Quantifying the Magnitude and Mechanisms Driving Pacific Herring (*Clupea pallasi*) Egg Loss on the Central Coast of British Columbia, Canada

by

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B.Sc., University of British Columbia, 2009

Thesis Submitted in Partial Fulfillment of the
Requirements for the Degree of
Master of Resource Management

Report No. 568

in the
School of Resource and Environmental Management
Faculty of Environment

SIMON FRASER UNIVERSITY

Spring 2013

Approval

Name:	**Brittany Elizabeth Keeling**
Degree:	**Master of Resource and Environmental Management**
Report No.:	**568**
Title of Thesis:	***Quantifying the Magnitude and Mechanisms Driving Pacific Herring (Clupea pallasi) Egg Loss on the Central Coast of British Columbia, Canada***
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Abstract

Pacific herring (*Clupea pallasi*) play a fundamental ecological and socio-economic role in marine ecosystems and have exhibited declining trends in British Columbia, Canada, over the past decade. The rate of herring egg loss following spawning events is a key parameter used to estimate population productivity, however, it is highly uncertain. We quantified the magnitude, spatial variation and mechanisms driving egg loss along BC's Central Coast using observational surveys and an experiment. Depending on the modeling approach, we estimated regional egg loss rates (Z) ranging from 0.152 ± 0.022 to 0.177 ± 0.027, the equivalent of 59-75% eggs loss over 6.8 days, the average lag between spawn deposition and survey. Loss rates varied 4.5 fold among sites. Spawn area was found to positively influence egg loss rates based on our observational study, while evidence from our experiment suggests that predation and habitat type were strong drivers of loss. Modeling approach, parameter uncertainty, and site-level variability in egg loss rates need to be accounted for when estimating Pacific herring abundance and its associated uncertainty.

Keywords: Pacific herring; forage fish; egg loss rate; fisheries management; Central Coast; predation

Acknowledgements

Without the amazing guidance of a fantastic committee my work would be nowhere near the level it is today. Thank you to Jon Moore for providing extremely valuable feedback over the past two years. I am so grateful to have had Margot Hessing-Lewis on my team. Margot, you have been instrumental throughout the entire process, from field work to final draft, and more than I could have asked for as a mentor and friend. A big thank you to Anne Salomon for introducing me to this project; one that has exposed me to more than I ever would have expected when I first started. Anne, your continued enthusiasm and interest have been absolutely inspiring, and for this, and much more, I am so very thankful.

I have had the privilege of working with amazing Heiltsuk people of Bella Bella who have welcomed me into their territory and community, guided my research questions, and facilitated my work in the field. A special thanks to our invaluable captain, Clark Housty, as well as members of the Heiltsuk Integrated Resource Management Department, the Gladstone Reconciliation Team, Cal Humchitt, and the remaining Heiltsuk community. I have had the pleasure of conducting two amazing field seasons, both with great field crews that made the process more successful and enjoyable than I could have hoped. Stefan Dick, Ryan Cloutier, Yago Doson Coll, and Scott Wallace, thank you for indulging in long days on the water, and for providing continual entertainment. We also had fantastic logistical support and amazing food provided by the Hakai Beach Institute and their staff.

I am grateful to have received financial support from the National Sciences and Engineering Research Council, Simon Fraser University, and the Hakai Network.

From the outset, I have had plenty of great feedback on my research. Thank you to the CMEC lab, Marine Group, Hakai Scholars, Steve Martell, Brendan Connors, Ruth Joy, Eric Buhle, Jake Schweigert, Chris Rooper, and Andy Cooper for your valuable intellectual support.

Special thanks to all of my amazing friends for providing such critical emotional support throughout this journey; it would not have been nearly as enjoyable without you. Finally, I would like to thank and dedicate this thesis to both my loving family and to John Schmidt. Your continued enthusiasm and support for my fishy pursuits are the greatest gifts you could ever give. Love you all.

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1. Introduction

Forage fish play a fundamental ecological role in temperate marine ecosystems as conduits of energy from low to upper trophic level species (Cury et al. 2000). As prey to a diversity of piscivorous fish, sea birds and marine mammals, fluctuations in forage fish abundance can have extensive ecosystem impacts (Smith et al. 2011). Furthermore, because marine predators are often commercially and/or recreationally valuable, declines can have profound indirect economic repercussions (Smith et al. 2011, Pikitch et al. 2012). Despite these implications, global catch of these species has increased over the past 60 years, and now accounts for one third of global fisheries production (Alder et al. 2008). The historic collapse of Peruvian anchovetta, California sardine and other forage fish provide demonstrable evidence that these low trophic-level fisheries are prone to abrupt decline (Barange et al. 2009, Pinsky et al. 2011). These abrupt declines highlight the challenge of managing forage fish, in part due to their highly variable population fluctuations and schooling behaviour driving high catchability and uncertainty in population forecasts (Pikitch et al. 2012). To reduce our uncertainty in population estimates of Pacific herring (*Clupea pallasi*), a dominant forage fish in the northeastern Pacific, we empirically estimate the spatial variation in herring egg loss rates and the mechanisms driving them with repeated field surveys and a large-scale field experiment.

Pacific herring are a low trophic-level forage fish species that have long played critical ecological, social and economic roles in British Columbia (BC), Canada (Anderson et al. 2006, Boas 1932, Brown and Brown 2009, Willson and Womble 2006). Archaeological evidence suggests that First Nations communities have harvested herring in BC for at least 3000 yrs BP (Speller et al. 2012). In the last century, herring and herring roe have been harvested using a variety of techniques to supply a range of markets. A reduction fishery from early 1930s to the late 1960s saw record catches followed by collapses in herring populations (DFO 2012a). The collapse resulted in a termination of the fishery at significant socio-economic costs to coastal communities (Brown and Brown 2009). Herring populations experienced sufficient recovery through the 1970's and 80's to permit the reopening of the commercial herring fishery with the food and bait, sac roe, and spawn-on-kelp (SOK) herring fisheries (DFO 2012a). Conflict between these commercial fisheries and the First Nations SOK fishery led to a precedent setting Supreme Court of Canada case, that recognized the aboriginal right of the Heiltsuk to a commercial SOK fishery (Harris 2000). Despite area closures and changes to the management framework, herring populations have exhibited instability and predominantly declining trends over the last sixty years (DFO 2012a). Due to pronounced population declines over the past decade, commercial herring fisheries have been closed on the Central Coast, West Coast of Vancouver Island, and Haida Gwaii, BC for the past 5, 7, and 10 years, respectively (DFO 2012a). Current declines have prompted coastal communities and scientists to seek improvements to the current Fisheries and Oceans Canada (DFO) herring stock assessment and management framework.

In BC, estimates of Pacific herring spawning stock biomass are based on estimates of the number of eggs spawned by female herring along coastlines each spring. Although a pelagic fish, in the spring herring migrate to the coast and spawn on benthic substrates, with spawn events occurring sequentially in space and time, progressing from the low latitude coastlines of northern California, Oregon then Washington, through British Columbia and northwards to Alaska (Haegele and Schweigert 1985a, Lok et al. 2012). The spatial distribution of spawned eggs within the intertidal and subtidal can vary in length and width, as well as in egg layer thickness (Hay 1985). Eggs are deposited on various marine vegetation types (including low growing macroalgae and seagrass, as well as species that occupy the water column like kelp) and rocky substrates (Fort et al. 2009, Haegele et al. 1981, Haegele and Schweigert 1985b).

To estimate herring abundance, eggs are quantified annually with dive surveys (for survey details see DFO sampling protocol, Fort et al. 2009). However, there is often a time lag (1-17 days) between spawn events and the dive team assessment (Martell et al. 2012), during which time, egg loss can occur due to wave action, predation and other possible factors. Egg loss prior to spawn surveys can result in underestimates of the actual number of eggs originally spawned, leading to underestimates of spawning stock biomass. This underestimation of spawners given the same number of recruits can translate to overestimates of overall stock productivity; which may lead to setting harvest rates too high (Walters and Martell 2004). Consequently, egg loss rates remain a key source of uncertainty in current Pacific herring stock assessment models (Martell et al. 2012).

Herring eggs are susceptible to a variety of factors that remove them from the substrate on which they are spawned. Eggs are primarily deposited at relatively shallow depths (+3m to -11m chart datum (Taylor 1971)) and are particularly vulnerable throughout the two to four week incubation period (Fort et al. 2009, Rooper et al. 1999). Intertidal and shallow subtidal spawn can be exceptionally susceptible to consumption by predators, such as birds in the intertidal (Bishop and Green 2008; Haegele and Schweigert 1991; Outram 1958; Rooper et al. 1999), and invertebrates, fish, diving birds and marine mammals in the subtidal (Haegele 1993; Haegele and Schweigert 1989; Palsson 1984; Rooper 1996). Physical removal by wave action has also been documented as a driver of egg loss (Hay and Miller 1982, Rooper et al. 1999). The influences of predation and wave exposure on egg loss are associated with depth, making depth an important predictor of egg loss (Rooper et al. 1999). Therefore, the depth at which eggs are spawned, and the extent to which these physical and biological drivers are present, will influence the rate at which eggs are lost throughout the incubation period.

Egg loss rates have been estimated for herring spawn events in southeast Alaska and on Vancouver Island; however, no studies have investigated egg loss rates on British Columbia's Central Coast (one of five regional DFO management areas in BC). Currently, DFO informs herring stock assessment models for all regions (Martell et al. 2012) using a mean egg loss rate estimated from three studies. These studies provide a comprehensive examination of egg loss across multiple substrates and multiple biological and physical factors; however, spatially, represent few areas (Prince William Sound, Alaska (Rooper et al. 1999), Georgia Straight, BC (Haegele and Schweigert 1991), and Barkley Sound, BC (Haegele and Schweigert 1989)) within the range of herring spawn locations. Instantaneous egg loss rates range from 0.042 to 0.083 across these three studies, equating to 67-99.99% loss over a 21 day incubation period (Rooper et al. 1999), 58% over a 14 day incubation period (Haegele and Schweigert 1991), and 68.8% over a 14 day incubation period (Haegele and Schweigert 1989). The disparity in these estimates, and the mounting evidence for the context-dependence of ecological dynamics (Agrawal et al. 2007), highlights the need to quantify region-specific estimates of herring egg loss. Adjusting spawn survey estimates with a regionally relevant, empirically-based daily egg loss rate would reduce the uncertainty in current stock assessment models and enhance the validity of management recommendations.

