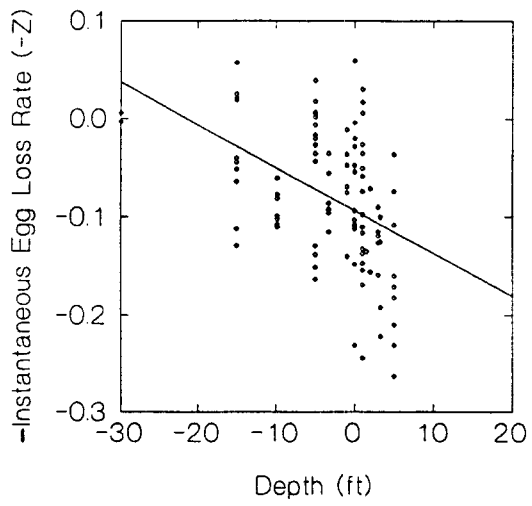
1995 Transects



**Figure 35.** Egg loss rates for each year, 1994 and 1995. Egg loss rates are plotted against both depth and air exposure. Data taken from rocky and boulder substrates only.



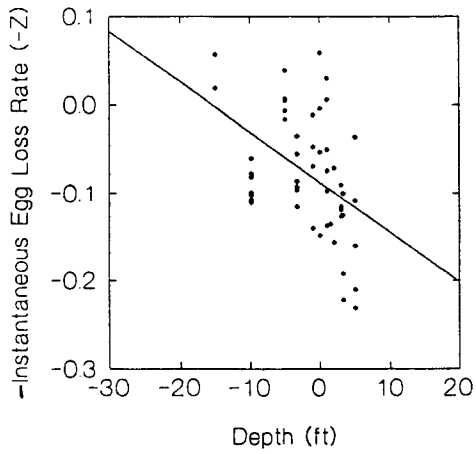
**Figure 36.** Egg loss rates in each kelp type category for 1994 and 1995 combined. LBK dominant refers to quadrats inhabited predominantly by large brown kelp (LBK) species, and LBK non-dominant refers to quadrats dominated by other vegetation types. Egg loss rates are plotted against both depth and air exposure, and are taken from rocky and boulder transects only.



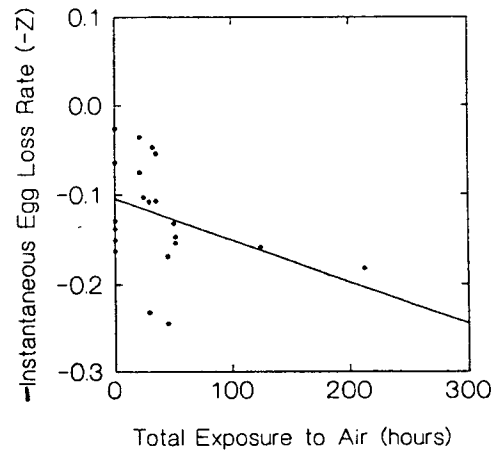
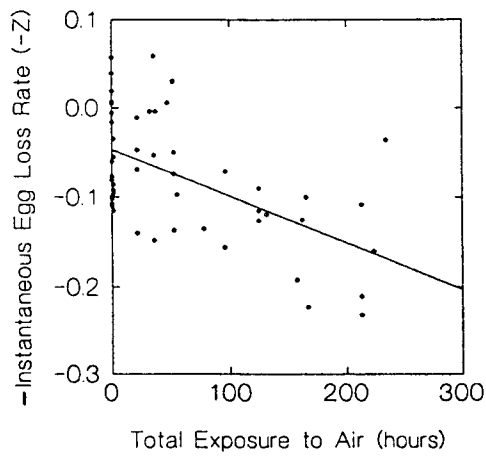
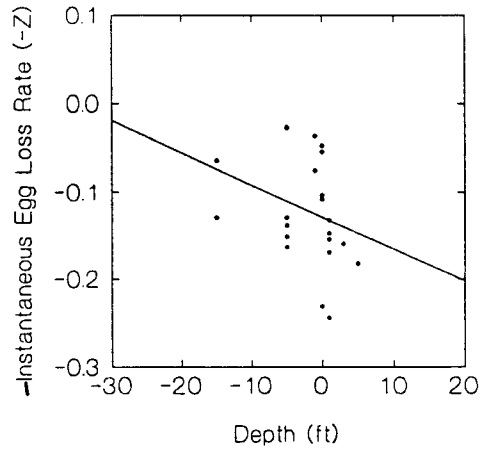
**Figure 37.** Egg loss rates against depth and air exposure for 1994 and 1995 combined. Data taken from rocky and boulder substrates only.



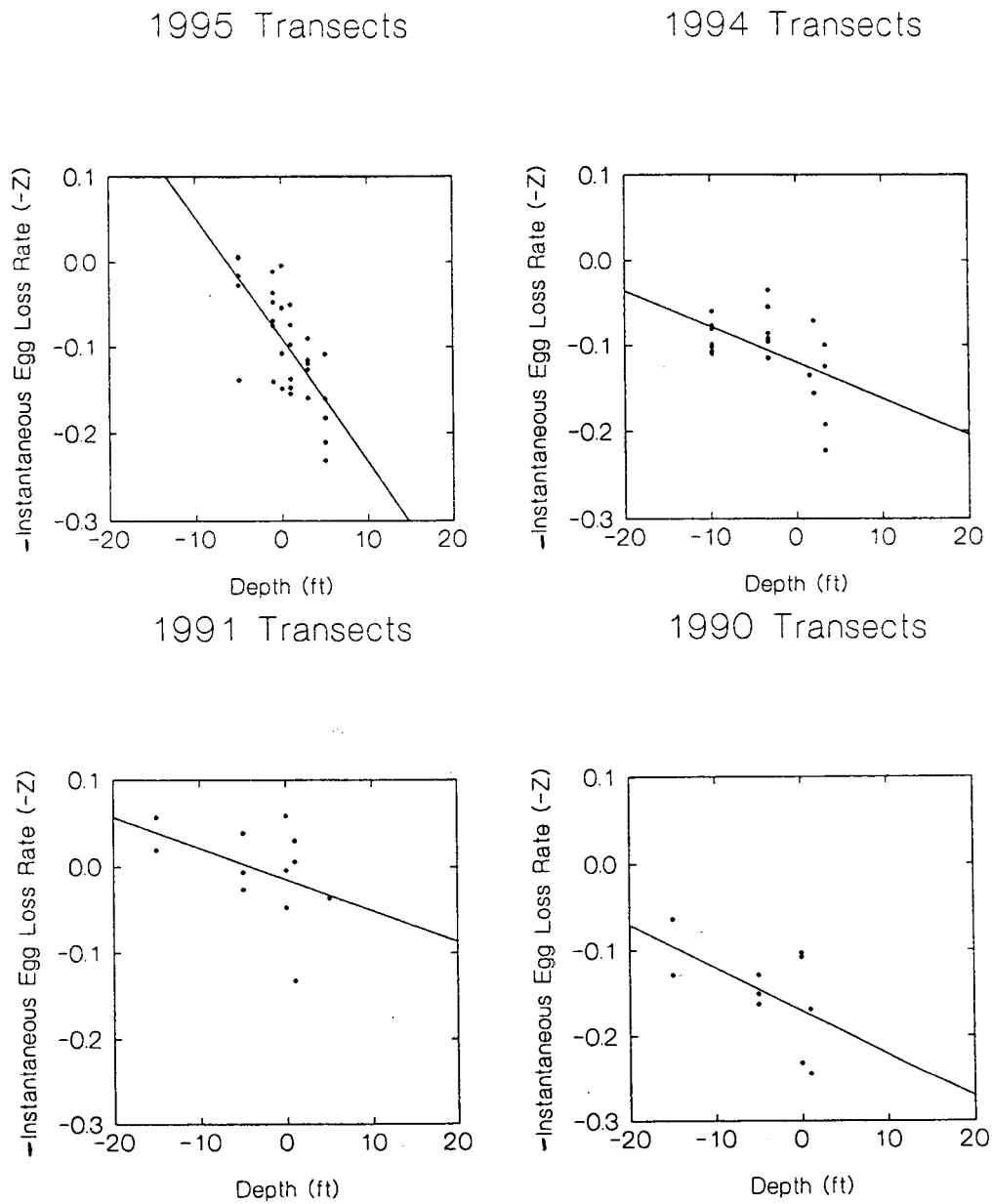
Exposed Transects



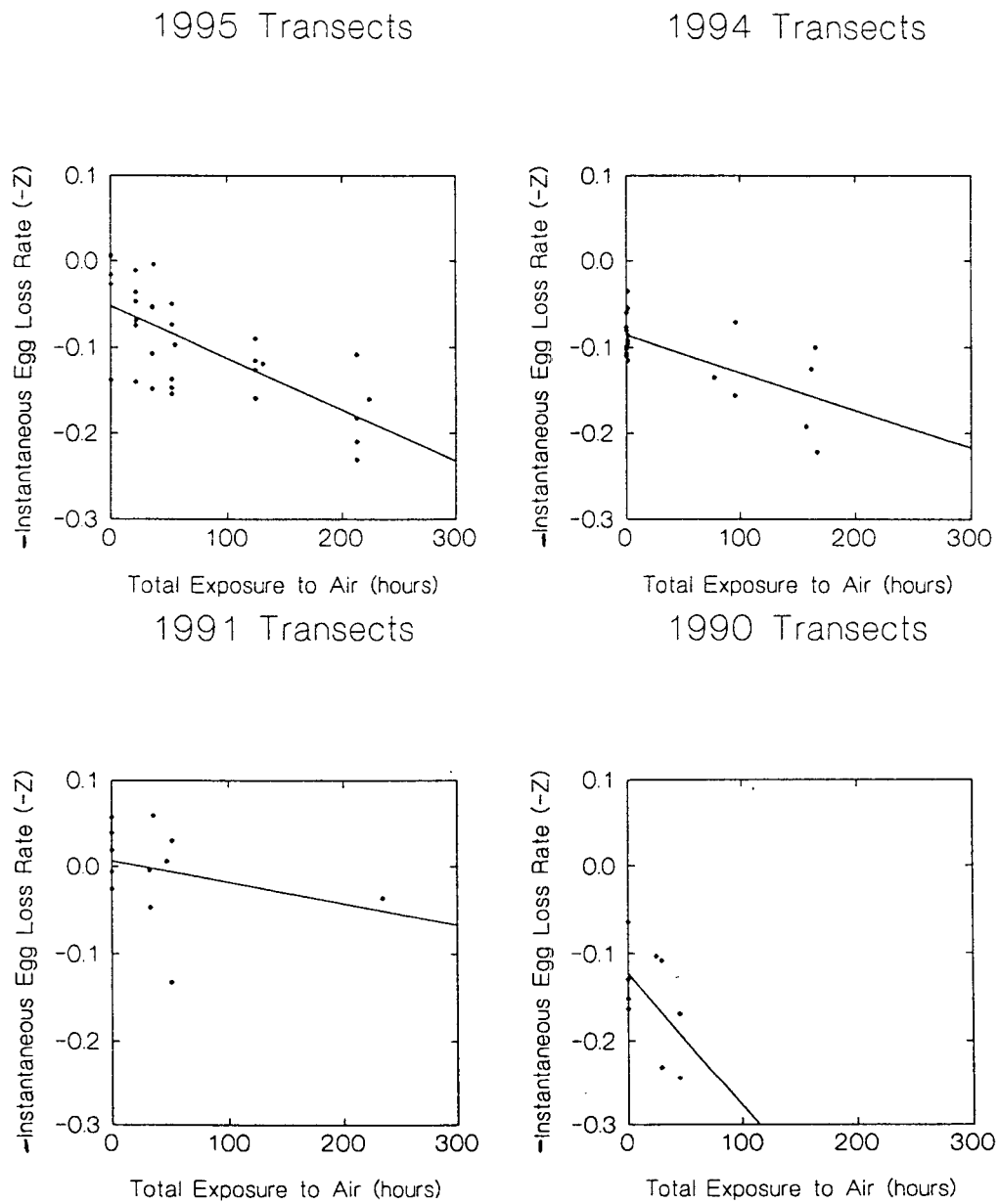
Protected Transects



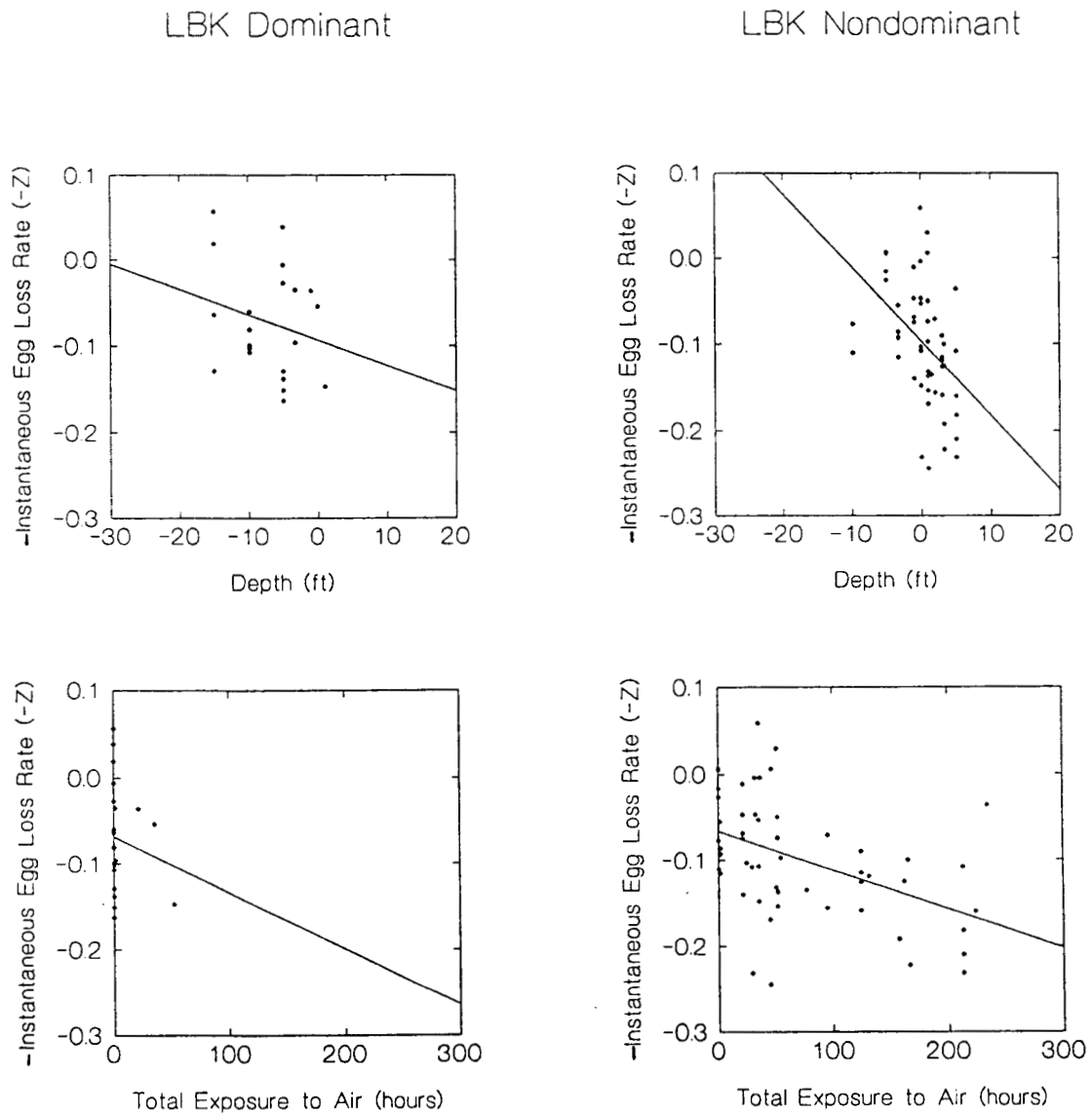
**Figure 38.** Egg loss rates for wave-exposed and wave-protected transects on Montague Island. Egg loss rates are plotted against both depth and air exposure. Data taken from all years, on rocky and boulder substrates only.



