


RESEARCH ARTICLE

Factors driving spatial variation in egg survival of an ecologically and culturally important forage fish

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Abstract

1. Low trophic-level forage fish are experiencing global declines, influencing coupled human-ocean systems worldwide. Along the northwest coast of North America, declining trajectories of Pacific herring (*Clupea pallasii*) have prompted interest in improving the understanding of its population and community dynamics to better guide future conservation and management strategies.
2. To improve future population estimates and understanding of the ecological factors governing herring egg survival, the magnitude, spatial variation and mechanisms driving herring egg loss rates were quantified. This was achieved by way of repeated observational field surveys and a predator exclusion experiment.
3. Observational surveys revealed that regional egg loss rates (Z) were substantial and ranged from 0.101 ± 0.019 to 0.134 ± 0.028 , the equivalent of 88–94% egg loss over a 21 day incubation period, or 50–60% egg loss over 6.8 days, the average time lag between spawn deposition and annual egg surveys. Furthermore, spatial variation was high, with egg loss rates varying 5-fold among study sites. Depth, time since spawn, and spawn area were primary spatial drivers of egg loss, but predator abundance and exposure were secondarily important.
4. Experimental evidence showed that benthic predation and habitat type were strong drivers of egg loss, suggesting that a high proportion of eggs, particularly those spawned on benthic substrates, are consumed by predators.
5. These results have important conservation implications for managers and ecologists seeking to estimate herring biomass and to understand the environmental influences on predator-prey interactions that affect herring dynamics.

KEYWORDS

Clupea pallasii, coastal habitat, egg loss, forage fish, predator-prey dynamics, subtidal

1 | INTRODUCTION

Forage fish provide a vital link in ocean food webs, yet are experiencing global declines (Pikitch et al., 2014; Pinsky, Jensen, Ricard, & Palumbi, 2011; Smith et al., 2011). As prey to a diversity of piscivorous fish, seabirds and marine mammals, declines in low trophic level fish can have extensive ecosystem-wide consequences, with knock-on social and economic effects (Cury et al., 2000; Pikitch et al., 2014). Yet managing forage fish is often complicated by their dramatic population fluctuations, erratic recruitment dynamics and schooling

behaviour, making their populations difficult to estimate and predict (Pikitch et al., 2012). These challenges and downward trajectories have catalysed widespread interest in improving the understanding of the ecological factors driving the population dynamics of these fish, which are a critical component of temperate coupled human-ocean systems worldwide.

Along the northwest coast of North America, Pacific herring (*Clupea pallasii*) are a dominant species of forage fish that play a pivotal ecological role in pelagic and coastal foodwebs (Anderson, Lovvorn, Esler, Boyd, & Stick, 2009; Fox, El-Sabaawi, Paquet, & Reimchen,

2014; Fox, Paquet, & Reimchen, 2015; Lok et al., 2012; Willson & Womble, 2006; Womble, Sigler, & Willson, 2009) and have significant cultural and socio-economic value (Brown & Brown, 2009; O'Donnell et al., 2013). Archaeological and ethnographic evidence suggests that indigenous communities have harvested herring, in some places, for more than 10 000 years (McKechnie et al., 2014). Importantly, Pacific herring have been foundational to coastal social-ecological systems in this area for millennia, representing a true ecocultural icon in the North Pacific (Brown & Brown, 2009). Over the last century, herring and herring eggs have also become the target of industrial harvest, supplying a range of national and international markets (DFO, 2013). However, spawning populations of this formerly abundant forage fish have declined considerably over the past decade across much of its range in the Northeast Pacific (Benson, Cox, & Cleary, 2015; Cleary, Cox, & Schweigert, 2010; Schweigert, Boldt, Flostrand, & Cleary, 2010; Siple & Francis, 2016). Low biomass, decreased size-at-age and adult survivorship (Martell, Schweigert, Cleary, & Haist, 2012), and a lack of recovery despite fishery closures (Schweigert et al., 2010), have prompted investigations into the factors driving herring population dynamics.