In collaboration with the Heiltsuk First Nation, we quantified the loss of Pacific herring eggs following annual spawning events on British Columbia's Central Coast. We quantified change in egg abundance through time across nine sites and asked; 1) What is the loss rate (Z) of Pacific herring eggs following annual spawning events on British Columbia's Central Coast?, 2) What is the magnitude of spatial variation in herring egg loss rates in this region? and 3) What physical and biological factors drive these loss rates? Specifically, is there evidence that wave exposure, predation, and/or predator swamping drive variation in egg loss rates among sites? To quantify the spatial variation in Z, we conducted repeated dive surveys at the same nine sites, at five intervals after initial spawn deposition. To explicitly test the effect of habitat and predation on egg loss rates, we conducted a field experiment manipulating predator access to herring eggs in three habitats.

2. Methods

2.1. Observational Study of Egg Loss

2.1.1. Study Area

We monitored herring egg loss following a spawn event for up to 22 days at 9 sites on the Central Coast of British Columbia (BC), Canada in the spring of 2012 (Fig. 1). On BC's Central Coast, spawn dates range from the beginning of March through the end of May, with a majority of spawn events occurring in late March and early April (Hay et al. 2008).

We chose sites based on daily Department of Fisheries and Oceans Canada (DFO) herring spawn reports and observations by local Heiltsuk First Nation collaborators in Bella Bella, BC. We surveyed nine spawn sites (Fig. 1C) all of which were dominated by rocky substrate and attached vegetation. Sites varied in wave exposure and total spawn area and ranged in depth from +4.6m to -5.31m chart datum (Appendix A: Fig. 1).

2.1.2. Field Surveys

A team of four divers conducted visual surveys at each site between March 27th and April 25th, 2012. At each site (Fig. 1C), we established four replicate vertical transects running perpendicular to shore on the first day after spawn completion. Transects were made of lead line and covered the width (vertical gradient) of the spawn. These permanent lines were attached at the shore and ran from the intertidal to the maximum subtidal depth of the spawn. The lead lines were anchored throughout with rocks to minimize the chances of displacement.

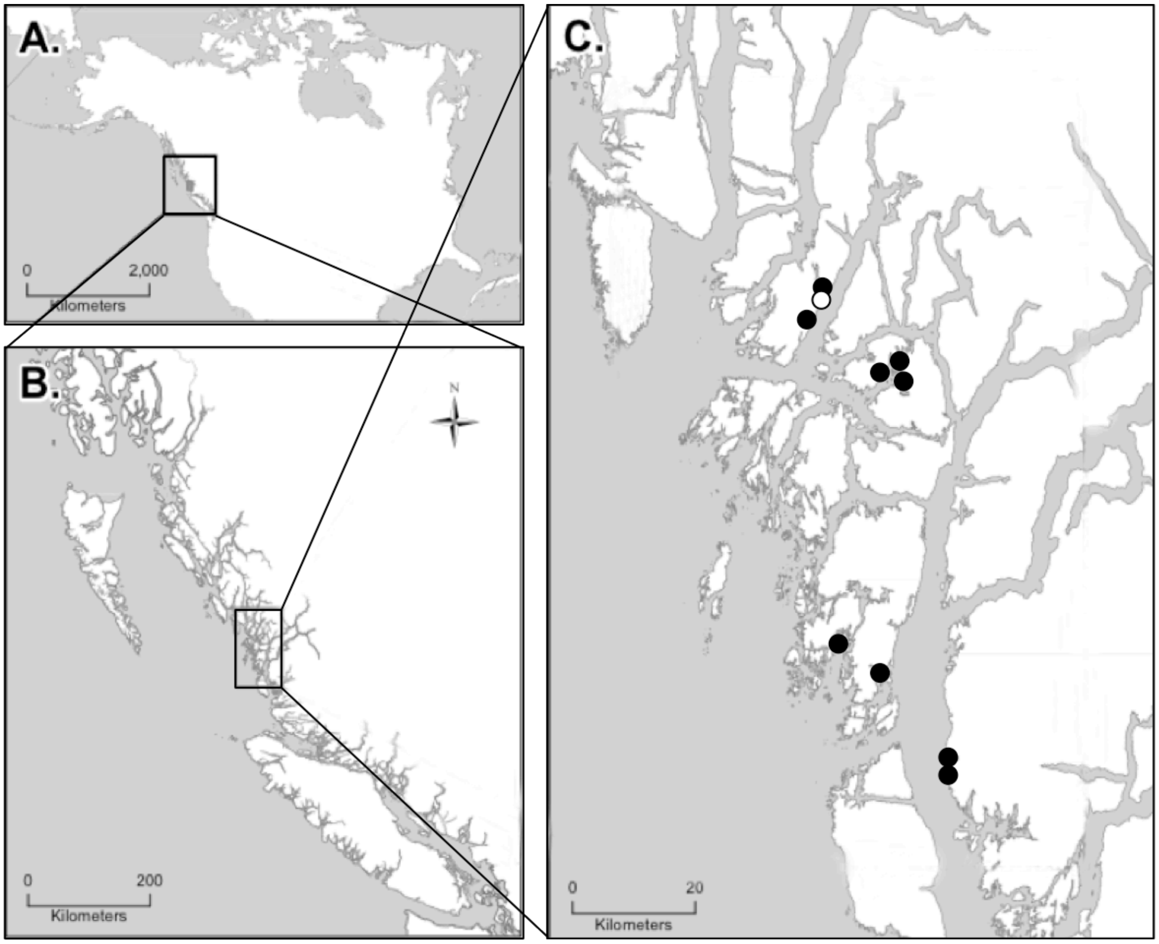


Figure 1. A and B. Central Coast, British Columbia, Canada. C. Locations of nine Pacific herring spawn survey sites (solid circles) and our experimental site (open circle).

We estimated the number of herring eggs on various substrate types within 0.5m^2 quadrats placed at permanent locations marked at 2-meter intervals along our transects based on methodology employed by DFO (Fort et al. 2009). Because spawn width (max and min depth) varied among sites and the number of quadrats sampled was a function of the spawn width, more quadrats were sampled across wider, more expansive spawns. In each quadrat, we noted the time, depth and estimated the percent cover of each substrate type (vegetation and benthos type), the percent cover of eggs on each of those substrates, and the number of egg layers. Divers returned to re-evaluate these specific variables at the same quadrat location every 3 to 5 days throughout the egg incubation period (18 to 22 days), visiting each site a total of 5 times. We used the WWW Tide/Current Predictor (Pentcheff 2012) to convert observed depths to Chart

Datum depths based on data generated from Bella Bella and Namu tide stations. Here, Chart Datum is considered to be mean lower low water.

To quantify potential herring egg predator density and biomass, we conducted surveys of fish and benthic invertebrates at all survey locations. Abundance and maximum length of all identified species were recorded along 30 x 4m horizontal belt transects (n= 3-6 per site) across a shallow (approximately 1-7m) and deep (approximately 7-15 m) depth range at each site. Based on these surveys, predator biomass was estimated for each site. Length-weight relationships, determined on a per species basis (Appendix B: Table 1), were combined with visual size and abundance estimates to calculate a mean total biomass for predators within the shallow and deep ranges of each site. Site level biomass was calculated by taking the mean of the shallow and deep biomass estimates.

2.1.3. Egg Density Estimation

Total egg density within each sampling quadrat was summed from estimates of eggs on vegetation and bottom substrate using procedures outlined in Schweigert 2001.

Eggs on Vegetation - Egg abundance for each category of vegetation (Appendix C: Table 1) found within the quadrat was estimated using the equation:

$$\text{Eggs}_{ij} = 1033.6694 L_{ij}^{0.7137} P_{ij}^{1.5076} V_{ij} Q_j$$

Eggs_{ij} = estimated number of eggs in thousands per m^2 on vegetation type i in quadrat j.

L_{ij} = number of layers of eggs on algal substrate i in quadrat j.

P_{ij} = proportion of quadrat covered by algal substrate i in quadrat j.

V_{1j} = 0.9948 parameter for sea grasses in quadrat j.

V_{2j} = 1.2305 parameter for rockweed in quadrat j.

V_{3j} = 0.8378 parameter for flat kelp in quadrat j.

V_{4j} = 0.9948 parameter for other brown algae in quadrat j.

V_{5j} = 0.9824 parameter for leafy red and green algae in quadrat j.

V_{6j} = 1.0000 parameter for stringy red algae in quadrat j.

Q = 0.5020 parameter for 0.5m^2 quadrats.

Total egg abundance on vegetation (thousands of eggs per m^2) for each quadrat was estimated by summing across all vegetation types.

$$Eggs_j = \sum_i eggs_{ij}$$

Eggs on Bottom Substrate - Bottom substrate included bedrock, boulders, cobble, pebbles and sand, as well as algae measuring less than 2cm. Egg abundance on bottom substrate was the product of percent of the bottom substrate within the quadrat covered in eggs, the number of egg layers, and an assumed density of 340,000 eggs/m^2 (Haegele et al. 1979).

2.1.4. Wave Exposure

During months when herring typically spawn, the Central Coast of British Columbia experiences intense storms with high winds and seas, and strong currents (Crawford et al. 2007, Haggarty et al. 2003), all of which can increase removal of eggs from nearshore substrates.

Winter and early spring winds in this region are primarily from the Southeast (Crawford et al. 2007). Based on physical relevance, we selected average fetch length within the Southeast quadrat as a measure of exposure for each site. Average fetch length was calculated using fetch values determined every 3 degrees at each site. We explored other metrics of exposure; however, found no difference in candidate models based on strength of evidence using Akaike's Information Criterion (AIC) (Appendix D. Table1).