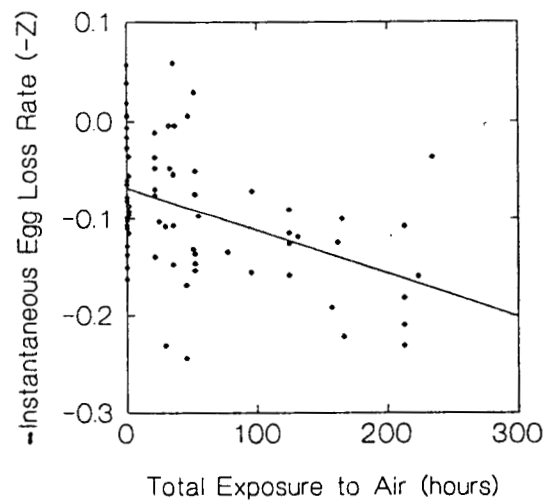
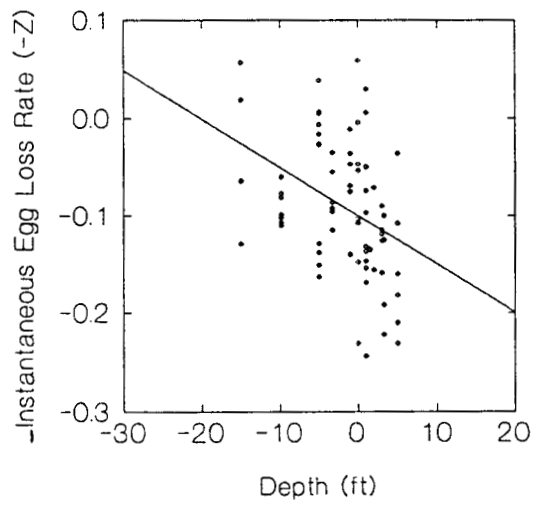
**Figure 39.** Egg loss rates from Montague Island transects for each year against depth. Data taken from rocky and boulder transects only.



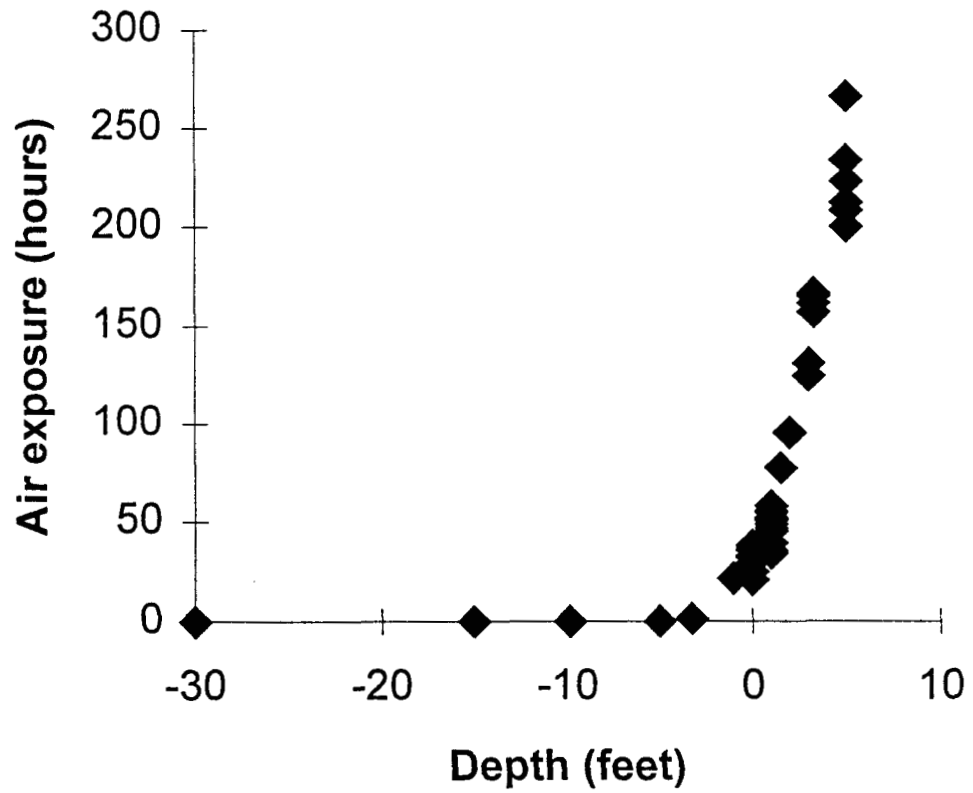
**Figure 40.** Egg loss rates at transects on Montague Island from each year against air exposure. Data from rocky and boulder transects only.



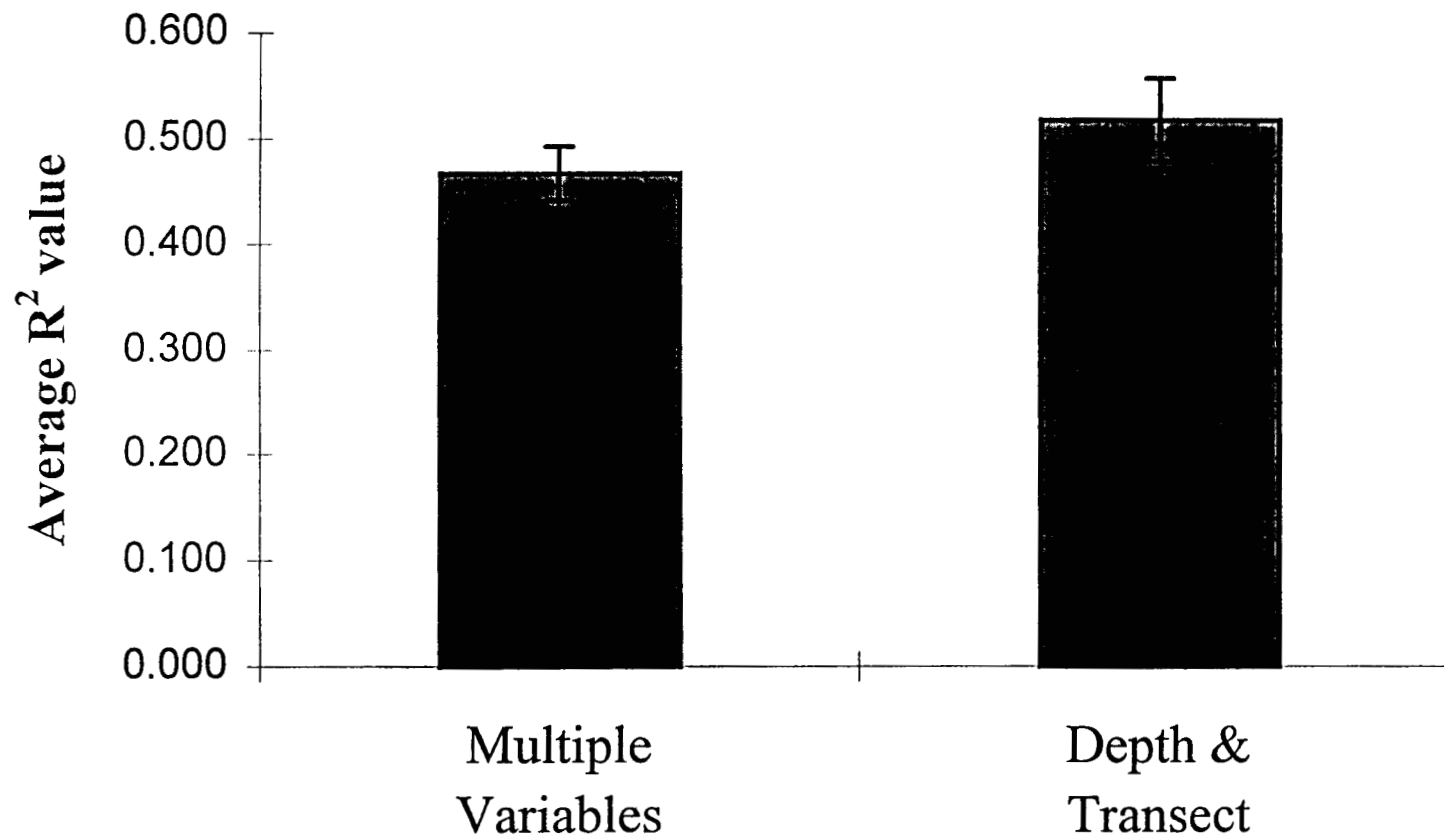
**Figure 41.** Egg loss rates from Montague Island in each kelp type category. LBK dominant refers to quadrats inhabited predominantly by large brown kelp (LBK) species, and LBK non-dominant refers to quadrats dominated by other vegetation types. Data plotted against both depth and air exposure, and taken from rocky and boulder transects only.



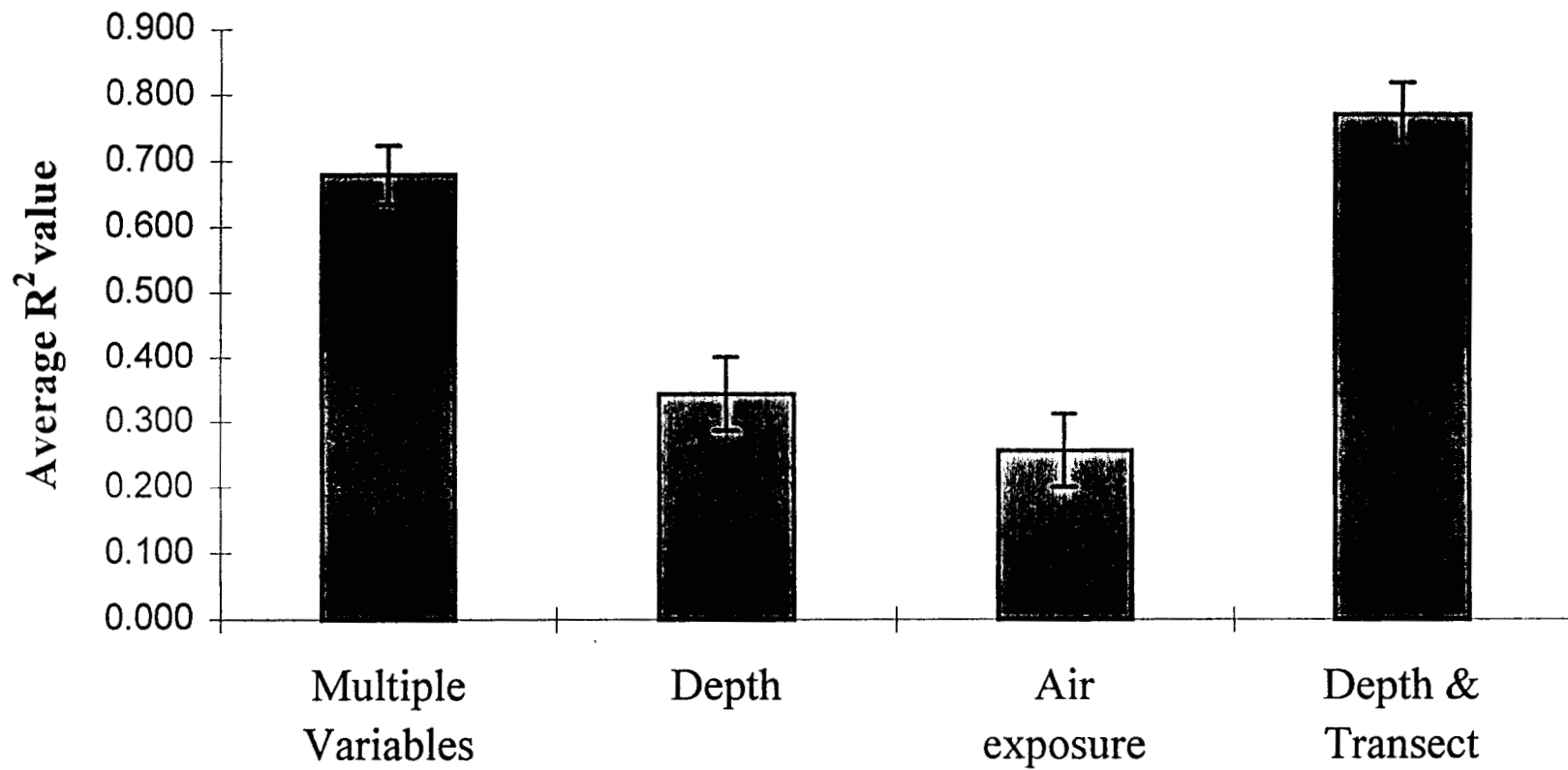
**Figure 42.** Egg loss rates from Montague Island transects against depth and air exposure. Data taken from all years, rocky and boulder substrates only.



**Figure 43.** Air exposure against depth. Air exposure is the cumulative exposure, in hours, over the herring egg incubation period at each depth sampled during the egg loss study.

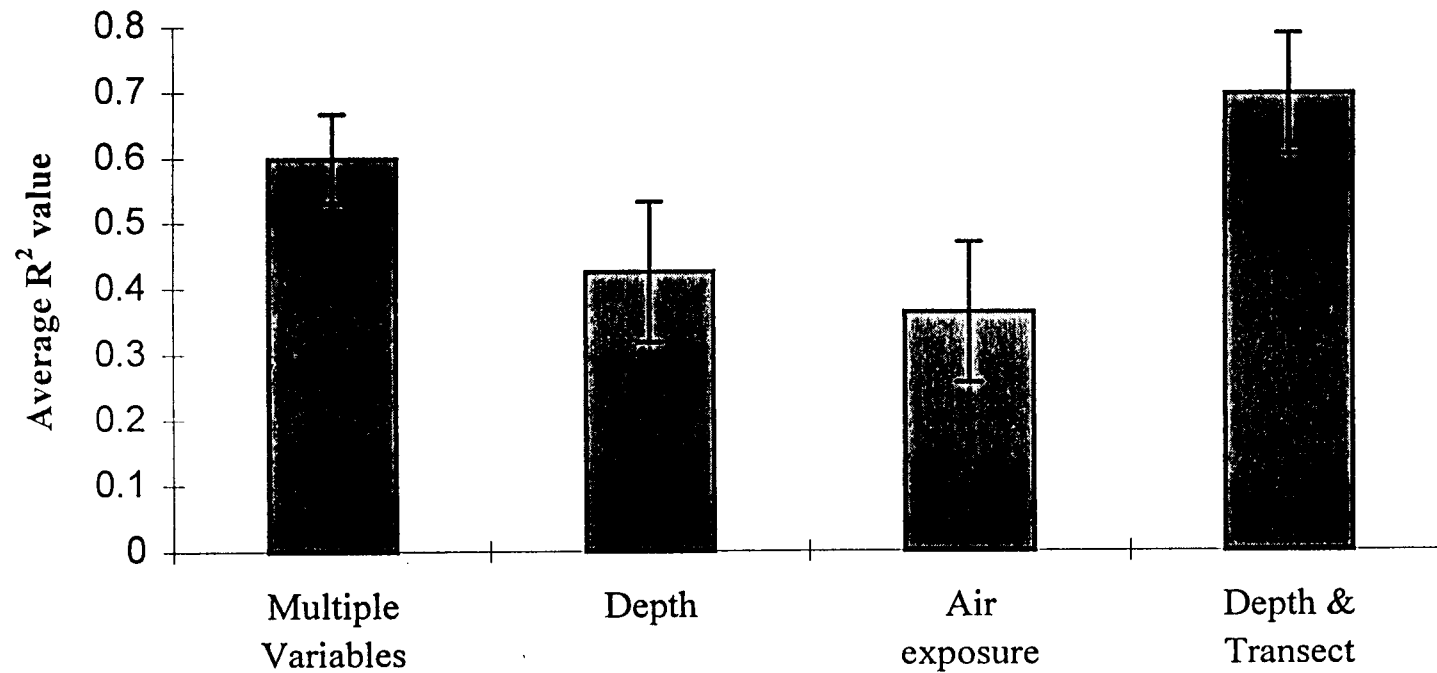


**Figure 44.** Average R<sup>2</sup> values for analyses of covariance models. The graph shows models with habitat variables, and models with transect and depth only.



