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An Egg-Loss Correction for Estimating Spawning Biomass of Pacific Herring in Prince William Sound, Alaska

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ABSTRACT: Spawning biomass of Pacific herring *Clupea pallasi* populations is commonly estimated from surveys that quantify their egg deposition. Because surveys occur after spawning, a correction for egg loss is required. We estimated this correction factor for the 1995 herring stock in Prince William Sound, Alaska, using an egg-loss model. The model was based on the cumulative time of exposure to air during egg incubation. The correction factor for the percentage of eggs lost between spawning and spawn-deposition surveys was estimated at 31% (SE = 2.2%). This value is much higher than the value previously assumed for Alaska stocks. Because interannual variability in the egg-loss correction may occur, we suggest that future spawn surveys be accompanied by egg-loss studies.

INTRODUCTION

The number of Pacific herring *Clupea pallasi* eggs spawned each year represents the full potential of recruits to the population in future years. Because environmental factors have been shown to influence herring recruitment (Wespestad 1991; Schweigert 1995; Zebdi and Collie 1995) the egg stage may be an important source of variation in recruitment if the number of eggs surviving to hatch is influenced by environmental conditions experienced during incubation.

Pacific herring spawn in intertidal and shallow subtidal habitats and have a demersal egg stage typically lasting from 14 to 21 d; consequently substantial egg removals may occur because of physical and biological influences. Significant egg removals have been attributed to wave action (Hart and Tester 1934; Hay and Miller 1982; Rooper 1996) and predation. Documented predators of Pacific herring eggs include birds (Cleaver and Franett 1946; Outram 1958; Steinfeld 1971; Haegele and Schweigert 1989; Haegele and Schweigert 1991), marine mammals (Haegele and Schweigert 1989), fish (Palsson 1984; Rooper 1996) and invertebrates (Haegele and Schweigert 1989; Haegele 1993).

Estimates of the number of eggs deposited are often used by management agencies to calculate the total spawning biomass of Pacific herring (Haegele et al. 1981; Biggs and Funk 1988). Egg numbers are typically estimated by scuba surveys of the spawning beds. Because these surveys occur from several days to a couple weeks after spawning, egg loss may reduce the biomass estimate, making a correction necessary to estimate egg biomass. A correction factor of 10% has previously been applied to Prince William Sound, Alaska, stocks (Biggs and Funk 1988). Recent herring research in Alaska and British Columbia suggests that egg loss is higher than previously thought and variable across years and sites (Blankenbeckler and Larson 1987; Biggs-Brown and Baker 1993; J. Schweigert, Pacific Biological Station, personal communication). The objective of this study was to improve the estimation of the biomass correction for Prince William Sound herring. We used an egg-loss model (Rooper 1996) based on cumulative time of air exposure to calculate egg-

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loss rates. From the egg-loss rate, we calculated the correction factor for egg deposition data in 1995.

METHODS

Alaska Department of Fish and Game personnel collected egg-loss data at 31 transects within herring spawning beds in Prince William Sound in 1990, 1991, 1994, and 1995. The data consisted of visual estimates, by scuba divers, of the number of eggs within permanently secured 0.1-m^2 quadrats. The quadrats were secured at 4–6 predetermined depths at each transect, and visual estimates were repeated every 2–5 d throughout incubation. To accurately describe the depth distribution and total abundance of spawn at each transect, a spawn-deposition survey was carried out at the same location as each 1995 egg-loss transect (Figure 1). For spawn-deposition surveys, divers visually estimated the number of eggs in 0.1-m^2 quadrats every 5 m along each transect, which extended perpendicularly from the beach. The methods for Prince William Sound spawn-deposition surveys are detailed in Biggs and Funk (1988). Visual estimates of egg numbers were calibrated for each diver before data analysis was undertaken (Biggs-Brown and Baker 1993).