2.1.5. Statistical Analysis

Modeling Egg Loss Through Time - We used linear mixed-effects models (LME) to determine the extent of herring egg loss across our study sites on the Central Coast, BC. Model structure was determined *a priori* based on the ecology of our study and our experimental design (Burnham and Anderson 2002). We estimated egg loss rate (*Z*) in three ways, assuming exponential decay (Eq 1). First, by taking the natural log of both sides of this equation (Eq 2), we estimated instantaneous egg loss rate (*Z*) from the slope of the linear model of log transformed egg abundance as a function of time (Eq 3):

$$N_t = N_0 * e^{-Zt} e^{\varepsilon} \qquad \text{(Eq 1)}$$

$$ln(N_t) = ln(N_0) + ln\ (e^{-Zt}) + ln(e^{\varepsilon}) \qquad \text{(Eq 2)}$$

$$ln(N_t) = ln(N_o) - Zt + \varepsilon \qquad \text{(Eq 3)}$$

where N_t is the number of eggs at day *t*, N_0 is the number of eggs initially deposited, *Z* is the instantaneous egg loss rate, and ε is a random error term with mean 0 and constant variance. Using this modeling approach, we evaluated two different ways to deal with undefined values of ln(0) resulting from zero-egg values (i.e., no eggs recorded); first (Approach 1) was to add half of the lowest non-zero egg abundance (90 eggs) to all values; second (Approach 2), was to model egg abundance through time to the smallest non-zero number of eggs. Approach 2 effectively removed all zeros from the dataset (<10% of data) and follows both DFO dive spawn survey protocols, which specify that zero values are not to be recorded, as well as the methods of Rooper et al. (1999).

In order to calculate the proportion of eggs lost over various time intervals, output parameters (intercept and slope) from our models were substituted into Eq 1 (where $N_0 = e^{\text{intercept}}$ and Z = -1(slope)) to determine N_t, which was then used to calculate the proportion lost given N_0. We calculated loss over 1, 6.8 and 21 days to represent the percentage of eggs lost daily, the percentage lost over the mean time lag between initial spawn and survey, and the percentage lost over the 21 day incubation period, respectfully.

Our third approach (Approach 3) was to model egg loss rates (Z) directly from our data:

$$Z = \frac{ln(N_0 \; - N_t)}{t} \qquad \text{(Eq 4)}$$

Rather than deriving a single egg loss (Z) parameter estimate from a linear model, in this approach we calculated instantaneous egg loss rates (Eq 4) for each time step in our survey (n= 4 decay periods). Here, *t* is the elapsed time between sampling periods.

Model Structure - In Approaches 1 and 2, transformed egg abundance (response variable) was modeled as a function of time (days) as a fixed effect and quadrat nested within transect, nested within site as random effects. To investigate how egg loss rates differed among our study sites, we added site to the model as a fixed effect. We allowed both intercept and slope to vary among all quadrats in the nested structure of our model. To quantify the effects of physical and biological factors on egg loss rates in models of egg abundance, we examined the standardized coefficients and relative variable importance (RVI) of the second order interaction terms between these factors and time. We accounted for the temporally auto-correlated nature of our time series data by incorporating a continuous correlation structure of order 1, with a continuous time covariate, to our variance covariance matrix using the corCAR1 function in the *nlme* package (Pinheiro and Bates 2012).

In Approach 3, we modeled instantaneous egg loss rate (Z) as the response variable, while quadrat, transect and site remained nested random effects. Site was included as a fixed effect to determine individual egg loss rates for each site. To identify the strength of evidence for biological and physical factors as key drivers of egg loss, we incorporated additional fixed effects (predator abundance, total spawn area, wave exposure, and depth) and examined the standardized coefficients and RVI factors directly. We used the lme function from the *nlme* package (Pinheiro and Bates 2012) in R (R Development Core Team 2012) for all analyses.

Model Selection - To determine the strength of evidence among alternative hypothesized causal factors driving Pacific herring egg loss rates on BC's Central Coast, we took an information-theoretic approach (see Burnham & Anderson 2000). To assess the strength of evidence for each explanatory variable in driving regional variation in our response variables, we compared alternative candidate models with small-sample bias-corrected Akaike's Information Criterion (AICc), standardized to the most parsimonious model to produce (ΔAICc) values, and used multimodel inference (Burnham and Anderson 2002, Grueber et al. 2011). We normalized the model likelihoods to a set of positive Akaike weights (w_i), representing the strength of evidence in favour of a given model relative to the set of candidate models. From our candidate model set, we calculated multi-model averaged parameter estimates and RVI using the *MuMIn* package in R (Barton 2012). RVI for a given factor is determined by summing the Akaike weights across all models in the candidate set where the factor occurs (Burnham and Anderson 2002). To easily interpret the relative importance of each factor in our candidate model set, we standardized our predictors to a common scale by subtracting their mean and dividing by 2 standard deviations (Gelman 2007).

2.2. Predator Exclusion Experiment

2.2.1. Experimental Design

We conducted a predator exclusion experiment to specifically determine the effect of predation and habitat on egg loss rates. Our experimental location in Spiller Channel (Fig.1C) was selected as an area where herring had spawned in the past and roe had been harvested by local Heiltsuk First Nation collaborators from Bella Bella, BC.

Sixty 13 x 10cm pieces of herring roe-on-kelp (*Macrocystis integrifolia*) were randomly assigned to four predator exclusion treatments (15 replicates per treatment); large size predator exclusion (25 x 25mm vexar mesh), large and medium sized predator exclusion (7 x 7mm vexar mesh), all sized predator exclusion (1mm nitex mesh), and all predators present (no enclosure).

A single line was suspended across the bay, from which individual lines were sunk vertically, mimicking the traditional spawn-on-kelp fishery. Each treatment was attached to a vertical line at 3 habitats: subsurface (2m), midwater (8m) and benthic sea floor (13m) (Fig. 2). This experimental design was replicated five times across the length of the bay, each replicate considered one block in the design. To quantify egg abundance over time, each piece of spawn-on-kelp was weighed and the percent egg cover and egg layer thickness assessed every two to three days, for a total of 5 times over 14 days.

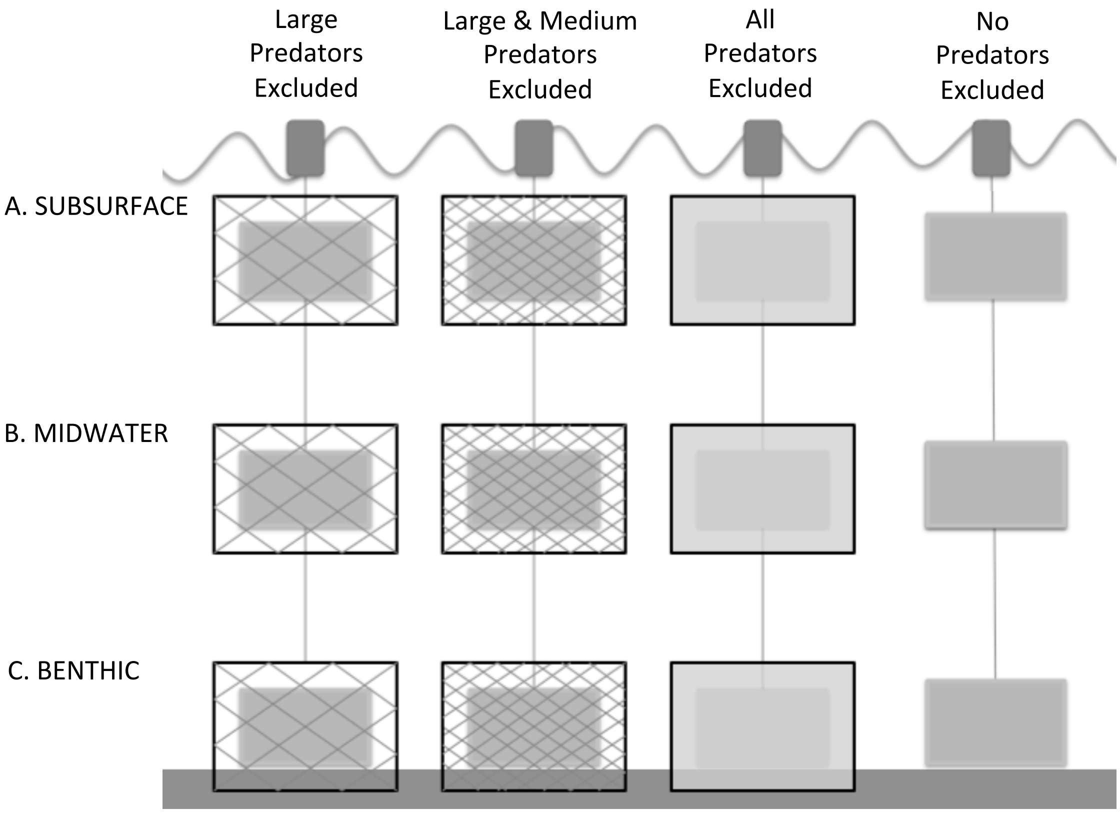


Figure 2. Experimental design used to test the effects of predation and habitat type on egg loss rates. Sixty 13 x 10cm sub-samples of SOK (herring spawn on giant kelp Macrocystis pyrifera (grey rectangle)) were assigned to one of 4 predator treatments and submerged to 3 different habitats (A. subsurface, B. midwater, C. benthic). Predator treatments included a large mesh to exclude large sized predators, a medium mesh to exclude large and medium sized predators, a fine mesh to exclude all predators, and an uncaged sample open to all predators. This design was replicated 5 times across a bay in Spiller Channel, near Bella Bella, BC.

2.2.2. Statistical Analysis

Modeling the effects of predation and habitat on egg loss – We used linear mixed effects models to assess the strength of evidence for the effects of predation and habitat on egg loss. Egg loss was evaluated using three different response variables; 1) percent cover, 2) egg layer number, and 3) instantaneous egg loss rate, as in Approach 3 of the observational study (Eq 4, n = 4 decay periods). We chose to exclude wet weight as a response variable due to the variability introduced by inconsistent exposure to air among samples and resulting desiccation.