Each spring, from the low latitude coastlines of northern California, through British Columbia and northwards throughout Alaska, Pacific herring mass along the coast to spawn on benthic substrates (Haegele & Schweigert, 1985a; Lok et al., 2012). Eggs are deposited on hard substrates and various species of marine vegetation, including low growing macroalgae and seagrass, as well as canopy forming kelps that occupy the water column (Fort, Daniel, & Thompson, 2009; Haegele, Humphreys, & Hourston, 1981; Haegele & Schweigert, 1985b). Population estimates of these pelagic fish are typically based on the number of observable eggs spawned by females along coastlines in the spring. However, there is often a time lag between when the eggs are deposited and when they are counted (Martell et al., 2012). During this time interval, eggs can be removed by predation, dislodgement by waves or other factors. Consequently, quantifying egg loss rates, the rate at which eggs are lost to the environment through time, is an important step in estimating spawning populations (Martell et al., 2012).

Herring egg loss rates, often denoted as the parameter Z in Pacific herring stock-assessment models, have been estimated in several regions across the Northeast Pacific based on the decay rate of eggs observed through time (Haegele & Schweigert, 1989, 1990; Rooper, Haldorson, & Quinn, 1999). These estimates are used to generate a universal value that is applied to population assessments across Canada's Northeast Pacific coast. Recently, however, egg loss rates have been shown to vary across sites in other regions of the Northeast Pacific (Washington State; Shelton, Francis et al., 2014), highlighting the coastwide need to quantify the spatial variation in egg loss rates and the mechanisms that drive it.

Empirical evidence suggests that the spatial distribution of spawned herring eggs within the intertidal and subtidal can vary in length, width, depth, as well as in egg layer thickness (Hay, 1985). Consequently, the deposition of eggs, as well as post-deposition mortality, is likely influenced by a range of biological and physical factors that interact to affect the rate and variability in egg loss. Waves and currents can dislodge herring eggs from substrates,

contributing to their loss from surveyed populations (Hart & Tester, 1934; Hay & Miller, 1982). Habitat alteration associated with urban development can also affect egg survivorship (Shelton, Francis et al., 2014). In addition to these physical factors, predation by a variety of subtidal predators, as well as terrestrial predators that can access the intertidal, have been found to influence herring egg survival (Bishop & Green, 2001; Haegele, 1993; Haegele & Schweigert, 1989; Outram, 1958; Rooper, 1996; Willson & Womble, 2006). These community-level interactions, from small beach-associated amphipods (Fox et al., 2014) to migratory sea ducks (Lok et al., 2012) and top predator bears (Fox et al., 2015), demonstrate the pivotal connections that herring, their eggs, and the harvest of herring-derived biomass play in the coastal environment. While these ecological linkages have been described, spatial variability in predatory effects and community-level interactions have not been well resolved geographically.

Although many factors may drive egg loss, to date, few studies have quantified the spatial variation in herring egg loss rates, tested the mechanisms driving them, or quantified the uncertainty associated with the methods commonly used for estimating egg loss rates (Haegele & Schweigert, 1989, 1990; Rooper et al., 1999; Shelton, Francis et al., 2014). This paucity of knowledge reduces the ability to forecast egg loss rates under a range of biotic and abiotic conditions. More broadly, ignoring environmental heterogeneity and measurement error associated with analytical tools can spur environmental controversies (Biggs, Carpenter, & Brock, 2009). Consequently, improving estimates of variability and uncertainty in Pacific herring egg loss is a critical step towards advancing the conservation and management of this ecologically, economically and culturally important forage fish.

Here, repeated subtidal surveys were used to assess the magnitude of spatial variation in Pacific herring egg loss rates and the physical and biological factors that drive loss rates along the central coast of northwestern Canada (Figure 1). Given the importance of egg loss in estimating adult herring populations, three unique quantitative models were used to assess the measurement error associated with egg loss estimates. Lastly, a large-scale field experiment, based on traditional indigenous herring egg harvest practices, was designed to explicitly test the degree to which habitat type and predation affect herring egg loss.