Rooper (1996) developed an egg-loss model from this data based on habitat characteristics of the herring spawning beds. Habitat characteristics included depth, cumulative time of air exposure during incubation, location, substrate type, vegetation type, wave exposure, bird predation, and fish predation. The model presented in Rooper (1996) assumes that a constant proportion of eggs is lost over time. The number of eggs at the time of the spawn-deposition survey is

$$N_t = N_0 e^{-Zt} \quad , \tag{1}$$

where N_0 is the number of eggs at the time of spawning, Z is the instantaneous egg-loss rate, and t is the time in days since spawning occurred. Equation (1) is rewritten as

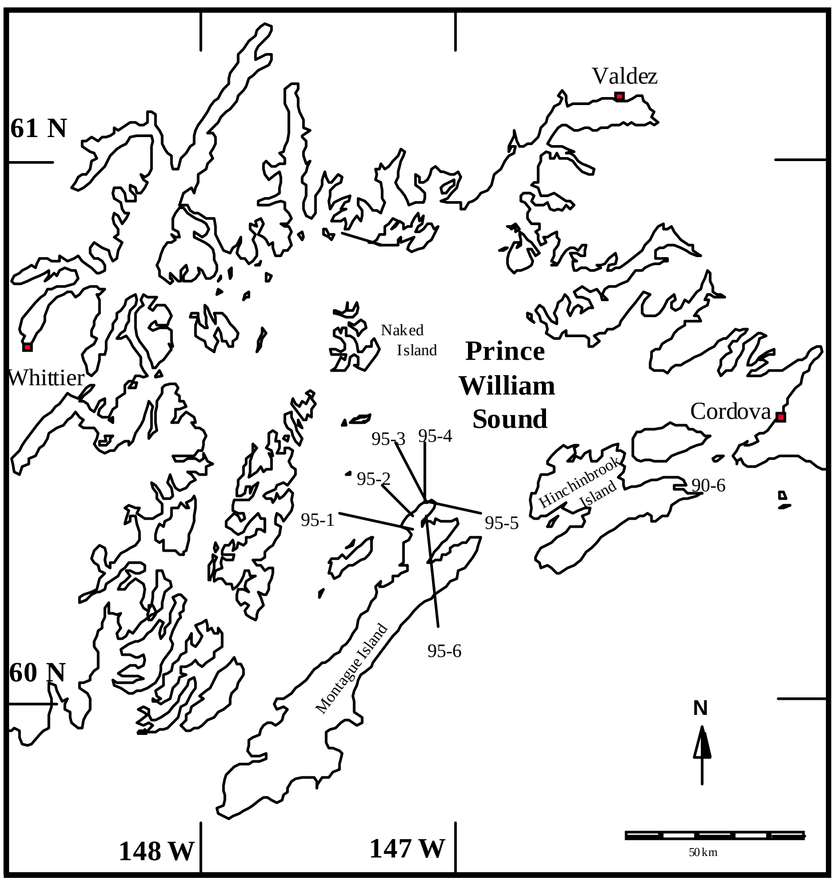

Figure 1. Prince William Sound, Alaska, showing location of egg-loss and spawn-deposition transects in 1990, 1991, 1994, and 1995.

$$N_0 = N_t e^{Zt} \quad , \qquad (2)$$

which provides an estimate of the number of eggs spawned. Evaluation of the egg-loss models presented in Rooper (1996) lead to the conclusion that cumulative time of air exposure was the most efficient way to predict egg-loss rates. Egg-loss rates for each time of air exposure could be calculated via linear regression. The egg-loss rate for each depth at which egg abundance was estimated during spawn-deposition surveys was calculated with the equation

$$Z_d = a + b \cdot AE_d \quad , \qquad (3)$$

where the independent variable, AE_d, is the cumulative time of air exposure over the egg incubation period at each depth and the parameter estimates are taken from Rooper (1996). Cumulative time of air exposure was determined from tide programs based on the date, time and depth of each tide stage during incubation (Tide1, Micronautics Inc.). At depths below -3.5 m mean low water, eggs were not exposed to air during incubation, thus AE_d is equal to zero.

Using equations (1–3) and the estimated number of eggs deposited from survey data, we estimated the original number of eggs deposited at transects in 1995. The number of eggs estimated at the time of the survey was then divided by the original number of eggs deposited to obtain the percentage of eggs lost at each depth.