Model Structure – Models of percent cover and egg layer number included time as well as all interactive combinations of habitat and predator treatment as fixed effects. Experimental block (n=5) was treated as a random effect. Both intercept and slope were allowed to vary among all quadrats in the nested structure of our model. We accounted for temporal-autocorrelation between repeated measures by including a correlation structure (corCAR1), and allowed variance in our residuals to differ through time by incorporating a variance structure (varExp) into our models. In models with instantaneous egg loss rate as the response, combinations of habitat and predator treatment were included as fixed effects, and block remained a random effect. All analyses were completed using the *nlme* package in R.

Model Selection Framework – To assess the strength of evidence for predation and habitat type driving variation in our response variables, we compared Akaike weights (w_i) of alternative candidate models using the same model selection approach as in the observational study analysis.

3. Results

3.1. Observational Study of Egg Loss

3.1.1. Observational Study of Egg Loss

Global instantaneous egg loss rates (*Z*) for Pacific herring spawn on BC's Central Coast were estimated as 0.177 ± 0.027, 0.152 ± 0.022, and 0.174 ± 0.024 for Approaches 1, 2 and 3, respectively (Fig. 3, 4), equating to a daily egg loss of between 12%-18%. Global and site-specific estimates of *Z* were consistent across statistical approaches based on overlapping standard errors (Fig. 4). Estimated values based on Approach 1, where 45 was added to all egg numbers as a constant prior to log transformation, were slightly greater than Approach 2, where all zeros were removed prior to transformation (except for Troup5layer). Estimated values based on Approach 2 were consistently lower than Approach 3, where egg loss rate was the response variable. For all three approaches, we found that egg loss rates differed between sites by a factor of up to 4.5 (Fig. 3, 4, Appendix E: Table 1).

3.1.2. Factors Affecting Egg Loss

There is no strong empirical support for one model of egg abundance over another given the ΔAIC_c values of <2 for the top 5 models (Table 1). However, model averaging (Approaches 1 and 2) suggests that time accounts for the greatest variation in egg abundance across our sample period (RVI = 1, Table 1, Fig. 5A). Furthermore, there is strong evidence that depth plays an important role in initial egg abundance (N_0) (RVI = 1, Table 1, Fig. 5A). Although the top set of models also include the effects of predator abundance, exposure and spawn area with depth (Table 2), model averaging gives confidence intervals for these parameter estimates that include zero, suggesting there is little evidence that these are important factors across models (Fig. 5A). Furthermore, the interactive effects of time with each of depth, predator abundance, exposure and spawn area on egg abundance have RVI = 0, or have bounds that cross zero, suggesting these parameters have little influence on egg loss rate, the slope of our model (Fig. 5A). We found relatively strong evidence that spawn area effects egg loss rates (RVI = 0.67), while our measures of predator abundance, depth and exposure had little influence (Fig. 5B, Table 1).

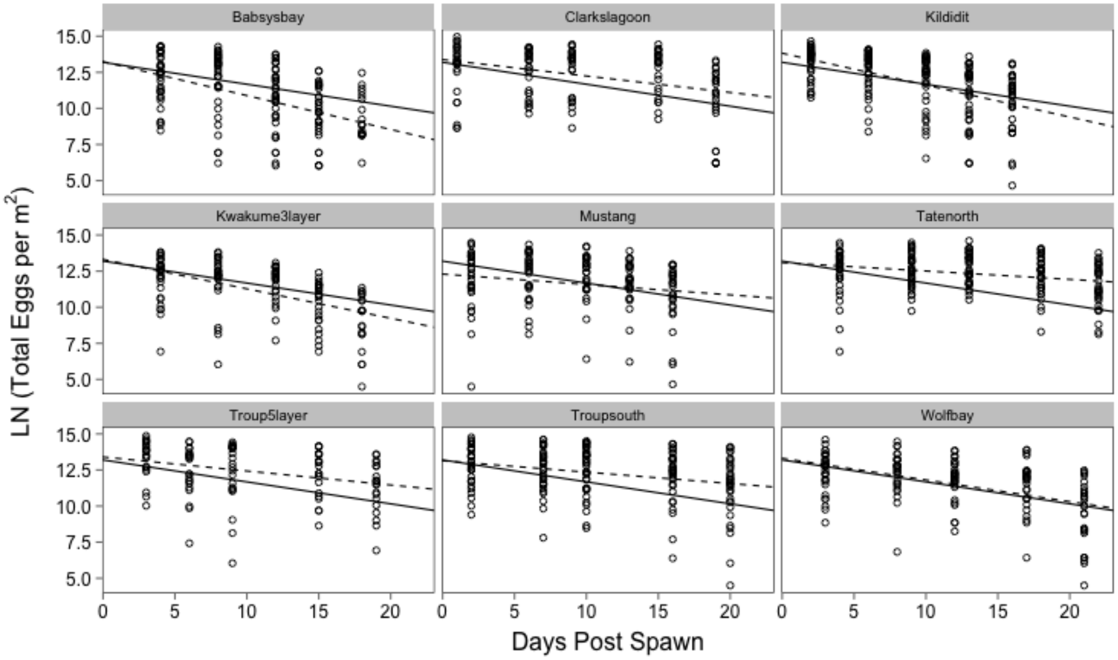


Figure 3. Density of Pacific herring eggs, log transformed, as a function of days post spawn at nine sites across British Columbia's Central Coast. The black line indicates the global model fit, while the dashed lines indicate site-specific model fits estimated by linear mixed effects models using modeling Approach 2 (all zeros removed from egg abundance data set prior to log transformation). Slope values are the modeled instantaneous egg loss rate (see Eq 3 & Appendix E: Table 1).

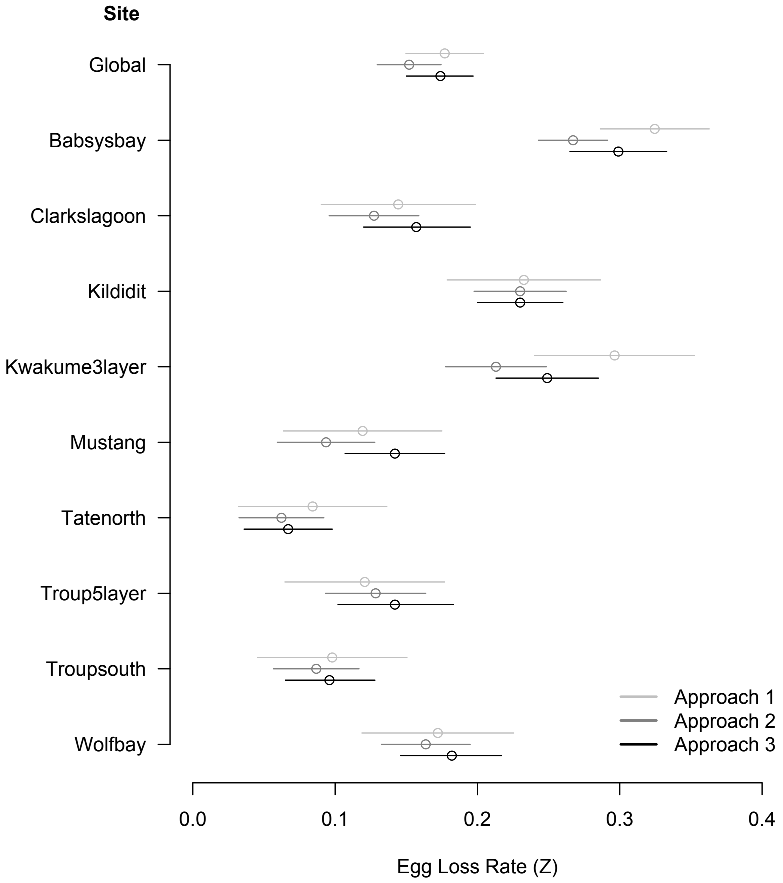


Figure 4. Estimates and standard errors of global and site-specific egg loss rates (Z) using three different modeling approaches. Modeled response variables include Approach 1: ln (egg abundance + 45); Approach 2: ln (egg abundance) with zeros removed prior to log transformation; Approach 3: egg loss rate calculated using $Z = ln(N_0 – N_t)/t$.

3.2. Predator Exclusion Experiment

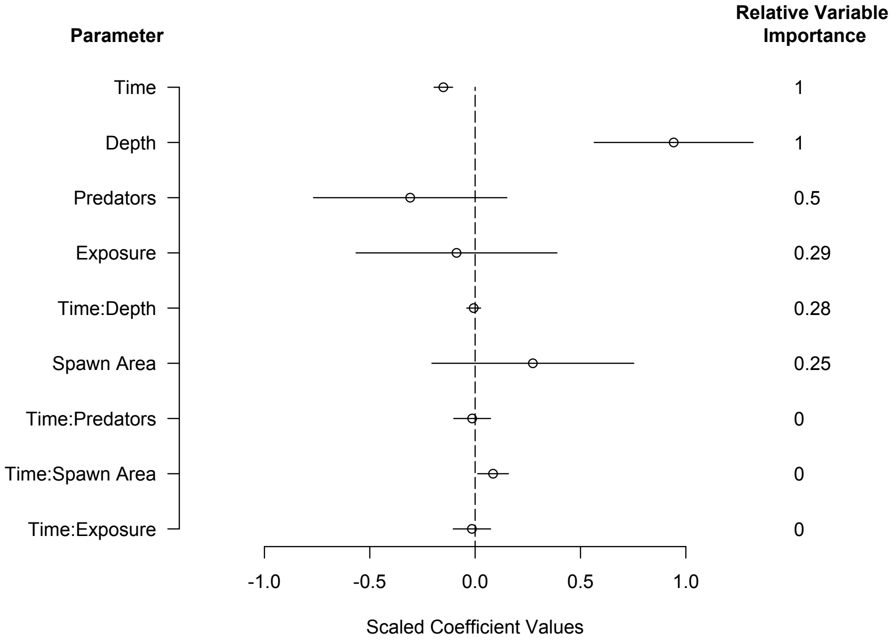
Our experiment shows strong evidence that both predation and habitat type influence egg loss rates (Fig. 6, Table 2). Specifically, we found that both percent cover and number of egg layers declined through time, most dramatically for eggs on kelp exposed to all predators in the benthic environment (Fig. 6). For models of percent cover and egg layer number, the interactive effects of predation and habitat have the greatest influence on egg abundance through time (percent cover w_i = 1; egg layers w_i = 0.9, Table 2). Similarly, there is strong empirical support from our field experiment suggesting that both predation and habitat type, in combination, drive instantaneous egg loss rates (w_i = 1.0,

Table 2). There is little empirical support that predation ($\Delta\text{AIC}_c = 9.2$) and habitat ($\Delta\text{AIC}_c = 13.3$) drive egg loss rates independently (Table 2).