**Figure 45.** Average R<sup>2</sup> values for analysis of variance models. Each bar represents the average R<sup>2</sup> value for different modeling techniques for comparison.





**Figure 46.** Average R<sup>2</sup> values for analysis of variance models for 1994 and 1995 only. Models using different explanatory variables are represented by each bar.

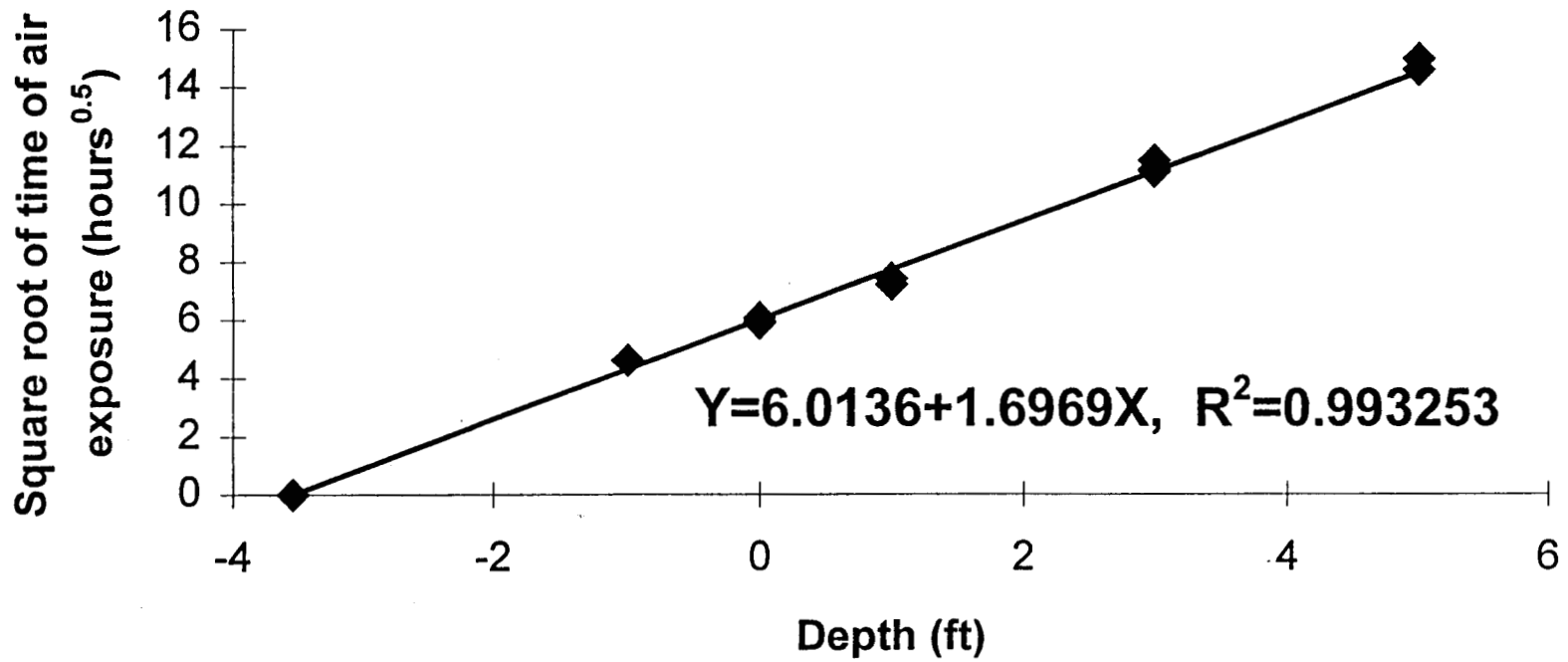
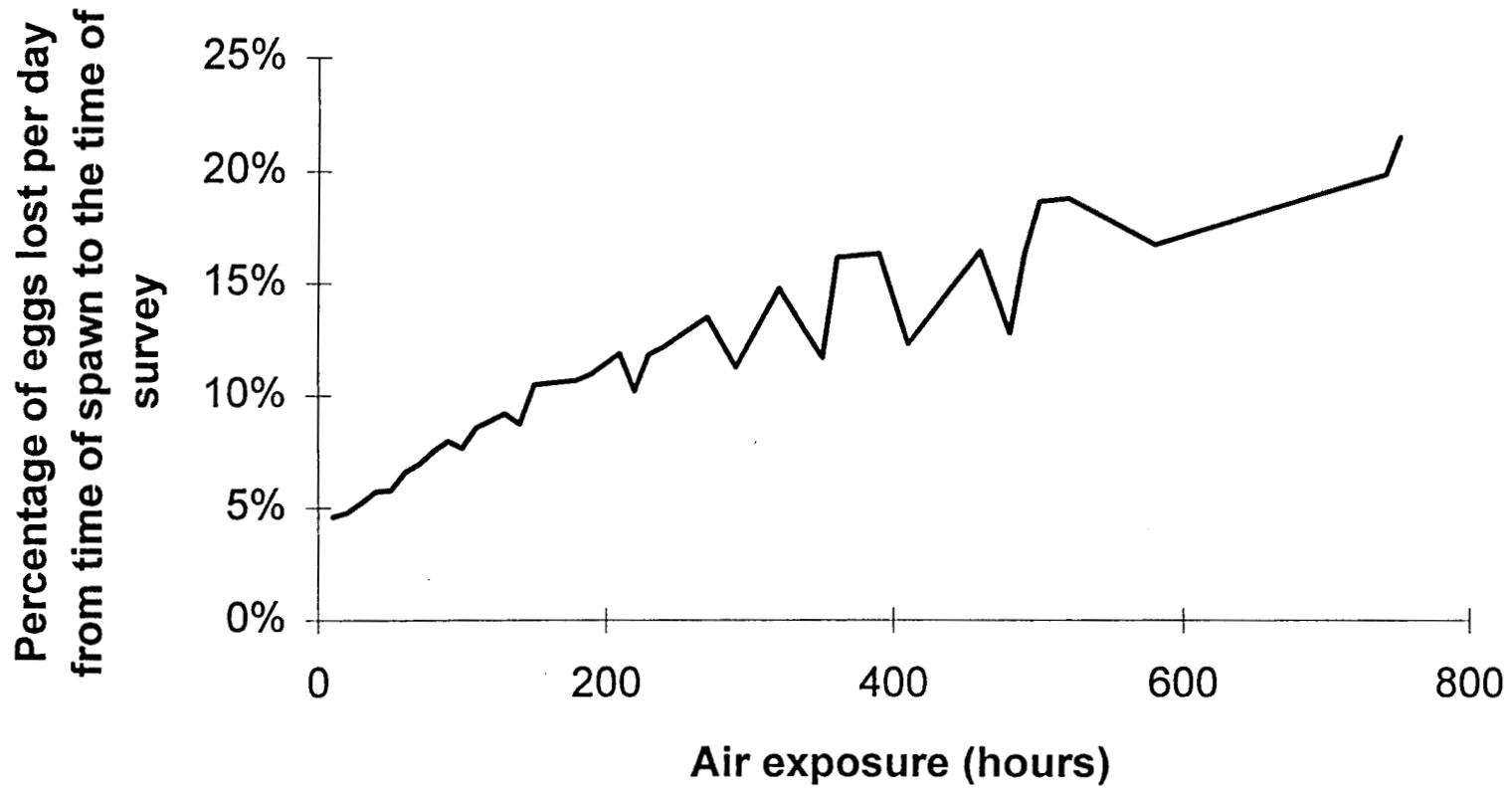
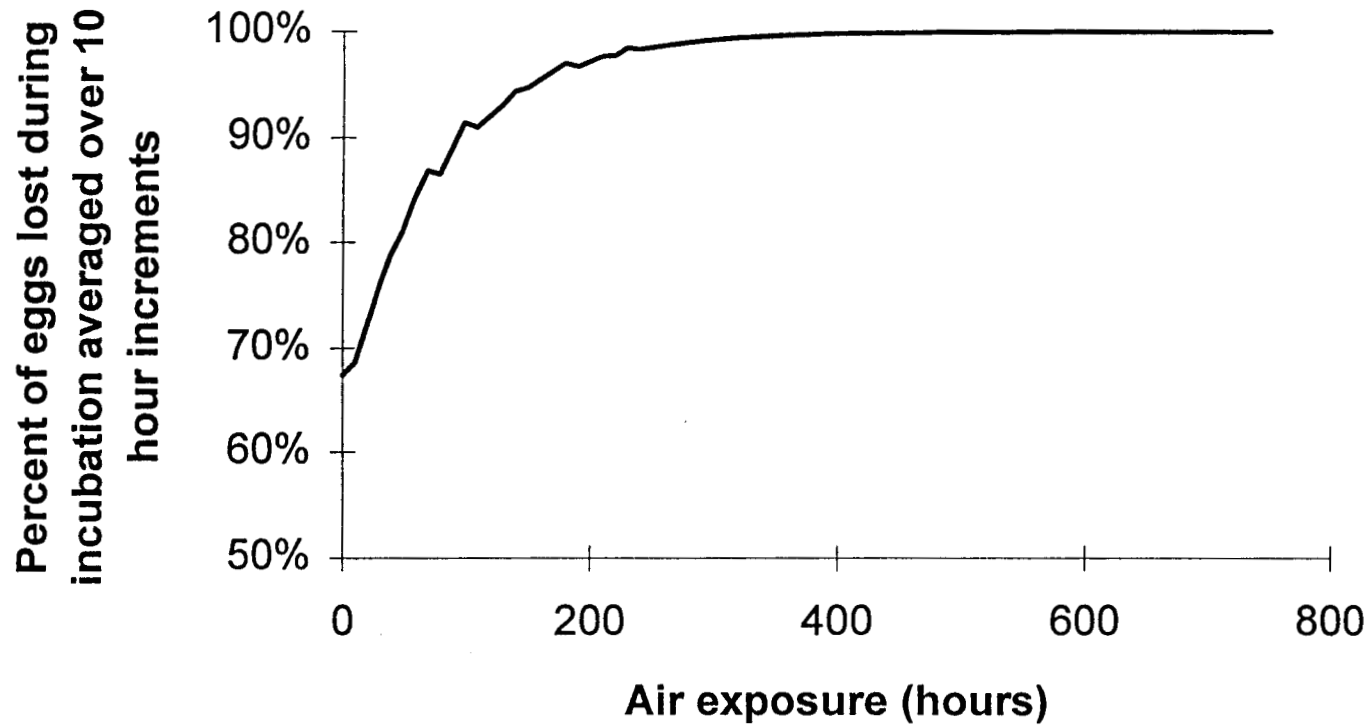


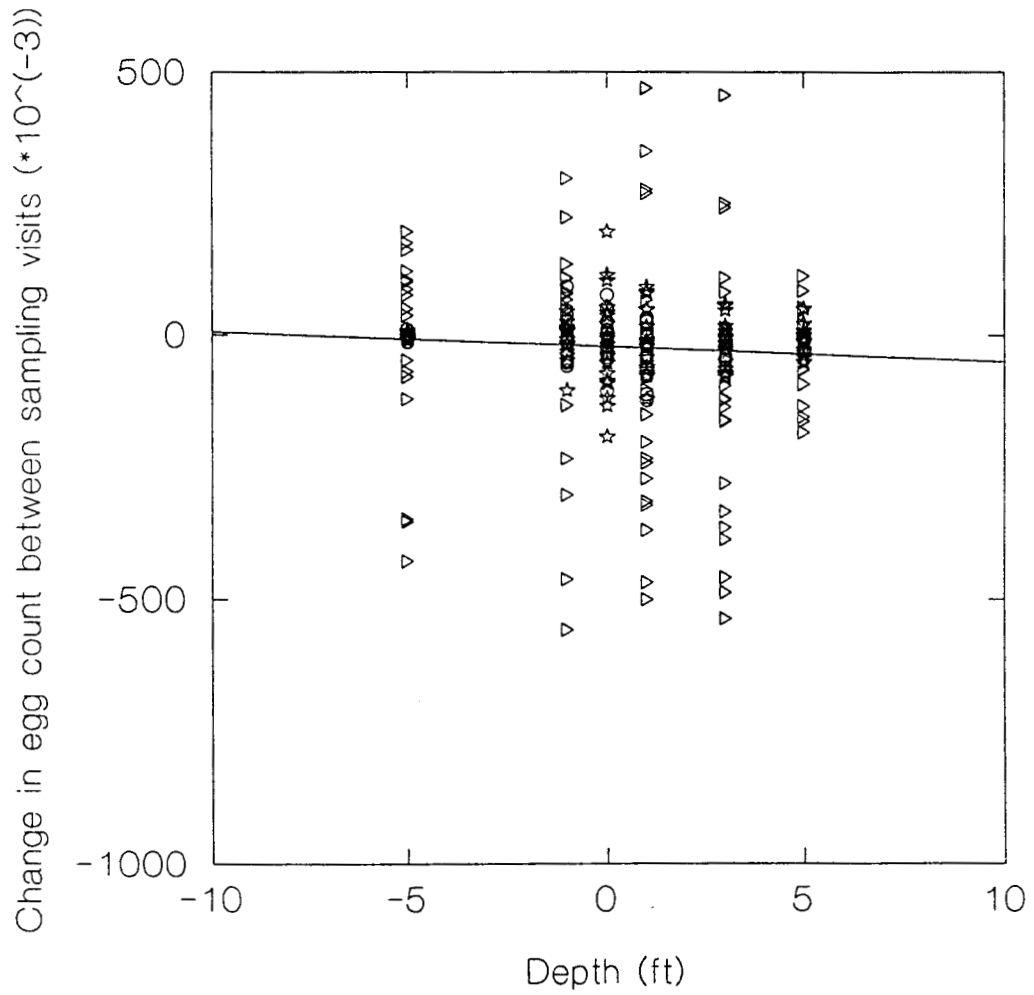
Figure 47. Regression of the square root of air exposure and depth for 1995.