2 | METHODS

2.1 | Observational study of egg loss

Herring egg loss was monitored following a spawn event for up to 22 days at nine sites on the central coast of British Columbia (BC), Canada in the spring of 2012 (Figure 1). On BC's central coast, spawn dates range from the beginning of March through to the end of May, with a majority of spawn events occurring in late March and early April (Hay, McCarter, & Daniel, 2008).

Sites were chosen based on daily Fisheries and Oceans Canada (DFO) herring spawn reports and observations by local Heiltsuk First Nation collaborators in Bella Bella, BC. Nine spawn sites (Figure 1c),

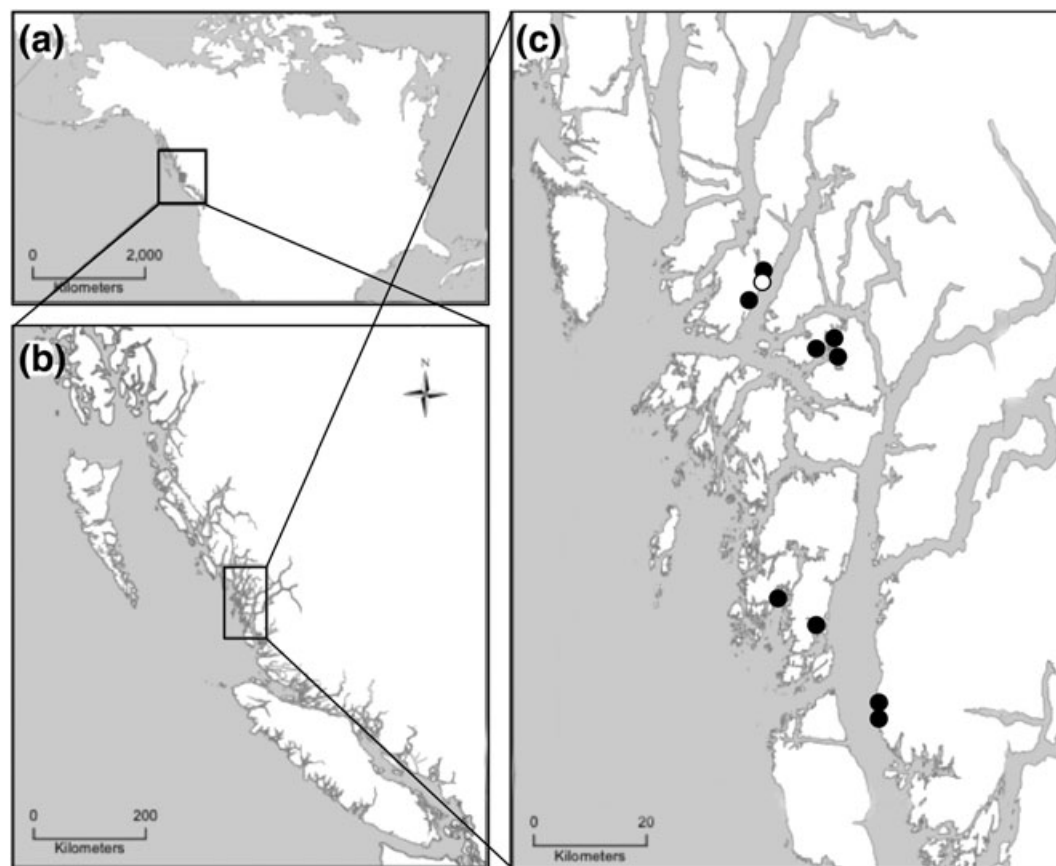


FIGURE 1 (a) and (b) The central coast of British Columbia, Canada. (c) Locations of nine Pacific herring spawn survey sites (solid circles) and predation experiment (open circle)

all of which were dominated by rocky substrate and attached vegetation, were surveyed five times. Sites varied in wave exposure and total spawn area, and ranged in depth from +4.6 m to -5.31 m chart datum.