RESULTS

We used 1995 egg-loss rates (Z) to estimate the parameters in equation (3); those rates ranged from -0.007 to 0.231 and averaged 0.096 (Figure 2). The parameters estimated in Rooper (1996) were a = 0.052357 and b = 0.000601. In 1995 the beginning of spawning ranged from April 27 to April 29, spawning at most transects beginning on April 28. The average time from the beginning of spawning to the spawn-deposition survey was 4.9 d and ranged from 4 to 7 d. The average time of the incubation period in 1995 was 21.1 d, ranging from 21 to 22 d. Based on the air-exposure model, 6.9% of the eggs were lost per day (SE = 0.53%) from the time of spawning to the time at which the spawn-deposition survey took place. This value ranged from 4.6% $\cdot$ d^{-1} at subtidal depths and no air exposure to 19.0% $\cdot$ d^{-1} at shallower depths and extensive air exposure (Figure 3). The average egg-loss es-

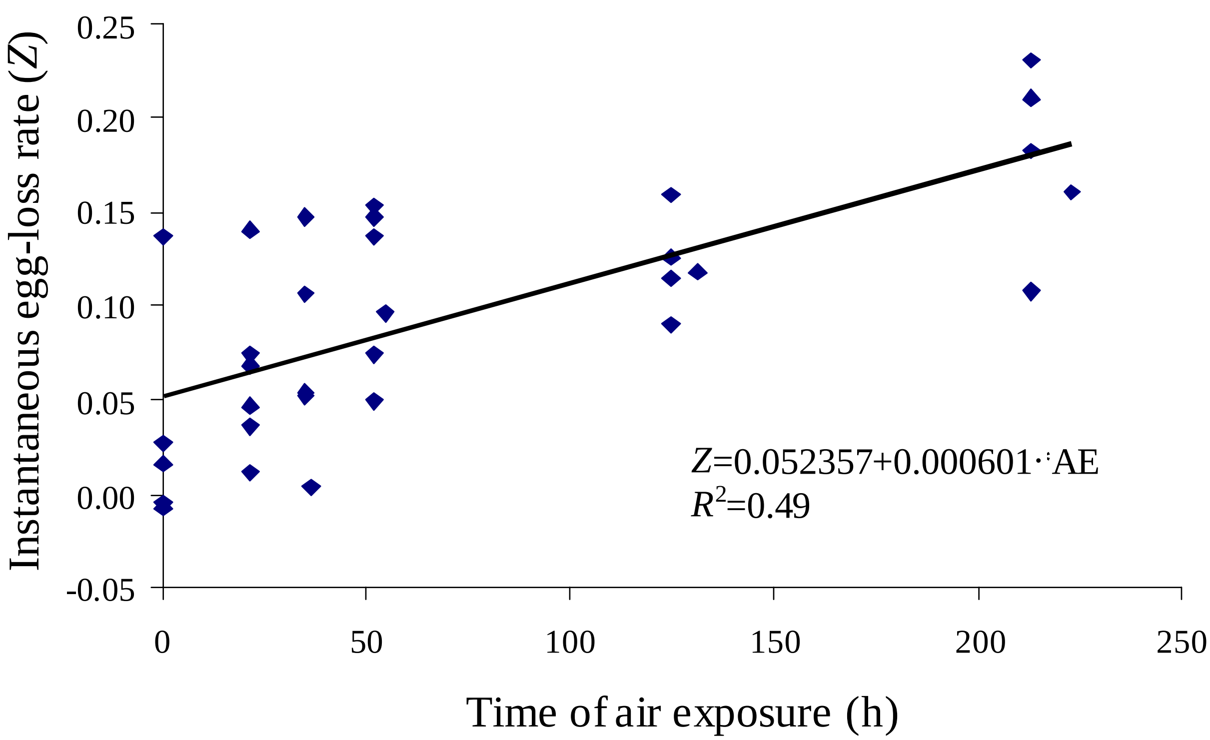

Figure 2. Regression of instantaneous egg-loss rate against cumulative time of air exposure during spawn incubation in 1995 (taken from Rooper 1996).

timate from the time of spawning until the survey was 31.0% (SE = 2.16%). This value ranged from 18.9% at deeper depths to 89.6% at the shallowest depths. Based on the original egg distribution, the majority of eggs lost were deposited in the region between 1.5 m and -5 m relative to mean low water (Figure 4).