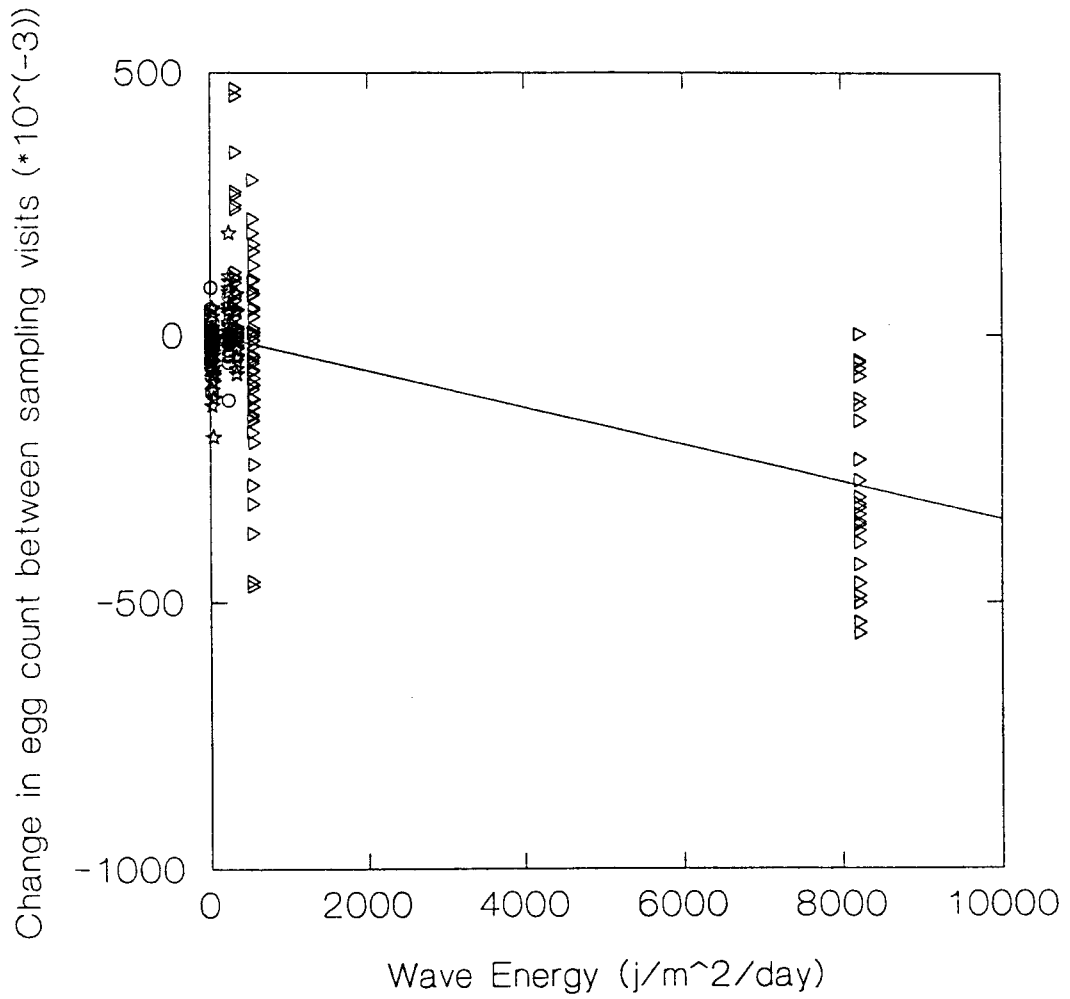
**Figure 48.** Percentage of eggs lost from time of spawning to time of survey in 1995. Percentages are predicted by the time of air exposure model. Percentages are averaged for ten hour increments of air exposure.



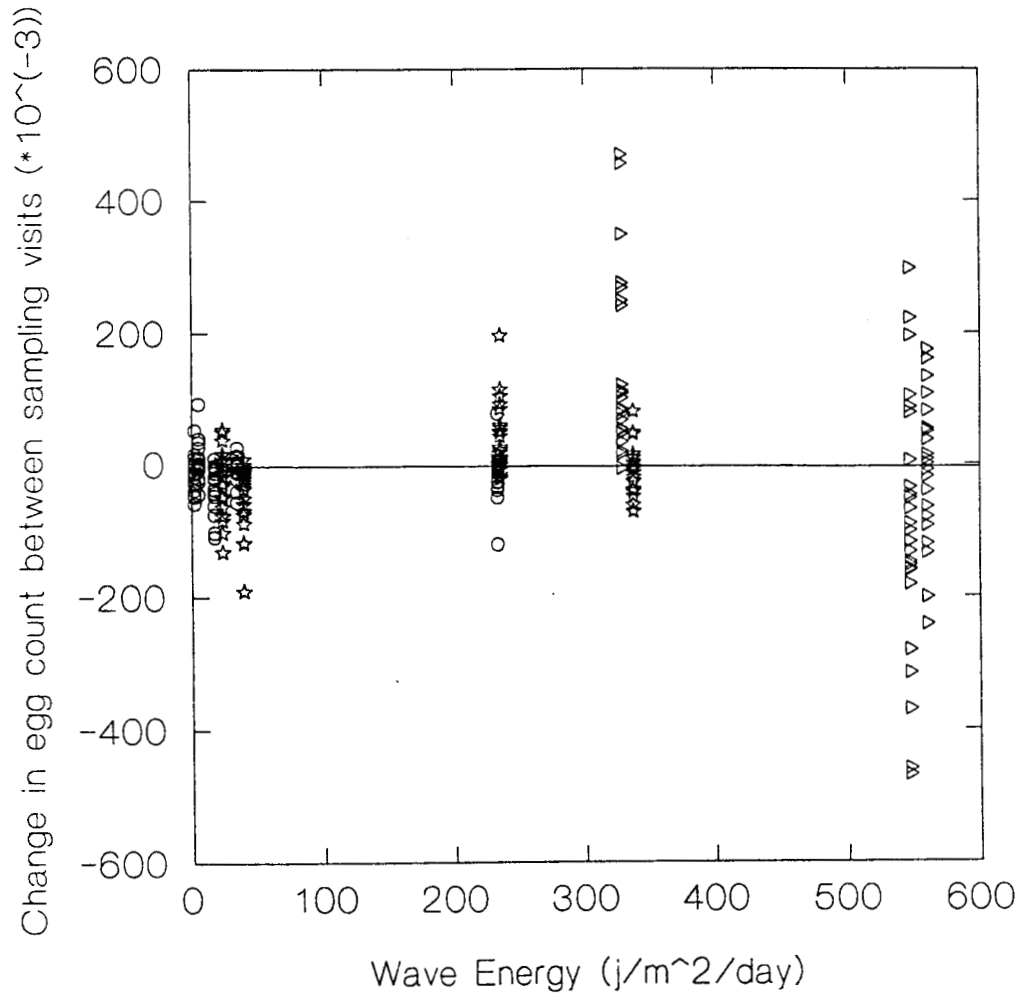
**Figure 49.** Percentage of eggs lost from time of spawning to time of hatching in 1995. Percentages are predicted for spawn deposition transects by the time of air exposure model. Percentages are averaged for ten hour increments of air exposure.



**Figure 50.** Change in egg abundance (in thousands of eggs) between sampling visits against depth in 1995. Triangles represent transect #6, stars represent transect #9 and circles represent transect #2.



**Figure 51.** Change in egg abundance (in thousands of eggs) between sampling visits against wave energy. Wave energy per day was measured at three transects by pressure sensors in 1995. Triangles represent transect #6, stars represent transect #9 and circles represent transect #2.



**Figure 52.** Changes in egg abundance (in thousands of eggs) between sampling visits against wave energies less than  $600 \text{ j} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$ . Wave energies were measured with pressure sensors at three 1995 egg loss transects. Triangles represent transect #6, stars represent transect #9 and circles represent transect #2.

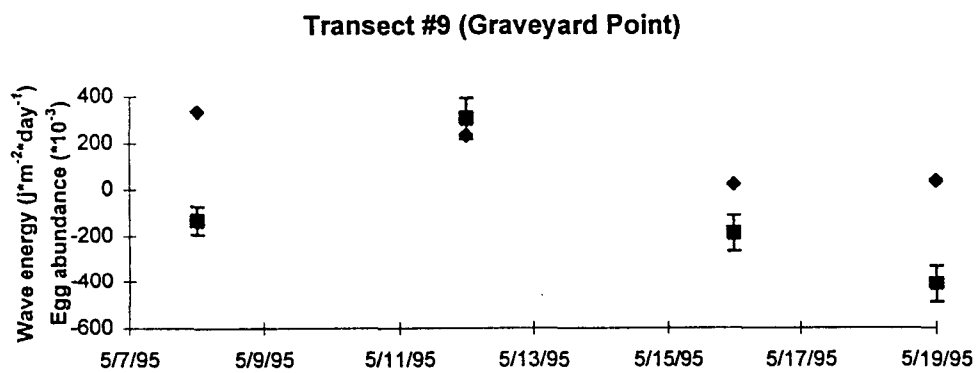
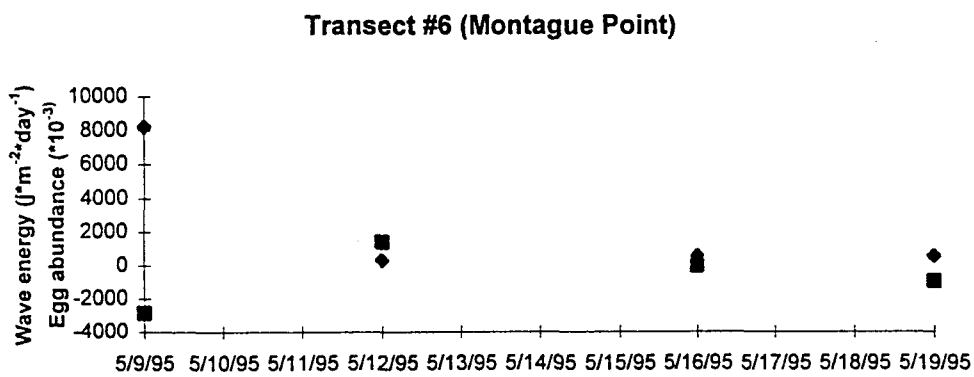
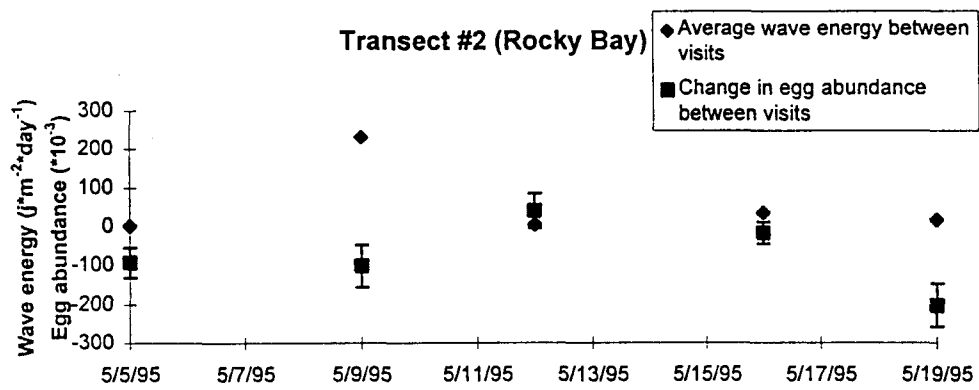


Figure 53. Average wave energy per day and average change in egg abundance between sampling visits against date sampled for 1995 transects.



**Table 1.** Summary of habitat variables available for each year of the egg loss study. + indicates these variables are confounded in 1994.

Habitat Variable	Year	1990	1991	1994	1995
Depths (ft)		-30, -15, -5, 0, 1, 5	-15, -5, 0, 1, 5	-10, -3, -2, 0, 2, 3	-5, -1, 0, 1, 3, 5
Air exposure		X	X	X	X
Wave exposure		X	X	X+	X
Oiled/Unoled		X	X		
Year		X	X	X	X
Substrate		X		X+	
Kelp Type		X	X	X	X
Average bird abundance				X	X
Average gull abundance				X	X
Cumulative loose eggs				X	
Fish abundance					X

**Table 2.** Summary of 1990 egg loss regressions from each transect by depth. R=Rocky substrate, G=Gravel substrate, B=Boulder substrate, P=wave-protected, E=wave-exposed, O=oiled area, and C=unoiled area.

Depth	Transect Habitat classifications	22	2	6	18	20	3	23	24	21
		O,E,R	C,P,R	C,P,R	O,P,R	O,P,R	C,P,G	O,P,G	O,P,G	O,P,B
5	slope (-Z)	-0.171					0.003	-0.134	-0.088	
	intercept	6.301					3.115	5.212	4.435	
	R <sup>2</sup>	0.408					0.000	0.476	0.328	
	p-value	0.000					0.887	0.000	0.000	
1	slope (-Z)	-0.116	-0.110	-0.035	-0.244		-0.005	-0.010	-0.035	-0.169
	intercept	6.817	4.772	4.869	7.553		4.770	3.112	1.591	7.136
	R <sup>2</sup>	0.405	0.136	0.042	0.482		0.001	0.001	0.012	0.515
	p-value	0.000	0.010	0.100	0.000		0.777	0.769	0.434	0.000
0	slope (-Z)	-0.110	-0.020	-0.094	-0.231	-0.103	-0.043	-0.085	-0.121	-0.108
	intercept	6.936	3.176	6.143	7.414	0.733	5.585	2.394	3.895	6.530
	R <sup>2</sup>	0.414	0.007	0.353	0.516	0.096	0.112	0.079	0.217	0.386
	p-value	0.000	0.557	0.000	0.000	0.079	0.007	0.031	0.000	0.000
-5	slope (-Z)	-0.020	0.002	0.018	-0.151	-0.129	-0.030	-0.016	-0.088	-0.163
	intercept	5.808	4.938	5.046	3.272	3.457	3.444	0.503	5.053	6.496
	R <sup>2</sup>	0.049	0.001	0.056	0.201	0.193	0.025	0.004	0.281	0.281
	p-value	0.090	0.772	0.057	0.005	0.003	0.214	0.645	0.000	0.000
-15	slope (-Z)	-0.040	0.025	0.021		-0.064	-0.035	-0.150	-0.141	-0.129
	intercept	6.337	3.814	4.499		3.889	5.075	3.168	2.930	4.822
	R <sup>2</sup>	0.189	0.028	0.069		0.154	0.108	0.262	0.185	0.287
	p-value	0.000	0.174	0.029		0.005	0.008	0.001	0.003	0.000
-30	slope (-Z)		-0.003	0.006						
	intercept		4.042	4.171						
	R <sup>2</sup>		0.001	0.007						
	p-value		0.795	0.509						

**Table 3.** Results of analysis of covariance of 1990 ln(egg abundance) data. All habitat variables and all possible interaction terms are included in the analysis.