A team of four divers conducted visual surveys at each site between 27 March and 25 April 2012. At each site (Figure 1c), four replicate vertical transects were established running perpendicular to shore on the first day after spawn completion. Transects were marked with lead line and covered the width (vertical depth 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. Lead lines were anchored throughout with rocks to minimize the chance of displacement.

The number of herring eggs was estimated on various substrate types within 0.5 m² quadrats. Quadrats were placed at permanent locations marked at 2 m intervals along the transects, based on established DFO methodology (Fort et al., 2009). Because spawn width (max and min depth) varied among sites, and the number of quadrats sampled was a function of spawn width, more quadrats were sampled across wider, more expansive spawns. In each quadrat, time and depth were noted, and the percentage cover of each substrate type (vegetation and benthos type), the percentage cover of eggs on each of those substrates, and the number of egg layers were estimated. Divers returned to re-evaluate these variables at the same quadrat location every 3 to 5 days throughout the egg incubation period (18 to 22 days), visiting each site five times. WWW Tide

and Current Predictor (Pentcheff, 2012) was used to adjust observed depths to chart datum based on data from Bella Bella and Namu tide stations.

To quantify potential herring egg predator density and biomass, underwater visual surveys of benthic fish and macroinvertebrates were conducted (Table S1, Supporting material) at all survey locations. Abundance and maximum length of all identified species were recorded along 30 × 4 m horizontal belt transects ($n = 3-6$ per site) across a shallow (~1–7 m) and deep (~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 (Table S1), 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.

Total egg density was summed within each sampling quadrat from estimates of eggs on vegetation and bottom substrate using procedures outlined in Schweigert (2001) and Haegele, Hoursten, Humphreys, & Miller (1979) (Methods S1, Supporting material). Schweigert's egg abundance calculations were modified to consider the percentage cover of eggs on each vegetation type. These calculations were tested against Schweigert's original calculations (that include the percentage of the quadrat covered by each vegetation type and not the percentage cover of eggs on each vegetation type) and very similar modelling results were found, although parameter

estimates differed slightly (compare unmodified Schweigert calculations Table S3. A, B with modified results Table 1 and Table S4).

During months when herring typically spawn, BC's central coast experiences intense storms with high winds and seas (Haggarty et al., 2003; Lucas, Verrin, & Brown, 2007), all of which can increase egg loss from nearshore substrates. Winter and early spring winds in this region are primarily from the south-east (Lucas, Verrin, & Brown, 2007); therefore, average fetch length was selected within the south-east quadrant as a measure of exposure for each site (Burrows, Harvey, & Robb, 2008). Average fetch length was calculated from fetch values determined every 3° at each site.

2.1.1 | Statistical analysis

2.1.1.1 | Modelling egg loss through time

Linear mixed-effects models (LME) were used to determine the extent of herring egg loss across sites. Egg loss rate (Z) was estimated using three approaches, all of which assume exponential decay of egg abundance (Equation 1). For Approach 1 and 2, instantaneous egg loss rate (Z) was calculated by taking the natural log of both sides of Equation 1

and estimated from the slope of the linear model of log transformed egg abundance as a function of time (t) (Equations 2, 3):

$$N_t = N_0 \exp(-Zt) \exp(\epsilon_t) \quad (1)$$

$$\ln(N_t) = \ln(N_0) + \ln[\exp(-Zt)] + \ln[\exp(\epsilon_t)] \quad (2)$$

$$\ln(N_t) = \ln(N_0) - Zt + \epsilon_t \quad (3)$$

where N_t is the number of eggs at day t , N_0 is the number of eggs initially deposited (intercept), Z is the instantaneous egg loss rate (slope), and ϵ is a random error term with mean 0 and constant variance. Approach 1 and 2 simply use different strategies for managing undefined values of $\ln(0)$ resulting from zero-egg values (i.e. no eggs recorded). For Approach 1, half of the lowest non-zero egg abundance was added to all values. For Approach 2, egg abundance through time was modelled to the smallest non-zero number of eggs. Approach 2 removed all zeros from the dataset (<10% of data) and follows DFO dive spawn survey protocols, which specify that zero values not be recorded, as well as the methods of Rooper et al. (1999).