Table 1. Strength of evidence for alternative candidate models to examine the influence of biological and physical factors on egg abundance. Candidate models sets were determined using 3 different modeling approaches. Models with varying numbers of parameters (K), were compared with differences in Aikaike's Information Criterion (Δ_i), likelihood of the model given the data (Log($\mathcal{L}$)), normalized Akaike's weight (w_i) indicating the weight of evidence in favour of model i. We report the top 8 models in our candidate set.

Response and Model	**K**	**Log ($\mathcal{L}$)**	**AIC$_c$**	**Δ_i**	**w_i**
APPROACH 1: ln(Egg Abundance + 45)					
Time + Depth	14	-3078.9	6186.2	0	0.2
Time + Depth + Spawn Area	15	-3078.3	6186.9	0.7	0.2
Time + Depth + Predation	15	-3078.6	6187.6	1.4	0.1
Time + Depth + Exposure	15	-3078.7	6187.7	1.5	0.1
Time * Depth	15	-3078.8	6187.9	1.7	0.1
Time + Depth + Predation + Exposure	16	-3078.1	6188.6	2.5	0.1
Time * Depth + Spawn Area	16	-3078.2	6188.7	2.5	0.1
Time * Depth + Predation	16	-3078.4	6189.2	3.0	0.1
APPROACH 2: ln(Egg Abundance)					
Time + Depth + Predation	15	-2393.6	4817.5	0.0	0.2
Time + Depth	14	-2394.8	4818.0	0.5	0.2
Time + Depth + Spawn Area	15	-2394.1	4818.5	1.0	0.1
Time + Depth + Predation + Exposure	16	-2393.4	4819.1	1.6	0.1
Time * Depth + Predation	16	-2393.5	4819.4	1.9	0.1
Time * Depth	15	-2394.7	4819.8	2.3	0.1
Time + Depth + Exposure	15	-2394.8	4820.0	2.5	0.1
Time * Depth + Spawn Area	16	-2394.0	4820.3	2.8	0.1
APPROACH 3: Egg Loss Rate (Z)					
Spawn Area	6	-428.9	869.8	0	0.7
Intercept	5	-431.4	872.7	2.9	0.1
Predation	6	-431.0	874.0	4.2	0.1
Depth	6	-431.3	874.7	4.9	0.1
Exposure	6	-431.4	874.7	4.9	0.0
Spawn Area + Predation + Depth + Exposure	9	-428.6	875.2	5.4	0.0

A. Observational Study



B. Predator Exclusion Experiment

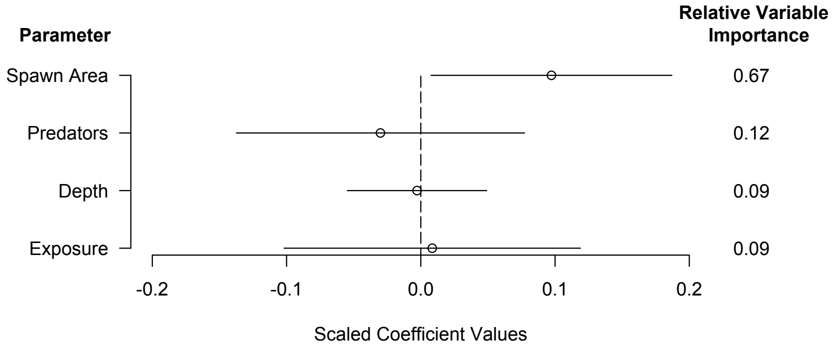


Figure 5. Scaled parameter estimates with 95% confidence intervals from averaging multiple linear mixed-effects models of A) egg abundance using model Approach 2 (response variable: ln(egg abundance) with zeros removed prior to log transformation) and B) Instantaneous egg loss rate (Z) using model Approach 3. Biological and physical parameters thought to drive egg loss (on left) are ranked by their relative variable importance (on right). Note: Modeling Approach 1 reveals similar results to those shown for Approach 2.

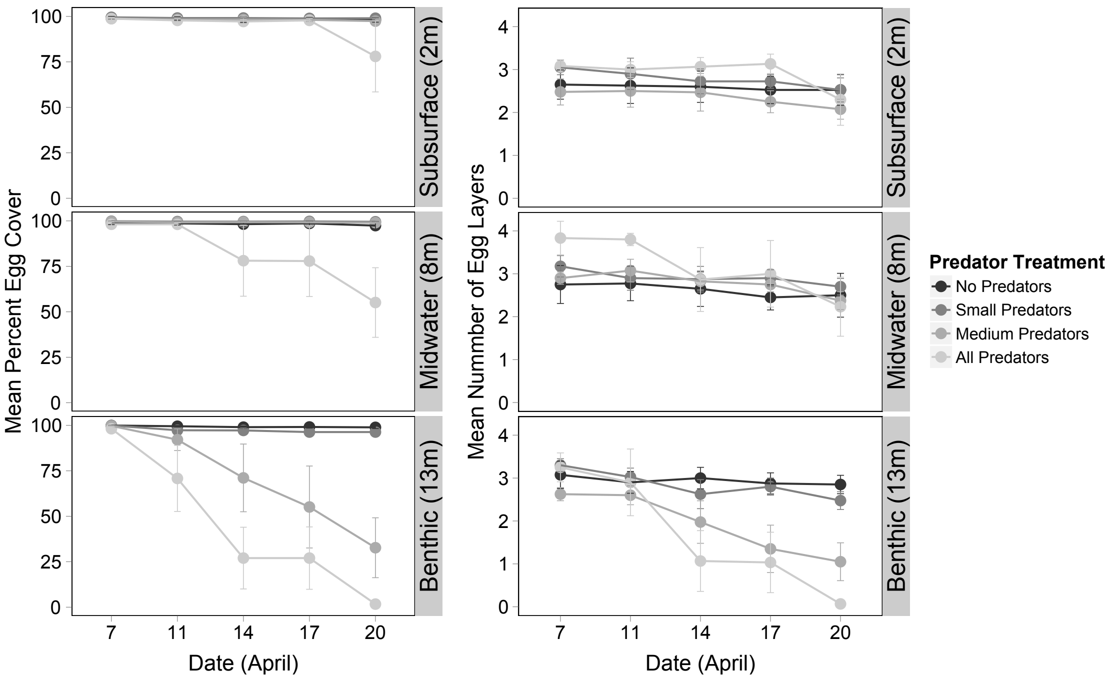


Figure 6. Mean percent egg cover (graphs on left) and mean number of egg layers (graphs on right) through time for pieces of roe on kelp under 4 different predator treatments and 3 habitats.

Table 2. Strength of evidence for alternative candidate models of the effect of predation and habitat type (benthic, midwater, subsurface) using different response variables (1. Percent Cover and 2. Egg Layers as measures of egg abundance, and 3. Egg Loss Rate, calculated using Eq 4. Note: Models showing multiple interaction terms also include the individual interactions.

Response and Model	**K**	**Log ($\mathcal{L}$)**	**AIC_c**	**Δ_i**	**w_i**
Percent Cover					
Time*Predation*Habitat	28	-1176.9	2415.9	0	1
Time*Predation	12	-1220.1	2465.3	49.4	0
Time*Habitat	10	-1224.6	2470.1	54.2	0
Time	6	-1238.3	2488.9	73.0	0
Egg Layers					
Time*Predation*Habitat	30	-277.2	621.5	0.0	0.9
Time*Predation	14	-298.9	627.3	5.8	0.1
Time*Habitat	12	-303.6	632.3	10.8	0.0
Time	8	-310.7	637.9	16.4	0.0
Egg Loss Rate (Z)					
Predation + Habitat	7	166.4	-318.2	0.0	1.0
Predation	6	160.7	-309.0	9.2	0.0
Habitat	4	156.5	-304.9	13.3	0.0
Intercept	3	152.3	-298.4	19.8	0.0

4. Discussion

This study shows strong evidence that Pacific herring eggs experience substantial loss rates following annual spawn events on BC's Central Coast. Our measure of daily egg loss rate equates to between 93-99% of the initial eggs deposited being lost over a 21 day incubation period, or 59-75% of eggs over a 6.8 day period, the average number of days between spawn deposition and spawn survey on the Central Coast (Martell et al. 2012). These loss rates vary spatially, from site to site, by up to a factor of 4.5, which translates to a range in daily egg loss of 6-28%, or 34-89% over 6.8 days. Furthermore, egg loss rates were influenced by total spawn area, predation and habitat type. Importantly, the rates of loss we document here are much higher than the estimates currently used to inform DFO's Pacific herring stock assessment (Martell et al. 2012), which are based on studies completed in Alaska (Rooper et al. 1999) and on the West Coast of Vancouver Island (Haegele and Schweigert 1989, 1991).

4.1. Implications of Egg Loss to Estimates of Population Productivity

Our estimate of egg loss rate is more than double the value (0.064±0.019) used broadly by DFO across all 5 management regions in the 2012 stock assessment (Martell et al. 2012). This could mean that spawning stock biomass on the Central Coast is currently being underestimated. Higher ranges of egg loss rates have been documented for other regions of the Pacific coast (ex. Rooper et al. 1999 document egg loss rates of up to 0.26, and Palsson 1984, up to 0.73), which could imply widespread underestimates of spawning stock biomass in BC. The relationship between spawning stock biomass and recruitment is informed by various parameters, one being the steepness (*h*) parameter, which describes the number of recruits when the virgin biomass is reduced to 20% (Francis 1992). Underestimation of spawning stock biomass can increase the steepness of the stock-recruit relationship and lead to overestimates of population productivity, which could alter key reference points for management (Martell et al. 2012).