**Analysis of Covariance**

Dependent Variable: Ln(egg abundance)

N: 2239

Multiple R: 0.660

Squared Multiple R: 0.436

<u>Source</u>	<u>Sum of Squares</u>	<u>DF</u>	<u>MS</u>	<u>F-Ratio</u>	<u>P</u>
Oiled/Unooled*Kelp type	281.781	1	281.781	121.058	0.000
Substrate type*Kelp type	36.579	2	18.289	7.857	0.000
Wave exposure*Kelp type	126.965	1	126.965	54.546	0.000
Wave exposure*days	3.812	1	3.812	1.638	0.201
Oiled/Unooled*days	64.148	1	64.148	27.559	0.000
Substrate*days	22.989	2	11.495	4.938	0.007
Kelp type*days	5.146	1	5.146	2.211	0.137
Depth*days	29.095	5	5.819	2.500	0.029
Days since spawn	53.660	1	53.660	23.053	0.000
Kelp type	0.000	1	0.000	0.000	0.991
Oiled/unooled	95.863	1	95.863	41.184	0.000
Wave exposure	159.067	1	159.067	63.338	0.000
Substrate	121.766	2	60.883	26.156	0.000
Depth	25.161	5	5.032	2.162	0.056
Error	5151.101	2213	2.328		

**Table 4.** Results of factorial analysis of 1990 egg loss rates. This model explains the most variation in the 1990 data. Data used in this analysis is from the rocky substrate.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate (Z)

N: 21

Multiple R: 0.924

Squared Multiple R: 0.85

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Oiled/Unoled	0.057	1	0.057	38.799	0.000
Wave exposure	0.016	1	0.016	11.058	0.005
Depth	0.042	5	0.008	5.698	0.005
Error	0.019	13	0.001		

**Table 5.** Results of factorial analysis of 1990 egg loss rates with air exposure in the place of depth. Egg loss rates are from the rocky substrate only.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate,

N: 21

Multiple R: 0.896

Squared Multiple R: 0.803

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Kelp type	0.035	1	0.035	23.159	0.000
Wave exposure	0.014	1	0.014	8.923	0.008
Oiled/Unoiled	0.059	1	0.059	39.282	0.000
Error	0.026	17	0.002		

**Table 6.** Summary of 1991 egg loss regressions from each transect by depth. R=rocky, P=wave-protected, E=wave-exposed, O=oiled area, and C=unoiled area.

Depth (ft)	Transect Habitat classification	26	28	12	15	21	25
		O,E,R	O,E,R	C,P,R	C,P,R	C,P,R	C,P,R
5	slope (-Z)		-0.036	-0.074		-0.263	
	intercept		4.430	4.303		6.155	
	R <sup>2</sup>		0.098	0.753		0.828	
	p-value		0.060	0.000		0.000	
1	slope (-Z)	0.006	0.030	-0.058	-0.026	-0.098	-0.132
	intercept	4.619	5.070	5.330	3.026	4.374	5.179
	R <sup>2</sup>	0.002	0.172	0.300	0.087	0.436	0.189
	p-value	0.792	0.013	0.005	0.152	0.002	0.030
0	slope (-Z)	-0.004	0.059	-0.028	-0.093	-0.112	-0.047
	intercept	4.555	4.315	6.142	5.127	5.325	3.682
	R <sup>2</sup>	0.001	0.436	0.173	0.590	0.583	0.014
	p-value	0.865	0.000	0.039	0.000	0.000	0.580
-5	slope (-Z)	-0.006	0.039	-0.035	-0.043	-0.017	-0.026
	intercept	4.639	3.396	6.253	4.553	4.679	3.336
	R <sup>2</sup>	0.002	0.142	0.240	0.352	0.021	0.017
	p-value	0.820	0.025	0.013	0.000	0.487	0.580
-15	slope (-Z)	0.057	0.019	-0.112	-0.051	-0.044	
	intercept	0.949	4.842	5.439	4.722	4.186	
	R <sup>2</sup>	0.166	0.030	0.370	0.275	0.121	
	p-value	0.039	0.320	0.001	0.002	0.088	

**Table 7.** Results of analysis of covariance of 1991 ln(egg abundance) data. All habitat variables and all possible interaction terms are included.

**Analysis of Covariance**

Dependent Variable: Ln(egg abundance)

N: 730

Multiple R: 0.641

Squared Multiple R: 0.4

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Wave exposure*Depth	50.245	4	12.561	11.069	0.000
Wave exposure*Kelp type	0.048	1	0.048	0.042	0.837
Wave exposure*Days	12.032	1	12.032	10.603	0.001
Oiled/unoiled*Days	0.115	1	0.115	0.101	0.751
Kelp type*Days	0.031	1	0.031	0.027	0.870
Depth*Days	14.997	4	3.749	3.304	0.011
Wave exposure	0.202	1	0.202	0.178	0.673
Oiled/Unoiled	2.591	1	2.591	2.283	0.131
Kelp type	1.207	1	1.207	1.063	0.303
Depth	12.022	4	3.006	2.648	0.032
Days since spawn	11.695	1	11.695	10.306	0.001
Error	804.605	709	1.135		

**Table 8.** Results of factorial analysis of 1991 egg loss rates. This model explains the most variability in the 1991 data.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate,

N: 26

Multiple R: 0.808

Squared Multiple R: 0.653

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Depth	0.025	4	0.006	3.168	0.036
Wave exposure	0.049	1	0.049	24.516	0.000
Error	0.040	20	0.002		



**Table 9.** Results of factorial analysis of 1991 egg loss rates with air exposure in the place of depth.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

N: 26

Multiple R: 0.792

Squared Multiple R: 0.628

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Air exposure	0.023	1	0.023	12.050	0.002
Wave exposure	0.052	1	0.052	27.617	0.000
Error	0.043	23	0.002		

**Table 10.** Summary of 1994 egg loss regressions from each transect by depth. Depths with no replicates are included in their nearest neighboring category. R=rocky, B=boulder, M=mud, S=sand, P=wave-protected, E=wave-exposed.

Depth (ft)	Transect Habitat classification	4	7	8	9	1	5	6	2	3	10	
		B,E	B,E	B,E	B,E	R,E	R,E	R,E	M,P	S,P	S,P	
3	slope (-Z)	-0.192			-0.100	-0.222	-0.125					
	intercept	6.483			5.180	6.125	5.975					
	R <sup>2</sup>	0.767			0.474	0.768	0.520					
	p-value	0.000			0.000	0.000	0.000					
2	slope (-Z)		-0.156	-0.071				-0.135				
	intercept		6.431	5.512				7.272				
	R <sup>2</sup>		0.566	0.502				0.770				
	p-value		0.000	0.000				0.000				
0	slope (-Z)								-0.063	-0.242	0.112	
	intercept								6.282	4.325	0.970	
	R <sup>2</sup>								0.688	0.645	0.231	
	p-value								0.000	0.000	0.003	
-2	slope (-Z)								-0.014		-0.101	
	intercept								3.180		6.720	
	R <sup>2</sup>								0.010		0.562	
	p-value								0.511		0.000	
-3	slope (-Z)	-0.086	-0.093	-0.035	-0.092	-0.096	-0.115	-0.055			-0.146	
	intercept	5.813	7.988	5.162	6.436	6.435	5.653	7.059			6.287	
	R <sup>2</sup>	0.050	0.693	0.275	0.409	0.430	0.111	0.227			0.668	
	p-value	0.282	0.000	0.001	0.000	0.000	0.067	0.008			0.000	
-10	slope (-Z)	-0.081	-0.099	-0.102	-0.077	-0.060	-0.107	-0.110	-0.125	-0.063	-0.033	
	intercept	4.255	6.066	5.362	3.861	5.000	4.830	7.196	5.758	5.199	3.459	
	R <sup>2</sup>	0.232	0.463	0.475	0.182	0.128	0.457	0.428	0.309	0.293	0.259	
	p-value	0.017	0.000	0.000	0.010	0.035	0.000	0.000	0.004	0.000	0.002	

**Table 11.** Results of analysis of covariance of 1994 ln(egg abundance) data, without the wave exposure variable.

**Analysis of Covariance**

Dependent Variable: Ln(egg abundance)

N: 1024

Multiple R: 0.637

Squared Multiple R: 0.406

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Substrate type*Kelp type	24.624	3	8.208	4.527	0.004
Substrate type*Days	24.118	3	8.039	4.434	0.004
Kelp type*Days	7.655	1	7.655	4.222	0.040
Depth*Days	53.002	5	10.600	5.846	0.000
Substrate type	44.133	3	14.711	8.113	0.000
Kelp type	12.695	1	12.695	7.002	0.008
Depth	87.980	5	17.596	9.705	0.000
Days since spawn	265.462	1	265.462	146.407	0.000
Error	1814.990	1001	1.813		

**Table 12.** Results of analysis of covariance of 1994 ln(egg abundance) data, without the substrate type variable.

**Analysis of Covariance**

Dependent Variable: Ln(egg abundance)

N: 1024

Multiple R: 0.614

Squared Multiple R: 0.37

<u>Source</u>	<u>Sum of Squares</u>	<u>DF</u>	<u>MSE</u>	<u>F-Ratio</u>	<u>P</u>
Wave exposure*Kelp type	17.483	1	17.483	9.261	0.002
Wave exposure*Days	0.789	1	0.789	0.418	0.518
Kelp type*Days	6.396	1	6.396	3.388	0.066
Depth*Days	50.109	5	10.022	5.309	0.000
Wave exposure	24.392	1	24.392	12.922	0.000
Kelp type	21.783	1	21.783	11.540	0.001
Depth	73.902	5	14.780	7.830	0.000
Days since spawn	545.587	1	545.587	280.449	0.000
Error	1900.884	1007	1.888		

**Table 13.** Results of factorial analysis of 1994 egg loss rates.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate,

N: 30

Multiple R: 0.936

Squared Multiple R: 0.87

<u>Source</u>	<u>Sum of Squares</u>	<u>DF</u>	<u>MSE</u>	<u>F-Ratio</u>	<u>P</u>
Depth*Average bird abundance	0.029	5	0.006	5.950	0.003
Wave exposure*Kelp type	0.013	1	0.013	12.865	0.003
Wave exposure	0.012	1	0.012	12.291	0.003
Kelp type	0.013	1	0.013	13.055	0.003
Depth	0.051	5	0.010	10.296	0.000
Average gull abundance	0.005	1	0.005	4.957	0.042
Error	0.015	15	0.001		

**Table 14.** Results of factorial analysis of 1994 egg loss rates, excluding the kelp type variable from the analysis.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

N: 30

Multiple R: 0.858

Squared Multiple R: 0.736

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Depth*Bird abundance	0.063	5	0.013	7.554	0.000
Depth	0.047	5	0.009	5.623	0.002
Error	0.032	19	0.001		

**Table 15.** Summary of 1995 egg loss regressions from each transect by depth. R=rocky substrate, P=wave-protected, E=wave-exposed.

Depth (ft)	Transect Habitat classificatio	1	2	6	9	11	12
		R,P	R,P	R,E	R,E	R,E	R,E
5	slope (-Z)		-0.182	-0.108	-0.160	-0.210	-0.231
	intercept		3.766	5.569	4.726	7.059	6.023
	R <sup>2</sup>		0.674	0.277	0.411	0.527	0.420
	p-value		0.000	0.003	0.001	0.000	0.009
3	slope (-Z)		-0.159	-0.126	-0.119	-0.115	-0.090
	intercept		4.238	6.735	5.004	5.598	6.100
	R <sup>2</sup>		0.381	0.455	0.335	0.336	0.408
	p-value		0.000	0.000	0.002	0.001	0.000
1	slope (-Z)	-0.154	-0.147	-0.050	-0.097	-0.137	-0.074
	intercept	3.166	5.438	6.511	4.998	6.006	7.158
	R <sup>2</sup>	0.338	0.364	0.324	0.174	0.557	0.402
	p-value	0.001	0.000	0.001	0.038	0.000	0.000
0	slope (-Z)	-0.107	-0.054		-0.004	-0.148	-0.053
	intercept	3.875	3.599		4.892	7.032	7.175
	R <sup>2</sup>	0.105	0.055		0.001	0.519	0.321
	p-value	0.080	0.213		0.899	0.000	0.001
-1	slope (-Z)	-0.075	-0.036	-0.011	-0.069	-0.140	-0.047
	intercept	3.638	2.734	5.538	4.455	5.771	6.763
	R <sup>2</sup>	0.259	0.010	0.009	0.093	0.213	0.089
	p-value	0.004	0.604	0.616	0.139	0.012	0.110
-5	slope (-Z)	-0.138	-0.027	0.007	-0.016		0.005
	intercept	1.669	1.011	4.780	2.768		3.522
	R <sup>2</sup>	0.194	0.015	0.002	0.023		0.001
	p-value	0.017	0.519	0.820	0.465		0.880

**Table 16.** Results of analysis of covariance of 1995 ln(egg abundance) data.

**Analysis of Covariance**

Dependent Variable: Ln(egg abundance)

n: 920

Multiple R: 0.762

Squared Multiple R: 0.580

<u>Source</u>	<u>Sum of Squares</u>	<u>DF</u>	<u>MSE</u>	<u>F-Ratio</u>	<u>P</u>
Wave exposure*Depth	33.164	5	6.633	3.575	0.003
Wave exposure*Kelp type	21.394	1	21.394	11.53	0.001
Wave exposure*Days	4.076	1	4.076	2.197	0.139
Kelp type*Days	0.520	1	0.520	0.280	0.597
Depth*Days	64.721	5	12.944	6.976	0.000
Kelp type	5.846	1	5.846	3.151	0.076
Wave exposure	62.194	1	62.194	33.520	0.000
Depth	94.803	5	18.961	10.219	0.000
Days since spawn	166.272	1	166.272	89.613	0.000
Error	1666.196	898	1.855		



**Table 17.** Results of factorial analysis of 1995 egg loss rates.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

N: 32

Multiple R: 0.886

Squared Multiple R: 0.784

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Depth	0.073	5	0.015	13.675	0.000
Bird abundance	0.030	1	0.030	28.449	0.000
Error	0.027	25	0.001		

**Table 18.** Results of factorial analysis of 1995 egg loss rates, excluding the average bird abundance variable.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

N: 32                      Multiple R: 0.734                      Squared Multiple R: 0.539

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Depth	0.067	5	0.013	6.075	0.001
Error	0.057	26	0.002		

**Table 19.** Results of analysis of covariance of the combined 1990 and 1991 ln(egg abundance) data.

**Analysis of Covariance**

Dependent Variable: Ln(egg abundance)

N: 2969

Multiple R: 0.649

Squared Multiple R: 0.421

Source	Sum of Squares	DF	MSE	F-Ratio	P
Kelp type*Oiled/unoiled*Year	8.484	1	8.484	4.041	0.045
Kelp type*Oiled/unoiled*Days	0.103	1	0.103	0.049	0.825
Kelp type*Wave exposure*Days	0.312	1	0.312	0.148	0.700
Kelp type*Year*Days	14.814	1	14.814	7.055	0.008
Kelp type*Substrate type*Days	13.627	2	6.813	3.245	0.039
Oiled/Unoiled*Year*Days	127.827	1	127.827	60.878	0.000
Wave exposure*Year*Days	8.355	1	8.355	3.979	0.046
Kelp type*Oiled/unoiled	61.854	1	61.854	29.458	0.000
Kelp type*Wave exposure	32.968	1	32.968	15.701	0.000
Kelp type*Year	1.784	1	1.784	0.849	0.357
Kelp type*Substrate type	11.417	2	5.709	2.719	0.066
Oiled/Unoiled*Year	74.966	1	74.966	35.703	0.000
Wave exposure*Year	5.868	1	5.868	2.794	0.095
Depth*Days	31.184	5	6.237	2.970	0.011
Year	126.239	1	126.239	60.122	0.000
Oiled/Unoiled	773.648	1	773.648	368.454	0.000
Substrate type	404.301	2	202.151	96.275	0.000
Kelp type	14.270	1	14.270	6.796	0.009
Wave exposure	1121.976	1	1121.976	534.347	0.000
Depth	12.447	5	2.489	1.186	0.314
Days since spawn	130.874	1	130.874	62.329	0.000
Error	6164.765	2936	2.100		

**Table 20.** Results of factorial analysis of combined 1990 and 1991 egg loss rates. Data from rocky and boulder substrates only, with all depths.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

n: 51

Multiple R: 0.882

Squared Multiple R: 0.777

Source	Sum of Squares	DF	MSE	F-Ratio	P
Kelp type*Substrate type	0.008	1	0.008	5.037	0.031
Kelp type*Year	0.008	1	0.008	4.775	0.035
Year*Oiled/Unoiled	0.043	1	0.043	26.391	0.000
Year	0.008	1	0.008	4.786	0.035
Oiled/Unoiled	0.026	1	0.026	15.841	0.000
Wave exposure	0.036	1	0.036	21.796	0.000
Depth	0.024	5	0.005	2.922	0.025
Error	0.064	39	0.002		

**Table 21.** Results of factorial analysis of combined 1990 and 1991 egg loss rates, with the kelp type\*substrate type interaction removed.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

n: 51                      Multiple R: 0.857                      Squared Multiple R: 0.734

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Year*Oiled/unoiled	0.046	1	0.046	24.649	0.000
Oiled/unoiled	0.025	1	0.025	13.627	0.001
Wave exposure	0.036	1	0.036	19.090	0.000
Year	0.009	1	0.009	4.828	0.034
Depth	0.054	5	0.011	5.753	0.000
Error	0.077	41	0.002		

**Table 22.** Average egg loss rates for 1990 and 1991 combined data for each significant habitat variable from factorial analysis. Estimates for rocky and boulder substrates only.