TABLE 1 Strength of evidence for alternative candidate models examining the influence of biological (predator abundance, spawn area) and physical (depth, wave exposure) factors on egg abundance. Candidate model sets were determined using three different modelling approaches. Models with varying numbers of parameters (K), were compared with differences in Akaike's Information Criterion (Δ_i), likelihood of the model given the data ($\text{Log}(L)$), and normalized Akaike's weight (w_i) indicating the weight of evidence in favour of model i . Reported are the top eight models in our candidate set. For approaches 1 and 2, all models allowed the intercept and time coefficients to vary randomly by site, transect within site, and quadrat within transect within site (6 random effects and $K = 9$ total random effects variance-covariance parameters). Approach 3 included the same structure, but only allowed the intercept to vary as there is no time covariate (leaving 3 random effects and $K = 3$ variance parameters).

Response and Model	K	Log (L)	AIC _c	ΔAIC_c	w_i
APPROACH 1: $\ln(\text{Egg Abundance} + 45)$					
Time * Depth + Predators	16	-2601.5	5235.3	0	0.2
Time + Depth + Predators	15	-2602.5	5235.4	0.1	0.2
Time + Depth	14	-2604.1	5236.5	1.2	0.1
Time * Depth	15	-2603.1	5236.6	1.2	0.1
Time * Depth + Predators + Exposure	17	-2601.4	5237.3	2.0	0.1
Time + Depth + Spawn Area	15	-2603.5	5237.3	2.0	0.1
Time + Depth + Predators + Exposure	16	-2602.5	5237.3	2.0	0.1
Time * Depth + Spawn Area	15	-2602.6	5237.6	3.2	0.1
APPROACH 2: $\ln(\text{Egg Abundance})$					
Time + Depth + Predators	15	-2108.9	4248.1	0	0.3
Time + Depth	14	-2110.3	4248.9	0.8	0.2
Time + Depth + Spawn Area	15	-2109.7	4249.7	1.6	0.1
Time + Depth + Predators + Exposure	16	-2108.8	4250.0	1.9	0.1
Time * Depth	15	-2110.0	4250.3	2.2	0.1
Time + Depth + Exposure	17	-2110.3	4250.9	2.8	0.1
Time + Depth + Predators + Exposure + Spawn Area	17	-2108.4	4251.3	3.1	0
Time * Depth + Predators + Exposure	16	-2108.6	4251.7	3.6	0
APPROACH 3: Egg Loss Rate (Z)					
Spawn Area	6	-205.2	422.5	0	0.3
Intercept	5	-206.3	422.6	0.1	0.3
Predation	6	-205.8	423.8	1.3	0.2
Depth	6	-206.2	424.5	1.9	0.1
Exposure	6	-206.3	424.6	2.1	0.1
Spawn Area + Predators + Depth + Exposure	9	-204.8	427.8	5.3	0

Models showing interaction terms also include all individual additive terms.

For the third approach, egg loss rates (Z) were calculated directly from the data (Equation 4):

$$Z_{t+\Delta t} = [\ln(N_{t+\Delta t}) - \ln(N_t)] / \Delta t \quad (4)$$

Rather than deriving a single egg loss (Z) parameter estimate from a linear model fit to the data, in this approach the average (instantaneous) egg loss rates (Equation 4) for each time interval in the survey ($n = 4$ decay periods) was calculated. Here, Δt is the elapsed time between sampling periods N_t and $N_{t+\Delta t}$.