4.2. Factors Influencing Egg Loss Rates

We detected strong evidence for context-dependence in instantaneous egg loss rates given the 4.5 fold difference in magnitude among our 9 sites (Fig. 4, Appendix E: Table 1). Our observational study revealed empirical evidence that spawn area has a positive effect on egg loss rate, such that sites with larger total spawn areas have higher egg loss rates (Fig. 5B, Table 1). Multiple alternative hypotheses can be invoked to explain this pattern. Larger spawns may cause an aggregative response, where predators concentrate in an area of high prey density (Krebs 2001). Alternatively, larger spawns may suffer more proportionally to wind driven storm events. Regardless, the direction of this relationship runs counter to our predicted hypothesis of predator swamping, a functional response where the quantity of prey is large enough to satiate the predator, thereby reducing the proportion of prey removed by predation (Darling 1938, Ims 1990). Furthermore, we did not detect an effect of predator abundance using our spawn survey data. This may be due to our metric and method of calculating predator abundance. Our estimate did not include avian predators, who have been found to account for large proportions of egg loss (31% Bishop and Green 2008, 30-55% Outram 1985). Additionally, fish and other marine mammal predators may have avoided divers and escaped our observation, or been more sporadic in abundance, resulting in diver observation bias (Sale and Douglas 1981). Similarly, we did not find an effect of exposure, which may have been due to our coarse estimate of this variable, or the weak effect of wave exposure in the semi-protected channels in which our study sites were located. Because we used average fetch within the southeast quadrat of our site, our estimate does not capture small-scale spatial differences in wave exposure or seasonal variability from storm events that are known to remove large quantities of eggs (40% Hart and Tester, 26% Hay and Miller 1982).

Our field experiment suggests that both subtidal predation and habitat type drive egg loss. These results, when compared to those from our observational study, highlight the power of field experiments to explicitly test the effects of factors rather than make inferences from observation alone. The influence of predation by fish and invertebrates on egg loss rates has been documented in several studies, which have attributed up to 30% of egg loss to subtidal predation (Haegele 1993, Haegele and Schweigert 1990, Rooper 1996). Our experiment provides strong evidence that the effect of predation is dependent on habitat, where eggs in the water column have a greater chance of survival than those in the benthic environment (Fig. 6). The target research area for this work was located in protected inland channels and bays, reflective of current herring spawn locations in the Central Coast region. However, historically, herring also spawned on the outer coast (DFO 2012b, Hessing-Lewis et al. 2012), where kelp forest substrate is more dominant. These results imply that kelp forests, and their vertical structure in the water column, may benefit herring eggs by decreasing the risk of predation while simultaneously improving water flow and reducing sedimentation, both factors known to improve herring egg survival (Alderdice and Hourston 1985, Griffin et al. 2009). Increasing available spawning habitat, and therefore surface area, may allow eggs to be deposited at lower densities (Haegele and Schweigert 1985) and thus increase egg viability through enhanced water movement and respiratory exchange within the egg mass (Taylor 1971). Consequently, reduction in kelp habitat following the extirpation of sea otters in the mid 1800s, and subsequent expansion in urchin barrens, may have had indirect effects on herring population dynamics in BC.

The empirical and experimental support for the influence of spawn area, predation and habitat type on egg loss rates may explain the magnitude of variability we found between study sites, as well as between the Central Coast region and previously studied regions. These biological and physical factors may vary on small spatial scales, raising the possibility of spatially explicit parameterization of stock assessment models. This study focuses on variation across space; however, variation across years might contribute substantially to differences in egg loss parameter estimates.

4.3. Ecosystem and Management Implications

The ecosystem impacts of herring management are widespread due to the foundational ecological role this forage fish plays transferring energy from lower to upper trophic levels in marine food webs. Many predators rely on herring as a food source, including commercially and culturally valuable species, such as salmon. This prompts the question: how can we continue to enjoy the economic benefits of higher trophic level species (ex. through commercial fisheries or tourism), while we simultaneously harvest their food source? In 2012, Pikitch et al. recommended adopting the Dependent Predator Performance Criterion, whereby management decisions are made to ensure that fishing forage fish will not deplete any dependent predator to IUCN's definition of vulnerable (with 95% confidence). Under these criteria, they suggest much more conservative targets for forage fish than commonly recommended and applied in the past in order to manage risks across entire ecosystems. Currently, the harvest control rule for herring in BC is set at 25% of unfished biomass (B_0). Pikitch et al. (2012) recommend that even with the best available knowledge and well-quantified estimates of uncertainty, forage fish biomass limits should be no less than 30% of B_0.

Biological diversity is fundamental in conferring resilience to both ecosystems (Chapin et al. 2000, Folke et al. 2004) and the individual species within them (Hutchinson 2008, Schindler et al. 2010), by buffering perturbations from harvest, ocean climate, competitors and predators. For Pacific herring, temporal and spatial variability of spawning events, as well as the use of multiple spawning habitats, may provide biocomplexity and stability to populations. Spatial and temporal management of forage fish populations, accomplished by restricting fishing effort in both space and in time, is valued as a means to ensure diversity and local productivity (Daunt et al. 2008, Hewitt et al 2004, Pichegru et al. 2009, Sherley et al. 2013). In order to safeguard this diversity, and ensure prey productivity to their numerous predators, further knowledge of herring population structure and variability should be incorporated into the current management framework (Hutchinson 2008). Managing for biocomplexity is limited by our ability to identify distinct spawning populations of herring and their regional variability. The use of new genetic analyses, and ancient herring DNA from midden sites, may provide further insight to spatial population structure and genetic diversity; as well as changes through time (Speller et al. 2012).

As with any modeling approach, there exists inherent uncertainty when forecasting population abundance and structure, and this uncertainty is often underestimated (Francis and Shotton 2007). Our analysis provides an example, where, not only did we demonstrate statistical variability (in the use of different modeling approaches), but also uncertainty in our modeled parameter estimates, and site-level variability. These various aspects of variability and uncertainty need to be accounted for when parameterizing models that influence management decisions at regional and transregional spatial scales.

Several analyses have now demonstrated that conventional management targets for forage fisheries are insufficient, and have recommended that current fishing pressure be cut in half and biomass left in the ocean be twice as large (Pikitch et al. 2012, Smith et al. 2011). If herring management in BC falls under the intermediate information tier, according to the three-tier precautionary approach outlined by Pikitch et al. 2012, harvest control rule is recommended to be set at 40% of B_0. This recommendation is echoed among First Nations communities, who support greater conservation measures and responsible stewardship of herring populations in BC (Brown and Brown 2009). Reduced fishing pressure, in combination with holistic ecosystem-based management that acknowledges the dependence of predators, the value of habitat, quantifies risk, and is precautionary, will help safeguard the long-term sustainability of herring stocks and the marine ecosystems upon which humans depend.

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Appendices

Appendix A. Depth distribution of herring eggs

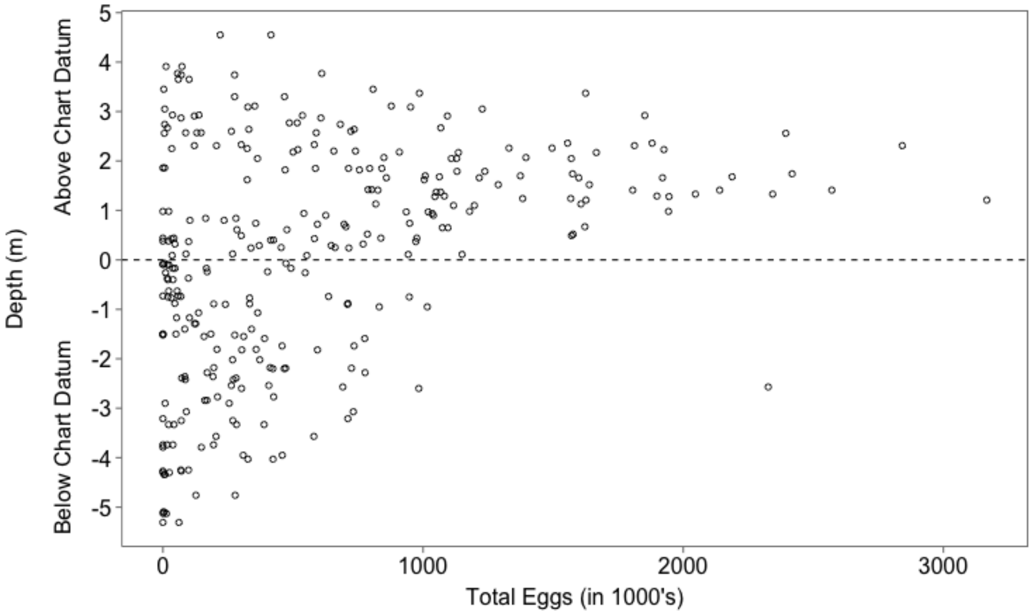

Figure A1. Depth distribution of egg deposition on the first sampling date across all sampled sites.