		1990	1991	Combined Years, Rocky and Boulder Substrates Only
<b>Wave exposed</b>	-Z			<b>-0.021</b>
	SE			0.018
	n			14
<b>Wave protected</b>	Z			<b>-0.079</b>
	SE			0.012
	n			37
<b>Oiled</b>	-Z	<b>-0.130</b>	<b>-0.003</b>	<b>-0.074</b>
	SE	0.016	0.015	0.017
	n	15	12	27
<b>Unoiled</b>	-Z	<b>-0.019</b>	<b>-0.075</b>	<b>-0.052</b>
	SE	0.015	0.017	0.013
	n	10	14	24
<b>1990</b>	-Z			<b>-0.086</b>
	SE			0.016
	n			25
<b>1991</b>	-Z			<b>-0.042</b>
	SE			0.013
	n			26

**Table 22 (continued).** Average egg loss rates for 1990 and 1991 combined data for each significant habitat variable from factorial analysis. Estimates for rocky and boulder substrates only.

		<b>Combined Years, Rocky and Boulder Substrates Only</b>	
<b>Depth</b>	5 ft	-Z	<b>-0.136</b>
		SE	0.051
		n	4
	1 ft	-Z	<b>-0.087</b>
		SE	0.024
		n	11
	0 ft	-Z	<b>-0.074</b>
		SE	0.021
		n	12
	-5 ft	-Z	<b>-0.044</b>
		SE	0.019
		n	12
	-15 ft	-Z	<b>-0.032</b>
		SE	0.019
		n	10
	-30 ft	-Z	<b>0.002</b>
		SE	0.005
		n	2

**Table 23.** Results of analysis of covariance of the combined 1994 and 1995 ln(egg abundance) data. Data from rocky and boulder substrates only.

**Analysis of Covariance**

Dependent Variable: Ln(egg abundance)

n: 1619

Multiple R: 0.734

Squared Multiple R: 0.538

Source	Sum of Squares	DF	MSE	F-Ratio	P
Kelp type*Wave exposure*Days	0.000	1	0.000	0.000	0.995
Kelp type*Year*Days	0.078	1	0.078	0.044	0.834
Kelp type*Substrate type*Days	0.038	1	0.038	0.022	0.883
Year*Days	1.769	1	1.769	1.000	0.318
Substrate type*Days	0.898	1	0.898	0.508	0.476
Kelp type*Days	0.002	1	0.002	0.001	0.975
Wave exposure*Days	2.205	1	2.205	1.247	0.264
Depth*Days	78.468	8	9.809	5.544	0.000
Kelp type*Wave exposure	1.047	1	1.047	0.592	0.442
Kelp type*Year	0.087	1	0.087	0.049	0.824
Kelp type*Substrate type	3.799	1	3.799	2.147	0.143
Year	0.038	1	0.038	0.021	0.884
Substrate type	2.202	1	2.202	1.143	0.285
Kelp type	8.127	1	8.127	4.594	0.032
Wave exposure	36.318	1	36.318	20.529	0.000
Depth	110.655	8	13.832	7.818	0.000
Days since spawn	277.492	1	277.492	156.850	0.000
Error	2807.644	1587	1.769		



**Table 24.** Results of factorial analysis of combined 1994 and 1995 egg loss rates, from the rocky substrate only.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

n: 41

Multiple R: 0.724

Squared Multiple R: 0.524

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Depth	0.076	8	0.010	4.400	0.001
Error	0.069	32	0.002		

**Table 25.** Results of factorial analysis of combined 1994 and 1995 egg loss rates from rocky and boulder substrates. For this analysis depth was replaced by time of air exposure.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

N: 53

Multiple R: 0.716

Squared Multiple R: 0.513

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Air exposure	0.080	1	0.080	49.659	0.000
Year	0.013	1	0.013	7.719	0.008
Wave exposure	0.007	1	0.007	4.122	0.048
Error	0.079	49	0.002		

**Table 26.** Average egg loss rates for significant habitat variables from the factorial analysis of 1994 and 1995 egg loss rates. Data from rocky and boulder substrates only.

		<b>1994 &amp; 1995 Combined, Rocky and Boulder Substrates Only</b>	
<b>Wave Exposure</b>	Exposed	-Z	<b>-0.098</b>
		SE	0.009
		n	43
	Protected	-Z	<b>-0.108</b>
		SE	0.018
		n	10
<b>Year</b>	1994	-Z	<b>-0.105</b>
		SE	0.010
		n	21
	1995	-Z	<b>-0.096</b>
		SE	0.011
		n	32

**Table 27.** Average egg loss rates for each depth for the combined years, 1994 and 1995. Data are from the rocky substrate only.

		1994 & 1995 Combined, Rocky Substrate Only	
Depth	5 ft	-Z	-0.178
		SE	0.021
		n	5
	3 ft	-Z	-0.137
		SE	0.016
		n	7
	2 ft	-Z	-0.135
		SE	-
		n	1
	1 ft	-Z	-0.110
		SE	0.017
		n	6
	0 ft	-Z	-0.073
		SE	0.025
		n	5
	-1 ft	-Z	-0.063
		SE	0.018
		n	6
	-3 ft	-Z	-0.089
		SE	0.018
		n	3
	-5 ft	-Z	-0.034
		SE	0.027
		n	5
	-10 ft	-Z	-0.092
		SE	0.016
		n	3

**Table 28.** Results of analysis of covariance of Montague Island ln(egg abundance) data. Data from rocky and boulder substrates only.

**Analysis of Covariance**

Dependent Variable: Ln(egg abundance)

n: 2432

Multiple R: 0.694

Squared Multiple R: 0.481

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Kelp type*Wave exposure*Days	0.409	1	0.409	0.193	0.660
Kelp type*Year*Days	25.283	3	8.428	3.981	0.008
Kelp type*Substrate type*Days	9.404	1	9.404	4.443	0.035
Year*Days	44.651	3	14.884	7.031	0.000
Substrate type*Days	7.709	1	7.709	3.641	0.056
Kelp type*Days	22.439	1	22.439	10.600	0.001
Wave exposure*Days	1.543	1	1.543	0.729	0.393
Depth*Days	137.732	9	15.304	7.229	0.000
Kelp type*Wave exposure	0.412	1	0.412	0.195	0.659
Kelp type*Year	22.216	3	7.405	3.498	0.015
Kelp type*Substrate type	4.007	1	4.007	1.893	0.169
Year	51.806	3	17.269	8.158	0.000
Substrate type	0.889	1	0.889	0.420	0.517
Kelp type	0.130	1	0.130	0.061	0.805
Wave exposure	35.715	1	35.715	16.872	0.000
Depth	163.882	9	18.209	8.602	0.000
Days since spawn	233.439	1	233.439	110.493	0.000
Error	5059.299	2390	2.117		

**Table 29.** Results of factorial analysis of Montague Island egg loss rates. Data from rocky transects only.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

N: 59

Multiple R: 0.845

Squared Multiple R: 0.715

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Wave exposure	0.018	1	0.018	8.704	0.005
Year	0.068	3	0.023	11.219	0.000
Depth	0.098	9	0.011	5.365	0.000
Error	0.091	45	0.002		

**Table 30.** Results of factorial analysis of Montague Island egg loss rates, with air exposure in the place of depth. Data from rocky transects only.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

N: 59

Multiple R: 0.819

Squared Multiple R: 0.672

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Wave exposure	0.020	1	0.020	10.275	0.002
Air exposure	0.084	1	0.084	42.416	0.000
Year	0.099	3	0.033	16.731	0.000
Error	0.105	53	0.002		

**Table 31.** Average egg loss rates for significant habitat variables from factorial analysis of Montague Island data. Data from the rocky substrate only.

			<b>Montague Island Data, Rocky Substrate Only</b>
<b>Wave Exposure</b>	Exposed	-Z	<b>-0.071</b>
		SE	0.012
		n	40
	Protected	-Z	<b>-0.116</b>
		SE	0.015
		n	19
<b>Year</b>	1990	-Z	<b>-0.154</b>
		SE	0.029
		n	6
	1991	-Z	<b>-0.003</b>
		SE	0.015
		n	12
	1994	-Z	<b>-0.114</b>
		SE	0.016
		n	9
	1995	-Z	<b>-0.096</b>
		SE	0.011
		n	32



**Table 32.** Average egg loss rates for each depth category for Montague Island data. Data from rocky substrate only.

		<b>Montague Island Data, Rocky Substrate Only</b>	
<b>Depth</b>	5 ft	-Z	-0.155
		SE	0.029
		n	6
3 ft	-Z	-0.137	
	SE	0.016	
	n	7	
2 ft	-Z	-0.135	
	SE	--	
	n	1	
1 ft	-Z	-0.100	
	SE	0.026	
	n	10	
0 ft	-Z	-0.069	
	SE	0.026	
	n	10	
-1 ft	-Z	-0.063	
	SE	0.018	
	n	6	
-3 ft	-Z	-0.089	
	SE	0.018	
	n	3	
-5 ft	-Z	-0.044	
	SE	0.022	
	n	10	
-10 ft	-Z	-0.092	
	SE	0.016	
	n	3	
-15 ft	-Z	0.004	
	SE	0.036	
	n	3	

**Table 33.** Analysis of variance of egg loss rates from subtidal depths using kelp type as the only explanatory variable. Depths selected were all deeper than +1 foot relative to mean low water.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

N: 89

Multiple R: 0.141

Squared Multiple R: 0.020

Source	Sum of Squares	DF	MSE	F-Ratio	P
Kelp type	0.010	1	0.010	1.767	0.187
Error	0.501	87	0.006		

**Table 34.** Comparison of residual sums of squares for models including depth and models including air exposure.

<b>Data set</b>	<b>RSS<sub>depth</sub></b>	<b>RSS<sub>air</sub></b>	<b>df<sub>depth</sub></b>	<b>df<sub>air</sub></b>	<b><math>\sigma^2</math></b>	<b>Calculated F</b>	<b>F statistic</b>	<b>p-value</b>
1990 data	0.019	0.038	13	17	0.0015	3.25	3.18	0.012
1991 data	0.040	0.043	20	23	0.0020	0.50	3.10	0.939
1994 data	0.032	0.103	19	27	0.0017	5.27	2.48	0.000
1995 data	0.057	0.064	26	30	0.0022	0.80	2.74	0.718
1990 and 1991 data	0.077	0.085	41	45	0.0019	1.06	2.60	0.417
1994 and 1995 data	0.069	0.080	32	39	0.0022	0.73	2.31	0.820
Montague Is. data	0.091	0.105	45	53	0.0020	0.87	2.15	0.689

**Table 35.** Summary of  $R^2$  values for analysis of covariance of  $\ln(\text{egg abundance})$  data. Models using habitat variables and models using only depth and transect are compared.

<b>Data Set</b>	<b><math>R^2</math> for Multiple Habitat Variables</b>	<b><math>R^2</math> for Depth &amp; Transect only</b>
1990 data (all substrates)	0.436	0.412
1991 data (rocky only)	0.411	0.476
1994 data (all substrates)	0.406	0.456
1995 data (rocky only)	0.580	0.662
1990 and 1991 data (all substrates)	0.421	0.413
1994 and 1995 data (rocky and boulder only)	0.538	0.628
Montague Is. data (rocky and boulder only)	0.481	0.578
<b>Average</b>	<b>0.468</b>	<b>0.518</b>
<b>SE</b>	<b>0.026</b>	<b>0.039</b>

**Table 36.** Summary of  $R^2$  values for the models of egg loss rates resulting from factorial analyses of each data set.

<b>Data Set</b>	<b>Habitat variables contained in model</b>	<b><math>R^2</math></b>
1990 data (rocky only)	Oiled/unoiled Wave exposure Depth	0.854
1991 data (rocky only)	Wave exposure Depth	0.653
1994 data (all substrates)	Bird*depth Depth	0.736
1995 data (rocky only)	Depth	0.539
1990 and 1991 data (rocky and boulder only)	Year*oiled/unoiled Oiled/unoiled Wave exposure Depth Year	0.734
1994 and 1995 data (rocky data only)	Depth	0.524
Montague Is. data (rocky data only)	Year Wave exposure Depth	0.715
	<b>Average</b>	<b>0.679</b>
	<b>SE</b>	<b>0.041</b>

**Table 37.** Summary of  $R^2$  values for each data set for models of egg loss rates containing only depth as an explanatory variable.

<b>Data Set</b>	<b>Habitat variable contained in model</b>	<b><math>R^2</math></b>
1990 data (rocky only)	Depth	0.418
1991 data (rocky only)	Depth	0.227
1994 data (all data)	Depth	0.211
1995 data (rocky only)	Depth	0.539
1990 and 1991 data (rocky and boulder only)	Depth	0.178
1994 and 1995 data (rocky data only)	Depth	0.524
Montague Is. data (rocky data only)	Depth	0.308
	<b>Average</b>	<b>0.344</b>
	<b>SE</b>	<b>0.057</b>

**Table 38.** Summary of  $R^2$  values for each data set for models of egg loss rates containing only air exposure as an explanatory variable.