DISCUSSION

The results of this study are based on a model by Rooper (1996), in which differences in egg loss arise from differences in time of air exposure of spawn, with higher egg-loss rates occurring at shallower depths. We applied the model to estimate a correction factor for survey-data estimates of the original abundance of herring eggs spawned. The average percentage of eggs lost from the time of spawning to the time of the survey in 1995 was estimated to be 31%. This is higher than the 10% egg loss estimated for Pacific herring in British Columbia (Haegele et al. 1981) and slightly higher than the 25% egg loss assumed for Southeast Alaska herring stocks (Blankenbeckler and Larson 1987). The egg-loss percentage is also much higher than the value of 10% currently used for management in Prince William Sound and higher than the range of values from 10 to 15% found previously for Prince William Sound (Biggs-Brown and Baker 1993). In their analysis Biggs-Brown and Baker (1993) excluded the highest depth station from their estimate of the correction factor. When that depth is included, their range of eggs lost from spawn to survey increases to 21–38%.

By using the time of air exposure from each depth where spawn is estimated during spawn-deposition surveys, it is possible to estimate an egg-loss rate at each 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 and depth data itself.

Air exposure is actually an indicator of other distinct processes, such as wave action and predation, which have variable effects at different depths. Gulls were the most common avian consumer of eggs in 1995 in Prince William Sound (M. A. Bishop and P. Green, U.S. Forest Service, Cordova, Alaska, unpublished data). Egg predation by gulls or other nondiving birds

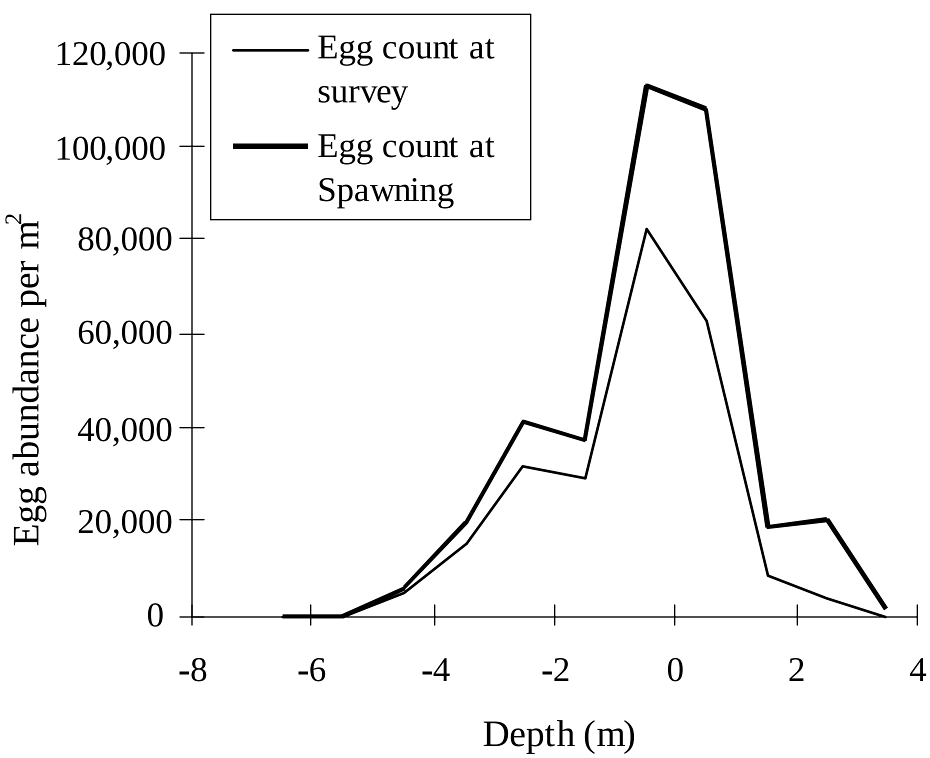

Figure 3. Percentage of eggs lost per day between the time of spawning and the time of spawn-deposition surveys in 1995; depth is relative to mean low water.

may be higher in the intertidal zone, where the eggs are accessible for longer periods, than in the subtidal zone, where eggs are never exposed. Wave action may also have varying effects on eggs at different depths; the crashing of waves may wash more eggs from beds in the intertidal zone than in the subtidal zone. The air exposure-based model is not meant to imply a specific mechanism for egg loss but instead seeks to represent a number of potential processes that are depth related.