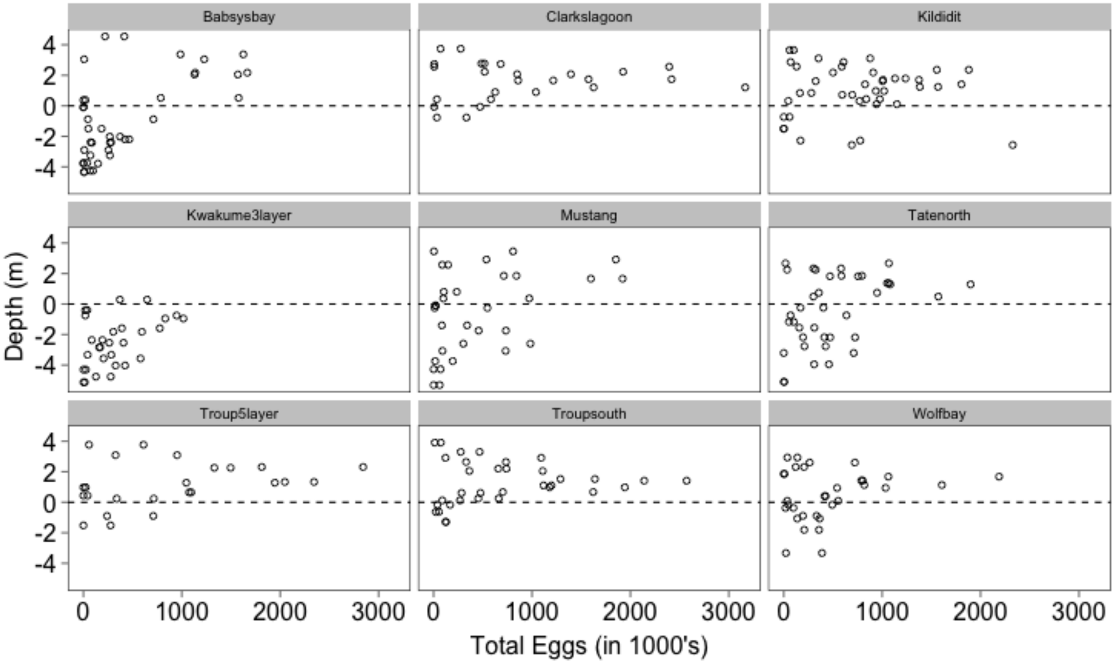

Figure A2. Depth distribution of deposited eggs at each site on the first sampling date. Differences likely reflect tidal height at time of spawning.

Appendix B. Length-weight parameters for species identified during predator surveys

Table B1. Length-weight relationship parameters used to estimate biomass for invertebrates and fish along belt-transects in 2012 surveys; weights in grams were calculated as LW_a*(total length)^LW_b.

Species	Scientific Name	LW_a	LW_b	Length Unit	Source
Invertebrates					
Leather Star	*Dermesterias*	0.045	2.835	cm	Dr. Rebecca Martone, UBC IRES, West Coast Vancouver Island, $R^2 = 0.90$
Blood Star	*Henrecia*	0.064	2.265	cm	Dr. Rebecca Martone, UBC IRES, West Coast Vancouver Island, $R^2 = 0.92$
Vermillion Star	*Mediaster*	0.004	3.849	cm	Dr. Rebecca Martone, UBC IRES, West Coast Vancouver Island, $R^2 = 0.97$
Rainbow Star	*Orthasterias*	0.030	2.509	cm	Dr. Rebecca Martone, UBC IRES, West Coast Vancouver Island, $R^2 = 0.88$
Sea Cucumber	*Parasticapus*	1.142	1.832	cm	*Isostichopus fuscus* parameters from Herrero-Pérezrulo et al. 1999, Baja California Sur Mexico, $R^2 = 0.71$
Pink Star	*Pisaster brevispinus*	0.015	1.784	mm	*Pisaster ochraceus* parameters from Christine Gruman, SFU REM, Gwaii Haanas
Purple Sea Star	*Pisaster ochraceus*	0.015	1.784	mm	Christine Gruman, SFU REM, Gwaii Haanas
Sunflower Star	*Pycnopodia helianthoides*	0.018	3.133	cm	Lynn Lee, SFU REM
Rose Star	*Crossaster papposus*	0.018	3.133	cm	*Pycnopodia helianthoides* parameters from Lynn Lee, SFU REM
Dawson's Sun Star	*Solaster Dawsoni*	0.039	2.741	cm	Dr. Rebecca Martone, UBC IRES,West Coast Vancouver Island, $R^2 = 0.98$
Fish					
Painted Greenling	*Oxylebius pictos*	0.016	3.000	cm	Fishbase.org
Copper Rockfish	*Sebastes caurnius*	0.016	3.020	cm	Rowan Trebilco, SFU

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Appendix C. Marine vegetation identified during surveys

Table C1. Common marine vegetation species identified during spawn surveys. Species were categorized under 5 different vegetation types, each represented with a parameter in Eq.

Vegetation Type	Common Species Identified
Seagrass	*Zostera marina*
	Phyllospadix spp.
Rockweed	*Fucus distichus*
Flat Kelp	*Agarum* sp.
	Alaria marginata
	Saccharina sessilis
	Egregia menziesii
	Laminaria spp.
Leafy Algae	*Porphyra* spp.
	Mastocarpus papillatus
	Chondracanthus exasperatus
	Mazzaella spp.
	Ulva spp.
	Halosaccion glandiforme
	Colpomenia peregrina
Stringy Algae	*Gracilaria* sp./*Gracilariopsis* sp.
	Neorhodomela spp.
	Odonthalia spp.
	Cyptosiphonia woodii
	Endocladia muricata
	Polysiphonia sp.
	Calithamnion pikeanum
	Corallina spp.
	Bosiella spp.

Appendix D. Alternative measures of exposure.

Table D1. Strength of evidence for alternative candidate models of egg abundance and various measures of exposure. Measures include maximum bottom velocity, maximum fetch, average fetch in the Northwest (NW) Quadrat (representing the direction of predominant summer winds on the Central Coast), and average fetch in the Southwest (SW) quadrat (representing direction of predominant winter winds). Fetch values were calculated every 3 degrees from the site.

Response and Model	**K**	**Log ($\mathcal{L}$)**	**AIC$_c$**	**Δ_i**	**w_i**
ln(Egg Abundance)					
Time + Maximum Fetch Value	14	-2409.1	4846.5	0	0.3
Time + Mean Fetch in NW Quadrat	14	-2409.3	4846.8	0.3	0.3
Time + Mean Fetch in SE Quadrat	14	-2409.5	4847.3	0.7	0.2
Time + Maximum Bottom Velocity	14	-2409.9	4848.0	1.5	0.2

Appendix E. Model output parameters for Approaches 1, 2, & 3

Table E1. Instantaneous egg loss rates (Z) estimated from model output parameters using 3 different modelling approaches. Modeled response variables include Approach 1: ln (egg abundance + 45); Approach 2: ln (egg abundance) with zeros removed prior to log transformation; Approach 3: egg loss rate calculated using $Z = ln(N_0 – N_t)/t$.

	Model Response					
	ln (eggs + 45)		ln (eggs)		$\frac{\ln(N_0 - N_t)}{t}$	
Site	**Z**	**SE**	**Z**	**SE**	**Z**	**SE**
Global	0.177	0.027	0.152	0.022	0.174	0.024
Babsysbay	0.325	0.038	0.267	0.024	0.299	0.034
Clarkslagoon	0.145	0.054	0.127	0.032	0.157	0.038
Kildidit	0.232	0.054	0.230	0.032	0.230	0.030
Kwakume3layer	0.296	0.056	0.213	0.035	0.249	0.036
Mustang	0.119	0.056	0.094	0.034	0.142	0.035
Tatenorth	0.084	0.052	0.062	0.030	0.067	0.031
Troup5layer	0.120	0.056	0.128	0.035	0.142	0.041
Troupsouth	0.098	0.053	0.087	0.030	0.096	0.032
Wolfbay	0.172	0.053	0.164	0.031	0.182	0.035

Appendix F. Plots of total egg abundance through time.

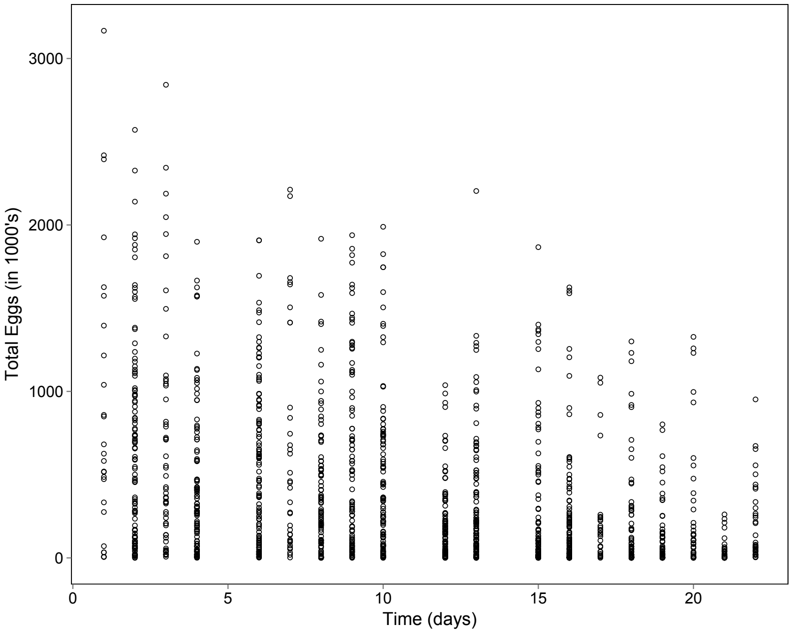

Figure F1. Total egg abundance through time for all survey sites.

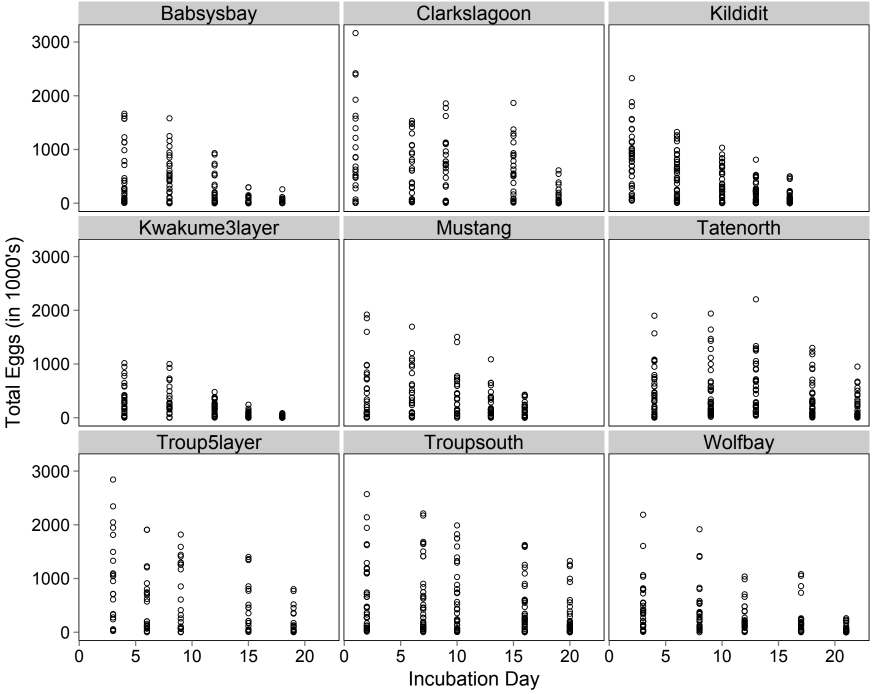

Figure F2. Total egg abundance through time by survey site.