<b>Data Set</b>	<b>Habitat variables contained in model</b>	<b><math>R^2</math></b>
1990 data (rocky only)	Air exposure	0.189
1991 data (rocky only)	Air exposure	0.181
1994 data (all substrates)	Air exposure	0.149
1995 data (rocky only)	Air exposure	0.486
1990 and 1991 data (rocky and boulder only)	Air exposure	0.118
1994 and 1995 data (rocky data only)	Air exposure	0.451
Montague Is. data (rocky data only)	Air exposure	0.222
	<b>Average</b>	<b>0.257</b>
	<b>SE</b>	<b>0.056</b>

**Table 39.** Summary of  $R^2$  values for each data set for models of egg loss rates containing transect and depth as explanatory variables.

<b>Data Set</b>	<b>Habitat variables contained in model</b>	<b><math>R^2</math></b>
1990 data (rocky only)	Depth Transect	<b>0.921</b>
1991 data (rocky only)	Depth Transect	<b>0.716</b>
1994 data (all substrates)	Depth Transect	<b>0.512</b>
1995 data (rocky only)	Depth Transect	<b>0.800</b>
1990 and 1991 data (rocky and boulder only)	Depth Transect	<b>0.807</b>
1994 and 1995 data (rocky data only)	Depth Transect	<b>0.776</b>
Montague Is. data (rocky data only)	Depth Transect	<b>0.854</b>
	<b>Average</b>	<b>0.769</b>
	<b>SE</b>	<b>0.052</b>



**Table 40.** Parameter estimates of depth and air exposure models for each data set.

Data Set	Egg Loss Rates at Depth		Air exposure parameters	
	Depth	-Z (SE)		
1990 data (rocky only)	-30	0.002 (0.005)	Constant (SE)	-0.0568 (0.0184)
	-15	-0.015 (0.022)	Slope (SE)	-0.0006 (0.0003)
	-5	-0.056 (0.035)		
	0	-0.112 (0.034)		
	1	-0.126 (0.043)		
	5	-0.171 (---)		
1991 data (rocky only)	-15	-0.026 (-0.029)	Constant (SE)	0.0238 (0.0147)
	-5	-0.015 (0.012)	Slope (SE)	0.0004 (0.0002)
	0	-0.038 (0.025)		
	1	-0.046 (0.025)		
	5	-0.124 (0.074)		
1994 data (all substrates)	-10	-0.086 (0.009)	Constant (SE)	0.0809 (0.0130)
	-3	-0.090 (0.012)	Slope (SE)	0.0004 (0.0002)
	-2	-0.058 (0.044)		
	0	-0.064 (0.102)		
	2	-0.121 (0.026)		
	3	-0.160 (0.028)		
1995 data (rocky only)	-5	-0.034 (0.027)	Constant (SE)	0.0524 (0.0115)
	-1	-0.063 (0.018)	Slope (SE)	0.0006 (0.0001)
	0	-0.073 (0.025)		
	1	-0.110 (0.017)		
	3	-0.122 (0.011)		
	5	-0.178 (0.021)		

**Table 40 (continued).** Parameter estimates of depth and air exposure models for each data set.

Data Set	Egg Loss Rates at Depth		Air exposure parameters	
	Depth	-Z (SE)		
1990 and 1991 data (rocky and boulder only)	-30	0.002 (0.005)	Constant (SE)	0.0530 (0.0100)
	-15	-0.032 (0.019)	Slope (SE)	0.0003 (0.0001)
	-5	-0.044 (0.019)		
	0	-0.074 (0.021)		
	1	-0.087 (0.024)		
	5	-0.136 (0.051)		
	1994 and 1995 data (rocky data only)	-10	-0.092 (0.016)	Constant (SE)
-5		-0.034 (0.027)	Slope (SE)	0.0005 (0.0001)
-3		-0.089 (0.018)		
-1		-0.063 (0.018)		
0		-0.073 (0.025)		
1		-0.110 (0.017)		
2		-0.135 (—)		
3		-0.137 (0.016)		
5		-0.178 (0.021)		
Montague Is. data (rocky data only)	-15	0.004 (0.036)	Constant (SE)	0.0676 (0.0092)
	-10	-0.092 (0.016)	Slope (SE)	0.0004 (0.0001)
	-5	-0.044 (0.022)		
	-3	-0.089 (0.018)		
	-1	-0.063 (0.018)		
	0	-0.069 (0.026)		
	1	-0.100 (0.026)		
	2	-0.135 (—)		
	3	-0.137 (0.016)		
5	-0.155 (0.029)			

**Table 41.** Results of analysis of covariance to determine the effect of wave energy on egg abundance. Changes in egg abundance between sampling visits was regressed against average wave energy per day between sampling visits.

**Analysis of Covariance**

Dependent Variable: Change in Ln(egg abundance) between sampling visits

N: 369

Multiple R: 0.590

Squared Multiple R: 0.348

Source	Sum of Squares	DF	MSE	F-Ratio	P
Regression	181.094*10 <sup>10</sup>	1	181.094*10 <sup>10</sup>	195.828	0.000
Error	339.387*10 <sup>10</sup>	367	0.924760*10 <sup>10</sup>		

**Table 42.** Results of analysis of covariance to determine the effect of high or low wave energy levels on egg abundance.

**Analysis of Covariance**

Dependent Variable: Change in Ln(egg abundance) between sampling visits

N: 369

Multiple R: 0.592

Squared Multiple R: 0.351

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>Mean Square</b>	<b>F-Ratio</b>	<b>P</b>
High energy/low energy	182.447*10 <sup>10</sup>	1	182.447*10 <sup>10</sup>	198.080	0.000
Error	338.034*10 <sup>10</sup>	367	0.92104*10 <sup>10</sup>		

**Appendix A.** Results of factorial analyses of subsets of each years data. Tables contained in this appendix summarize analyses not resulting in the best egg loss model.

Table A-1. Results of factorial analysis of egg loss rate (Z) for 1990 data from all substrates and all depths.

Table A-2. Results of factorial analysis of egg loss rates (Z) for 1990 data from rocky and boulder substrates, with all depths.

Table A-3. Results of factorial analysis of egg loss rates (Z) for 1990 data from all substrates, with the -30 foot depth removed.

Table A-4. Results of factorial analysis of egg loss rates (Z) for 1990 data from rocky and boulder substrates, with the -30 foot depth removed.

Table A-5. Results of factorial analysis of egg loss rates (Z) for 1990 data from the rocky substrate, with the -30 foot depth removed.

Table A-6. Results of factorial analysis of egg loss rates (Z) for 1990 data from all substrates, with the -30 and +5 foot depths removed.

Table A-7. Results of factorial analysis of egg loss rates (Z) for 1990 data from rocky and boulder substrates, with the -30 and +5 foot depths removed.

Table A-8. Results of factorial analysis of egg loss rates (Z) for 1990 data from the rocky substrate, with the -30 and +5 foot depths removed.

Table A-9. Results of factorial analysis of egg loss rates (Z) for 1990 data from all substrates with the depth variable replaced by air exposure.

Table A-10. Results of factorial analysis of egg loss rates (Z) for 1990 data from the rocky and boulder substrates, with air exposure in the place of depth.

Table A-11. Results of factorial analysis of egg loss rates (Z) for 1991 data, with the +5 foot depth excluded.

Table A-12. Results of factorial analysis of egg loss rates (Z) for the 1994 data from all substrates. Depths are combined into three categories.

Table A-13. Results of factorial analysis of egg loss rates (Z) for 1994 rocky and boulder data. Depths are combined into three categories.

Table A-14. Results of factorial analysis of egg loss rates (Z) for 1994 data from all substrates. Depths combined using similar times of air exposure.

Table A-15. Results of factorial analysis of egg loss rates (Z) for 1994 rocky and boulder data. Depths combined using similar times of air exposure.

Table A-16. Results of factorial analysis of egg loss rates (Z) for 1994 data from all substrates. Depths combined into closest 1990-1991 depth category.

Table A-17. Results of factorial analysis of egg loss rates (Z) for 1994 rocky and boulder data. Depths combined using closest depth category from 1990 and 1991.

Table A-18. Factorial analyses of egg loss rates from 1994 rocky and boulder substrates only. The two single depths were combined with closest neighbors into depth categories.

Table A-19. Factorial analyses of egg loss rates from 1994, with air exposure in the place of depth.

Table A-20. Factorial analyses of egg loss rates (Z) from 1994 rocky and boulder substrates only, with air exposure in the place of depth.

**Table A-1.** Results of factorial analysis of egg loss rate (Z) for 1990 data from all substrates and depths.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

n: 40

Multiple R: 0.772

Squared Multiple R: 0.595

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Kelp type*Substrate type	0.034	2	0.017	7.817	0.002
Oiled/Unoiled	0.070	1	0.070	32.471	0.000
Error	0.078	36	0.002		

**Table A-2.** Results of factorial analysis of egg loss rates (Z) for 1990 data from rocky and boulder substrates, with all depths.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

n: 25

Multiple R: 0.881

Squared Multiple R: 0.776

Source	Sum of Squares	DF	MSE	F-Ratio	P
Kelp type*Substrate type	0.030	1	0.030	19.810	0.000
Wave exposure	0.014	1	0.014	8.784	0.007
Oiled/Unoiled	0.049	1	0.049	10.833	0.004
Error	0.033	21	0.002		



**Table A-3.** Results of factorial analysis of egg loss rates (Z) for 1990 data from all substrates, with the -30 foot depth removed.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

n: 38

Multiple R: 0.752

Squared Multiple R: 0.566

Source	Sum of Squares	DF	MSE	F-Ratio	P
Substrate type*Kelp type	0.033	2	0.016	7.192	0.002
Oiled/Unoiled	0.066	1	0.066	29.039	0.000
Error	0.077	34	0.003		

**Table A-4.** Results of factorial analysis of egg loss rates (Z) for 1990 data from rocky and boulder substrates, with the -30 foot depth removed.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

n: 23

Multiple R: 0.866

Squared Multiple R: 0.750

Source	Sum of Squares	DF	MSE	F-Ratio	P
Kelp type*Substrate type	0.029	1	0.029	16.946	0.001
Wave exposure	0.014	1	0.014	8.026	0.011
Oiled/Unooled	0.069	1	0.069	39.925	0.000
Error	0.033	19	0.002		

**Table A-5.** Results of factorial analysis of egg loss rates (Z) for 1990 data from the rocky substrate, with the -30 foot depth removed.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

n: 19

Multiple R: 0.916

Squared Multiple R: 0.839

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Oiled/Unoled	0.057	1	0.057	35.890	0.000
Wave exposure	0.016	1	0.016	10.229	0.008
Depth	0.041	4	0.010	6.422	0.005
Error	0.019	12	0.002		

**Table A-6.** Results of factorial analysis of egg loss rates (Z) for 1990 data from all substrates, with the -30 and +5 foot depths removed.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

n: 34

Multiple R: 0.728

Squared Multiple R: 0.530

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Kelp type*Substrate type	0.029	2	0.015	5.851	0.007
Oiled/Unooled	0.056	1	0.056	22.251	0.000
Error	0.075	30	0.003		

**Table A-7.** Results of factorial analysis of egg loss rates (Z) for 1990 data from rocky and boulder substrates, with the -30 and +5 foot depths removed.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

n: 22

Multiple R: 0.874

Squared Multiple R: 0.764

Source	Sum of Squares	DF	MSE	F-Ratio	P
Substrate type*Kelp type	0.025	1	0.025	15.093	0.001
Wave exposure	0.017	1	0.017	10.432	0.005
Oiled/Unooled	0.069	1	0.069	42.091	0.000
Error	0.030	18	0.002		

**Table A-8.** Results of factorial analysis of egg loss rates (Z) for 1990 data from the rocky substrate, with the -30 and +5 foot depths removed.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

n: 18

Multiple R: 0.909

Squared Multiple R: 0.826

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Oiled/Unooled	0.057	1	0.057	35.890	0.000
Wave exposure	0.016	1	0.016	10.229	0.008
Depth	0.033	3	0.011	6.896	0.006
Error	0.019	12	0.002		

**Table A-9.** Results of factorial analysis of egg loss rates (Z) for 1990 data from all substrates with the depth variable replaced by air exposure.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

n: 40

Multiple R: 0.800

Squared Multiple R: 0.639

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Substrate type*Air exposure	0.042	2	0.021	10.503	0.00
Wave exposure*Air exposure	0.030	1	0.030	15.061	0.00
Oiled/Unoiled	0.094	1	0.094	47.309	0.000
Error	0.069	35	0.002		

**Table A-10.** Results of factorial analysis of egg loss rates (Z) for 1990 data from the rocky and boulder substrates, with air exposure in the place of depth.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

n: 25

Multiple R: 0.923

Squared Multiple R: 0.851

Source	Sum of Squares	DF	MSE	F-Ratio	P
Kelp type*Substrate type	0.023	1	0.023	19.969	0.000
Wave exposure*Air exposure	0.063	1	0.063	54.150	0.000
Oiled/unoiled*Kelp type	0.032	1	0.032	27.315	0.000
Wave exposure*Kelp type	0.015	1	0.015	12.919	0.002
Oiled/Unoiled*Air exposure	0.082	1	0.082	70.796	0.000
Error	0.022	19	0.001		



**Table A-11.** Results of factorial analysis of egg loss rates (Z) for 1991 data, with the +5 foot depth excluded.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

n: 23

Multiple R: 0.785

Squared Multiple R: 0.616

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Wave exposure	0.039	1	0.039	33.708	0.000
Error	0.024	21	0.001		

**Table A-12** Results of factorial analysis of egg loss rates (Z) for the 1994 data from all substrates. Depths are combined into three categories.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

n: 30

Multiple R: 0.767

Squared Multiple R: 0.589

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Depth (three catagories)*Bird abundance	0.020	2	0.010	4.898	0.016
Depth (three catagories)	0.023	2	0.012	5.665	0.010
Gull abundance	0.013	1	0.013	6.297	0.019
Error	0.050	24	0.002		

**Table A-13.** Results of factorial analysis of egg loss rates (Z) for 1994 rocky and boulder data. Depths are combined into three categories.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

n: 21

Multiple R: 0.722

Squared Multiple R: 0.522

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Gull abundance*Depth (three catagories)	0.015	1	0.015	14.955	0.001
Gull abundance	0.008	1	0.008	7.782	0.012
Error	0.018	18	0.001		

**Table A-14.** Results of factorial analysis of egg loss rates (Z) for 1994 data from all substrates. Depths combined using similar times of air exposure.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

n: 30

Multiple R: 0.623

Squared Multiple R: 0.388

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Kelp type*Wave exposure	0.016	1	0.016	5.79	0.023
Gull abundance	0.022	1	0.022	8.155	0.008
Error	0.074	27	0.003		

**Table A-15.** Results of factorial analysis of egg loss rates (Z) for 1994 rocky and boulder data. Depths combined using similar times of air exposure.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

n: 21

Multiple R: 0.681

Squared Multiple R: 0.463

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Depth	0.018	2	0.009	7.768	0.004
Error	0.020	18	0.001		



**Table A-17.** Results of factorial analysis of egg loss rates (Z) for 1994 rocky and boulder data. Depths combined using closest depth category from 1990 and 1991.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

n: 21

Multiple R: 0.681

Squared Multiple R: 0.463

Source	Sum of Squares	DF	MSE	F-Ratio	P
Depth	0.018	2	0.009	7.768	0.004
Error	0.020	18	0.001		

**Table A-18.** Factorial analyses of egg loss rates from 1994 rocky and boulder substrates only. The two single depths were combined with closest neighbors into depth categories.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

n: 21

Multiple R: 0.686

Squared Multiple R: 0.471

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Depth (closest neighbor)	0.018	3	0.006	5.045	0.011
Error	0.020	17	0.001		



**Table A-19.** Factorial analyses of egg loss rates from 1994, with air exposure in the place of depth.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

n: 21

Multiple R: 0.673

Squared Multiple R: 0.453

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Air exposure*Kelp type	0.017	1	0.017	15.739	0.001
Error	0.021	19	0.001		

**Table A-20.** Factorial analyses of egg loss rates (Z) from 1994 rocky and boulder substrates only, with air exposure in the place of depth.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

n: 30

Multiple R: 0.785

Squared Multiple R: 0.617

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Air exposure*Wave exposure	0.035	1	0.035	19.577	0.000
Air exposure*Kelp type	0.049	1	0.049	27.327	0.000
Air exposure	0.026	1	0.026	14.556	0.001
Error	0.046	26	0.002		

**Appendix B.** Results of factorial analyses of subsets of combined years data. Tables contained in this appendix summarize analyses not resulting in the best egg loss model.