To accurately estimate the herring biomass in Prince William Sound from spawn-deposition surveys, egg-loss studies should be carried out annually. The rationale for this recommendation is that interannual variability is likely to occur in the effects of ecological factors on egg loss, especially the occurrence of storms and the abundance of predators. To accurately estimate egg-loss rates, egg-loss studies also should fully represent the locations and environmental regimes found in the entire area covered by spawn. It is important to note that the relationship between air exposure and depth changes with both the length of the incubation period and with year because tides are different from year to year, depending on when spawning and hatching occur. For this reason it is important to know the relationship between time of air exposure and depth in each year, specific to the timing and duration of the herring egg-incubation period.

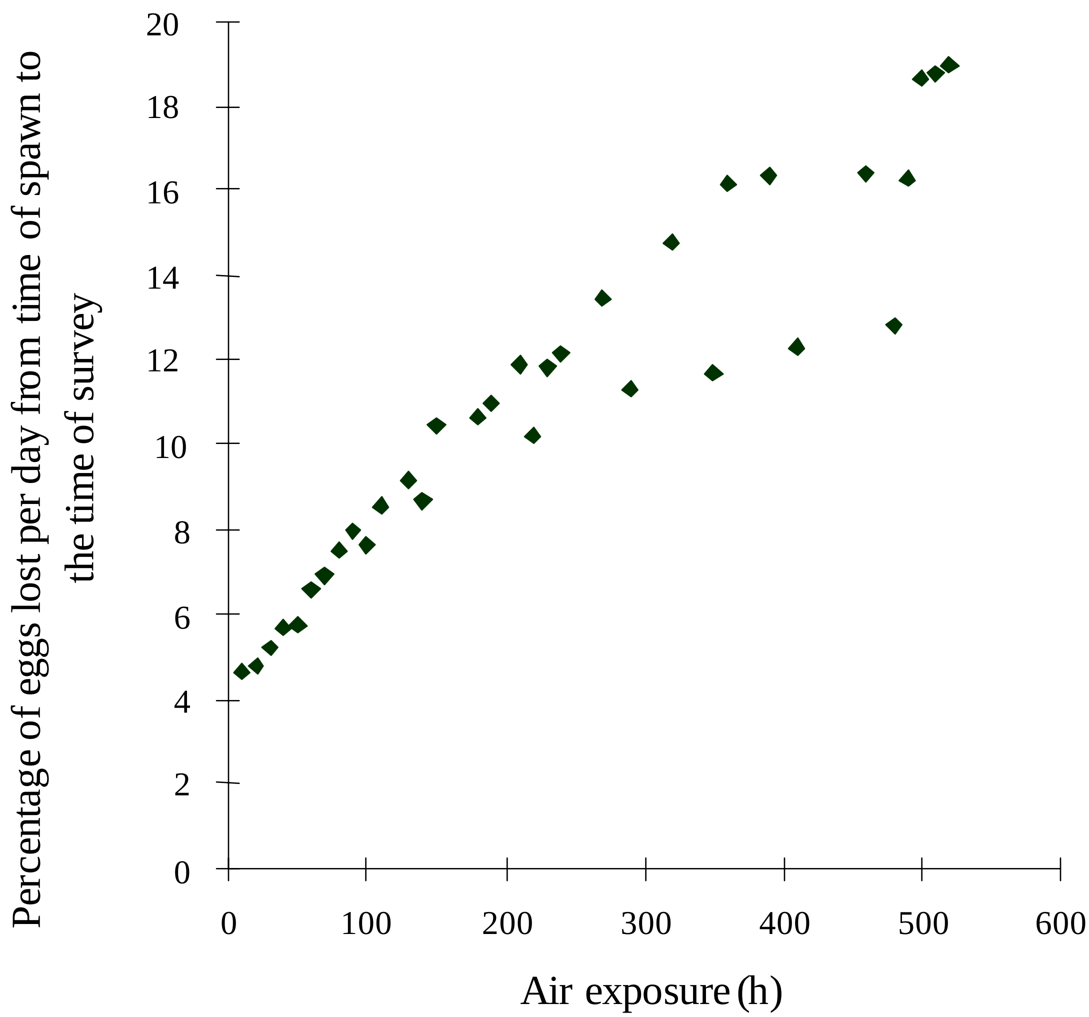

Figure 4. Depth distribution (0 = mean low tide) of eggs observed at the time of spawn-deposition survey and the number of eggs initially deposited, as predicted by the egg-loss model for 1995.

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