Using the estimated loss rate parameters from each approach, the expected proportion of eggs lost over specific time intervals was calculated. Specifically, for each model approach, expected egg loss after 1 day, 6.8 days (the mean time lag between initial spawn and the BC dive surveys), and 21 days (the average incubation period for the central coast of BC), was estimated.

2.1.1.2 | Model structure

To test the strength of evidence for the causal factors driving egg loss rates, alternative mixed effects models were constructed. For Approaches 1 and 2, transformed egg abundance was modelled as a function of time (days) and local covariates as fixed effects, allowing both the intercept and time coefficients to vary by nested random effects (site, transect within site, and quadrat within transect within site). Both intercept ($\ln(N_0)$) and slope (Z) varied among all quadrats in the nested structure of the model. The temporally auto-correlated nature of the time series data was accounted for by incorporating a continuous time first-order correlation structure in the variance covariance matrix using the *corCAR1* function in the *nlme* package (Pinheiro, Bates, DebRoy, Sarkar, & Core Team, 2015) in R (R Development Core Team, 2015).

For Approach 3, instantaneous egg loss rate (Z) was modelled as the response variable, with the intercept being allowed to vary as nested random effects (site, transect within site, and quadrat within transect within site). All mixed effects models in this study were estimated using the *nlme* package (Pinheiro et al., 2015) in R (R Development Core Team, 2015).

In order to investigate individual site-level differences in egg loss rate, a separate analysis was conducted with site as a fixed effect in the best model for each of the three approaches. This allowed for the estimate of loss rate at each site without sacrificing potential accuracy in estimating specific, site-level parameters, as is the case with the mixed effects model structure (Pinheiro & Bates, 2000). This analysis was conducted for illustrative purposes and not used for model selection.

2.1.1.3 | Model selection

To determine the strength of evidence among alternative, non-mutually exclusive, hypothesized causal factors driving Pacific herring egg loss rates, an information-theoretic approach was used (Burnham & Anderson, 2002). To assess the strength of evidence for each explanatory variable (predator abundance, total spawn area, wave exposure, and depth) in driving regional variation in the response variables, alternative candidate models were compared with small-sample bias-corrected Akaike's Information Criterion (AICc), standardized to the most parsimonious model ($\Delta AICc$), and with multi-model inference

(Burnham & Anderson, 2002; Grueber, Nakagawa, Laws, & Jamieson, 2011). The model likelihoods were normalized 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 the set of candidate models, multi-model averaged parameter estimates and relative variable importance (RVI), otherwise known as variable weights, were calculated using the *MuMIn* package in R (Barton, 2013). RVI for a given factor is determined by summing the Akaike weights (w_i) across all models in the candidate set where the factor occurs (Burnham & Anderson, 2002). To easily interpret the relative importance of each factor in the candidate model set, predictor parameters were standardized to a common scale by subtracting their mean and dividing by 2 standard deviations (Gelman, 2008).

2.2 | Predator exclusion experiment

To specifically test the effect of predation and habitat on egg loss rates, a predator exclusion experiment was conducted. The experimental location in Spiller Channel (Figure 1c) was selected as an area where herring had spawned in the past and spawn-on-kelp had been harvested by local Heiltsuk First Nation collaborators from Bella Bella, BC. Sixty 13×10 cm experimental units of herring spawn-on-kelp (*Macrocystis pyrifera*) were randomly assigned to four predator exclusion treatments (15 replicates per treatment); large size predator exclusion (25×25 mm vexar mesh), large and medium sized predator exclusion (7×7 mm vexar mesh), all sized predator exclusion (1×1 mm Nitex™ mesh), and all predators present (no enclosure). Where mesh was used to exclude predators, spawn-on-kelp units were placed freely in the envelope-type enclosure. Spawn-on-kelp units with no enclosure were affixed to lines using plastic tubing around the bulb at the stipe.