Table B-1. Results of factorial analysis of egg loss rates (Z) for combined 1990 and 1991 data from all substrates.

Table B-2. Results of factorial analysis of egg loss rates for 1990 and 1991 combined data from the rocky substrate.

Table B-3. Results of factorial analysis of 1990 and 1991 combined egg loss rates from all substrates, with depth replaced by air exposure.

Table B-4. Results of factorial analysis of 1990 and 1991 combined egg loss rates from the rocky and boulder substrates. For this analysis depth was replaced by air exposure.

Table B-5. Results of factorial analysis of combined 1990 and 1991 egg loss rates from the rocky substrate. For this analysis depth was replaced with air exposure.

Table B-6. Results of factorial analysis of combined 1994 and 1995 egg loss rates from rocky and boulder substrates.

Table B-7. Results of factorial analysis of combined 1994 and 1995 egg loss rates (Z) from all substrates.

Table B-8. Results of factorial analysis of combined 1994 and 1995 egg loss rates from the rocky substrate only. For this analysis depth is replaced with air exposure.

Table B-9. Results of factorial analysis of combined 1994 and 1995 data from all substrates. For this analysis depth was replaced by air exposure.

Table B-10. Results of factorial analysis of combined Montague Island egg loss rates from all substrates.

Table B-11. Results of factorial analysis of combined Montague Island egg loss rates from rocky and boulder substrates.

Table B-12. Results of factorial analysis of combined Montague Island egg loss rates from all substrates. For this analysis depth was replaced by air exposure.

Table B-13. Results of factorial analysis of combined Montague Island egg loss rates from rocky and boulder substrates. For this analysis depth was replaced by air exposure.

**Table B-1.** Results of factorial analysis of egg loss rates (Z) for combined 1990 and 1991 data from all substrates.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

n: 66

Multiple R: 0.765

Squared Multiple R: 0.586

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Oiled/Unooled*Year	0.056	1	0.056	24.317	0.000
Substrate type*Kelp type	0.044	2	0.022	9.453	0.000
Wave exposure	0.013	1	0.013	5.669	0.021
Oiled/unooled	0.010	1	0.010	4.204	0.045
Year	0.012	1	0.012	5.018	0.029
Error	0.136	59	0.002		

**Table B-2.** Results of factorial analysis of egg loss rates for 1990 and 1991 combined data from the rocky substrate.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

n: 47

Multiple R: 0.852

Squared Multiple R: 0.726

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Oiled/unoiled*Year	0.045	1	0.045	23.315	0.000
Kelp type*Year	0.011	1	0.011	5.562	0.024
Wave exposure	0.049	1	0.049	25.564	0.000
Depth	0.054	5	0.011	5.681	0.001
Oiled/Unoiled	0.034	1	0.034	17.840	0.000
Error	0.071	37	0.002		

**Table B-3.** Results of factorial analysis of 1990 and 1991 combined egg loss rates from all substrates, with depth replaced by air exposure.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

n: 66

Multiple R: 0.808

Squared Multiple R: 0.652

<u>Source</u>	<u>Sum of Squares</u>	<u>DF</u>	<u>MSE</u>	<u>F-Ratio</u>	<u>P</u>
Oiled/unoiled*Year	0.031	1	0.031	15.557	0.000
Year*Air exposure	0.018	1	0.018	9.104	0.004
Substrate type*Air exposure	0.068	2	0.034	17.209	0.000
Wave exposure*Air exposure	0.012	1	0.012	6.359	0.014
Wave exposure	0.031	1	0.031	15.918	0.000
Oiled/unoiled	0.033	1	0.033	16.935	0.000
Error	0.114	58	0.002		

**Table B-4.** Results of factorial analysis of 1990 and 1991 combined egg loss rates from the rocky and boulder substrates. For this analysis depth was replaced by air exposure.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

n: 51

Multiple R: 0.874

Squared Multiple R: 0.764

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Oiled/Unoiled*Year	0.046	1	0.046	28.910	0.000
Kelp type*Substrate type	0.012	1	0.012	7.536	0.009
Kelp type*Year	0.007	1	0.007	4.336	0.043
Air exposure	0.020	1	0.020	12.728	0.001
Wave exposure	0.037	1	0.037	23.398	0.000
Year	0.008	1	0.008	4.981	0.031
Oiled/unoiled	0.026	1	0.026	16.236	0.000
Error	0.068	43	0.002		



**Table B-5.** Results of factorial analysis of combined 1990 and 1991 egg loss rates from the rocky substrate. For this analysis depth was replaced with air exposure.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

n: 47

Multiple R: 0.850

Squared Multiple R: 0.723

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Oiled/unoiled*Year*Air exposure	0.030	1	0.030	15.339	0.000
Wave exposure*Year*Air exposure	0.027	1	0.027	13.893	0.001
Wave exposure*Year	0.030	1	0.030	15.329	0.000
Wave exposure*Kelp type	0.015	1	0.015	7.744	0.008
Oiled/unoiled*Air exposure	0.061	1	0.061	31.771	0.000
Wave exposure*Air exposure	0.068	1	0.068	35.216	0.000
Oiled/unoiled*Kelp type	0.025	1	0.025	12.961	0.001
Air exposure	0.025	1	0.025	13.098	0.001
Year	0.011	1	0.011	5.517	0.024
Error	0.072	37	0.002		

**Table B-6.** Results of factorial analysis of combined 1994 and 1995 egg loss rates from rocky and boulder substrates.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

n: 53                      Multiple R: 0.712              Squared Multiple R: 0.506

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Depth	0.083	8	0.010	5.641	0.000
Error	0.080	44	0.002		

**Table B-7.** Results of factorial analysis of combined 1994 and 1995 egg loss rates (Z) from all substrates.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

n: 62                      Multiple R: 0.603                      Squared Multiple R: 0.363

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Depth	0.089	9	0.010	3.296	0.003
Error	0.156	52	0.003		

**Table B-8.** Results of factorial analysis of combined 1994 and 1995 egg loss rates from the rocky substrate only. For this analysis depth is replaced with air exposure.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

n: 41                      Multiple R: 0.711                      Squared Multiple R: 0.505

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Year	0.008	1	0.008	4.120	0.049
Air exposure	0.071	1	0.071	37.567	0.000
Error	0.072	38	0.002		

**Table B-9.** Results of factorial analysis of combined 1994 and 1995 data from all substrates. For this analysis depth was replaced by air exposure.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

n: 62                      Multiple R: 0.537                      Squared Multiple R: 0.289

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Air exposure	0.071	1	0.071	24.366	0.000
Error	0.174	60	0.003		

**Table B-10** Results of factorial analysis of combined Montague Island egg loss rates from all substrates.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

n: 91                      Multiple R: 0.462                      Squared Multiple R: 0.214

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Year	0.130	3	0.043	7.881	0.000
Error	0.477	87	0.005		

**Table B-11.** Results of factorial analysis of combined Montague Island egg loss rates from rocky and boulder substrates.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

n: 75

Multiple R: 0.834

Squared Multiple R: 0.695

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Year	0.075	3	0.025	14.136	0.000
Wave exposure	0.018	1	0.018	10.216	0.002
Depth	0.103	9	0.011	6.506	0.000
Error	0.107	61	0.002		

**Table B-12.** Results of factorial analysis of combined Montague Island egg loss rates from all substrates. For this analysis depth was replaced by air exposure.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

n: 91

Multiple R: 0.667

Squared Multiple R: 0.445

Source	Sum of Squares	DF	MSE	F-Ratio	P
Wave exposure*Kelp type	0.030	1	0.030	6.909	0.010
Substrate type*Air exposure	0.117	4	0.029	6.788	0.000
Kelp type*Year	0.044	3	0.015	3.408	0.022
Wave exposure	0.052	1	0.052	12.091	0.001
Year	0.117	3	0.039	9.050	0.000
Error	0.337	78	0.004		



**Table B-13.** Results of factorial analysis of combined Montague Island egg loss rates from rocky and boulder substrates. For this analysis depth was replaced by air exposure.

**Analysis of Variance**

Dependent Variable: Instantaneous Egg Loss Rate, Z

n: 75                      Multiple R: 0.808                      Squared Multiple R: 0.653

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Year	0.116	3	0.039	21.849	0.000
Wave exposure	0.020	1	0.020	11.130	0.001
Air exposure	0.088	1	0.088	49.994	0.000
Error	0.122	69	0.002		

## **Appendix C. Predator Exclusion Devices**

### **Introduction**

This appendix reports the results of predator exclusion experiments conducted at egg loss transects in 1994 and 1995. These experiments were designed to measure the effects of bird predation on egg loss using treatment and control plots, with the objective of measuring the amount of eggs lost due to bird predation.

### **Methods**

In 1994 and 1995 predator exclusion devices were installed at all egg loss sites. The devices were designed to prevent large predators, specifically birds, from feeding on eggs within the frame. The devices consisted of netting stretched between the sides of a PVC frame to form a box open on one side. The frames were installed with the open side down on patches of vegetation with attached eggs. Control sites were established at the same depth on nearby patches of eggs. In 1994 predator exclusion frames and controls were installed at all depths at each egg loss transect, while in 1995 frames and controls were installed at the +5 foot, +1 foot and -1 foot depths only. The predator exclusion frames were permanently anchored to the substrate using a combination of rebar and large nails, and the area covered by the frames was the same as two standard 1 m<sup>2</sup> quadrats. The control sites were marked by rebar, so that two standard 1 m<sup>2</sup> quadrats could be placed over the same patch of eggs each time the site was visited. Eggs were counted during each sampling visit in both the controls and predator exclusion devices to determine the rate of egg loss over time.

In 1994 observations of the absence or presence of potential predators in and around both the control and exclusion frames were recorded. These predators ranged from birds (mostly Glaucous winged gulls) to invertebrates (snails, crabs, etc.) to fishes (greenlings, blennies, etc.). Since most of these individual predators were recorded only once or twice during sampling, a categorical variable was used in the data analysis. The categorical variable was either predator present or predator absent, and was used in the analysis of covariance performed on the 1994 predator data.

The data collected in each year was analyzed separately because of the different depths, and sampling techniques employed between years. Analysis of covariance predicting egg abundance over time was performed on each individual year of data. In 1994 three factors were used in the ANCOVA, the previously mentioned absence/presence of predator, treatment (either control or exclusion frame) and depth. In 1995 only two factors and their interaction term were available, depth and treatment.

## **Results**

In 1994 three variables were available for analysis; the treatment condition, depth and whether predators were observed or not observed at the site during sampling. An analysis of covariance predicting  $\ln(\text{egg abundance})$  with days since spawn as the covariate was performed with the three other variables. The results show all interaction terms: treatment\*predator, treatment\*depth and depth\*predator as well as all variables: depth, treatment and predator were significant with the covariate term explaining the most

variability in the data set (Table C-1). The analysis explains 45.4% of the variability in  $\ln(\text{egg abundance})$ .

Another analysis of covariance was also performed on the 1994 data, excluding the predator absence/presence term and examining only the treatment and control effects (Table C-2). Only depth and days since spawn were significant in this analysis, with treatment and treatment\*depth being insignificant. Again days since spawn explained most of the variability in  $\ln(\text{egg abundance})$ ; however, the analysis itself explained only 29.7% of the variability.

The analysis of covariance of the 1995 predator exclusion frame contained two significant terms, depth and the covariate days (Table C-3). The treatment term and the interaction term were both highly insignificant ( $p > 0.50$ ). The entire model explained only 10.9 % of the variability within the data set.

## **Discussion**

The most interesting result of the predator exclusion experiment is that there is not a significant difference in egg loss over time between the two treatments in either years. If large predators such as birds are important contributors to herring egg loss, the opposite result would have been predicted.

Egg loss caused by avian predation on Pacific herring eggs has been documented by previous exclusion experiments (Steinfeld, 1971). The fact that birds feed on herring eggs throughout the incubation period is confirmed by the stomach contents recovered in the avian predation component of the egg loss study. However, the intensity of the predation

may not be enough to offset the large abundance of herring eggs deposited. The quantity of total consumption by birds may make up only a fraction of the total deposits, making the effect undetectable in the analysis.

Another possible explanation for the lack of a significant treatment effect is that some other mechanism such as wave action, or predation by small predators may be affecting egg loss. The effects of bird predation may be lost in the presence of a force with a larger contribution to egg loss.

The other possibility is that the predator exclusion devices did not function correctly. The presence of the control, exclusion and decaquad frames in a relatively small area may have repelled predators from the entire site. However, the avian predation facet of the project recorded abundant birds at many of the transects, suggesting this did not occur. Another option is that the mesh of the exclusion frame netting was large enough so that the predators were able to enter or reach inside the exclusion devices. This may have been the case, however the effort required to reach into the exclusion device may have outweighed any possible gains from doing so since herring eggs were abundant throughout the egg loss sites as well as adjoining areas.

## **List of Tables**

Table C-1. Summary of analysis of covariance for 1994 predator exclusion frame data.

Table C-2. Summary of analysis of covariance for 1994 predator exclusion frames, excluding the predator present or absent variable.

Table C-3. Summary of analysis of covariance for 1995 predator exclusion frame data.

**Table C-2** Summary of analysis of covariance for 1994 predator exclusion frames, excluding the predator present or absent variable.

**Analysis of Covariance**

Dependent Variable: Ln(egg abundance)

N: 214

Multiple R: 0.522

Squared Multiple R: 0.272

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Treatment*Depth	12.227	5	2.445	1.713	0.133
Treatment	3.658	1	3.658	2.563	0.111
Depth	33.361	5	6.672	4.674	0.000
Days since spawn	72.002	1	72.002	50.440	0.000
Error	286.921	201	1.427		

**Table C-3.** Summary of analysis of covariance for 1995 predator exclusion frame data.

**Analysis of Covariance**

Dependent Variable: Ln(egg abundance)

N: 330

Multiple R: 0.327

Squared Multiple R: 0.107

<b>Source</b>	<b>Sum of Squares</b>	<b>DF</b>	<b>MSE</b>	<b>F-Ratio</b>	<b>P</b>
Treatment*Depth	2.018	2	1.009	0.285	0.752
Treatment	0.126	1	0.126	0.036	0.851
Depth	22.005	2	11.003	3.104	0.046
Days since spawn	115.998	1	115.998	32.728	0.000
Error	1144.817	323	3.544		