Appendix G. Model output parameters for various approaches used to handle zeros in the data

Table G1. Slope and intercept (ln(N_0)) values across all sites (global) and for each site from model outputs using different statistical approaches to handle zero egg values in the data. In the first three approaches (ln(Eggs+1); ln(Eggs+45) and ln(Eggs+90)), constants were added to all values of egg abundance. In the fourth approach (ln(Eggs)), zeros were removed from the data prior to log transformation. If we multiply the slope values by -1 we are left with the instantaneous egg loss rate (Z).

	ln (Eggs+1)		**ln (Eggs + 45)**		**ln (Eggs + 90)**		**ln (Eggs)** *Zeros Removed*	
Site	**ln(N_0)**	**Slope**	**ln(N_0)**	**Slope**	**ln(N_0)**	**Slope**	**ln(N_0)**	**Slope**
Global	13.084	-0.205	13.051	-0.177	13.044	-0.171	13.195	-0.152
Babsysbay	13.448	-0.415	13.120	-0.325	13.065	-0.307	13.378	-0.267
Clarkslagoon	13.268	-0.154	13.284	-0.145	13.281	-0.142	13.271	-0.127
Kildidit	12.968	-0.248	13.176	-0.232	13.210	-0.228	13.776	-0.230
Kwakume3layer	14.063	-0.355	13.676	-0.296	13.598	-0.283	13.288	-0.213
Mustang	12.056	-0.141	12.159	-0.119	12.180	-0.115	12.299	-0.094
Tatenorth	13.173	-0.098	13.086	-0.084	13.073	-0.081	13.026	-0.062
Troup5layer	12.348	-0.133	12.635	-0.120	12.690	-0.118	13.398	-0.128
Troupsouth	13.314	-0.110	13.222	-0.098	13.205	-0.095	13.149	-0.087
Wolfbay	13.142	-0.187	13.107	-0.172	13.098	-0.168	13.222	-0.164

Appendix H. Site-level measures of predator biomass, exposure and spawn area

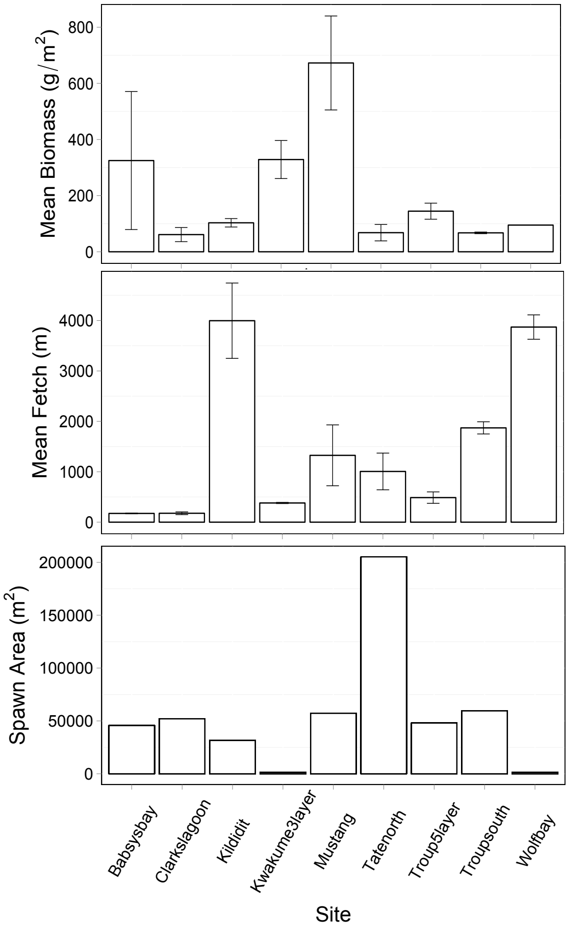

Figure H1. Site-level measures of factors hypothesized to influence egg loss rate. A. Predator biomass determined from fish and invertebrate surveys, B. mean fetch in the Southeast quadrat, reflecting dominant winter wind direction, C. total area covered by spawn.

Appendix I. Approach 3: Plots showing the relationship between biological and physical factors and egg loss rates

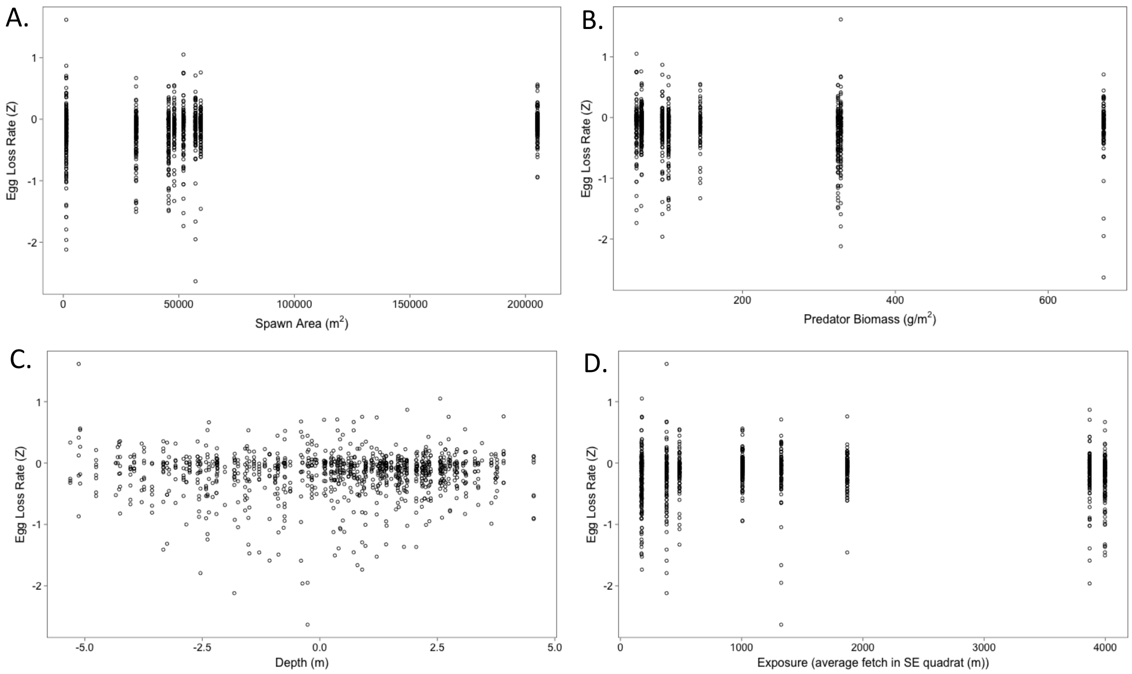

Figure I1. Relationship between measures of A. total spawn area per site, B. predator abundance measured as total biomass per site, C. depth, measured for per quadrat, and D. exposure, measured using average fetch in the SE quadrat per site, and egg loss rate (calculated per quadrat using Eq. 4).

Appendix J. Predator exclusion experiment using wet weight as a response variable

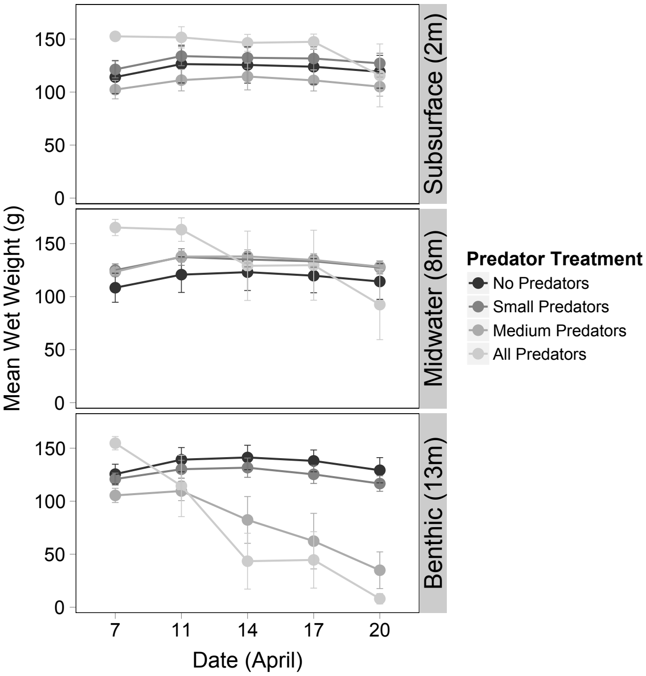

Figure J1. Egg biomass through time as measured by wet weight of pieces of roe-on-kelp under various habitat types and predator treatments. Weight was removed as a response variable from the primary analysis due to the variability introduced by inconsistent exposure to air among samples and resulting desiccation.

Table J1. Strength of evidence of alternative candidate models to determine the effect of treatment and depth on egg abundance through time as measured by weight.

Response and Model	**N**	**AICc**	**K**	**ΔAICc**	$\mathbf{w}_i$
Weight					
Time*Treatment*Depth	296	2637.5	30	0	1
Time*Treatment	296	2751.8	14	114.4	<0.001
Time*Depth	296	2785.3	12	147.9	<0.001
Time	296	2488.8	8	158.2	<0.001