A single line was suspended across a bay, from which individual lines were sunk vertically, mimicking the traditional indigenous spawn-on-kelp fishery. Each treatment was attached to a vertical line at three habitats: subsurface (2 m), midwater (8 m) and benthic sea floor (13 m) (Figure 2). This experimental design consisted of blocks of fully crossed replicates located at ~3 m intervals across the length of the bay (~75 m wide). To quantify egg abundance over time, each piece of spawn-on-kelp was weighed and assessed for percentage egg cover and egg layer thickness every 2–3 days, for a total of five times, and thus four decay periods over 14 days. Pieces of spawn-on-kelp were monitored for hatched eggs throughout the study period to ensure predation was not confused with larval hatch. Additionally, given the study period was less than the average incubation period in this region, hatching was expected to have little influence on the estimates of egg abundance.

2.2.1 | Statistical analysis

2.2.1.1 | Modelling the effects of predation and habitat on egg loss

Linear mixed effects models were used to assess the strength of evidence for the effects of predation and habitat type on egg loss in the experiment. Egg loss was evaluated using three different response variables: (1) percentage cover; (2) number of egg layers; and (3) instantaneous egg loss rate, as calculated in Approach 3 of the observational study (Equation 4, $n = 4$ decay periods). Wet weight was excluded as

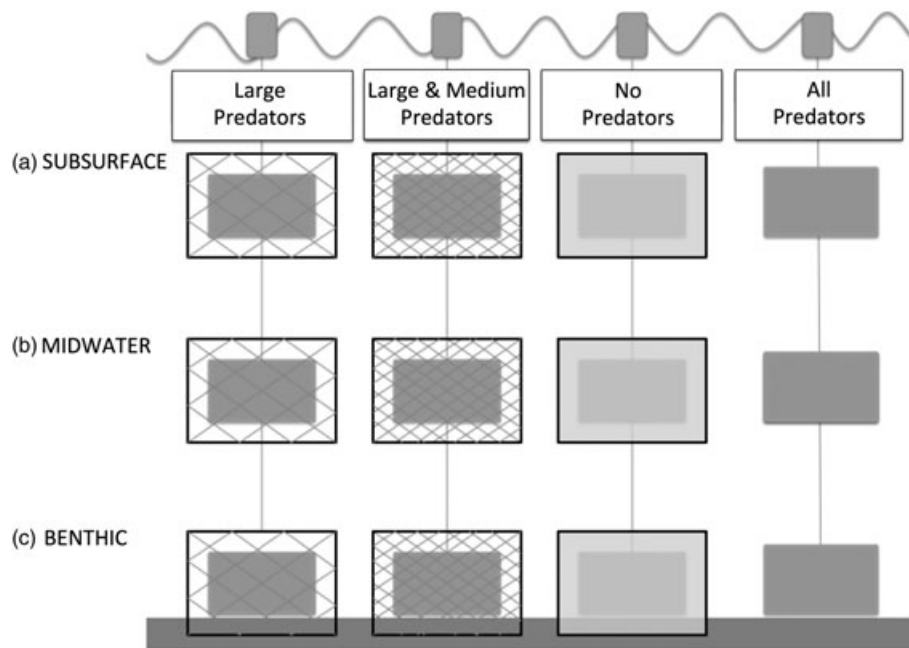


FIGURE 2 Experimental design used to test the effects of predation and habitat type on egg loss rates. Sixty 13×10 cm sub-samples of SOK (herring spawn on giant kelp *Macrocystis pyrifera* (grey rectangle)) were assigned to one of four predator treatments and submerged to three different habitats (A. 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 five times across a bay in Spiller Channel, near Bella Bella, BC

a response variable owing to the variability introduced by inconsistent exposure to air among samples and resulting desiccation.

2.2.1.2 | Model structure

Models of percentage cover and egg layer number included time as well as all additive and interactive effects of habitat and predator treatment as fixed effects. Experimental block ($n = 5$) was treated as a random effect, with the intercept varying by block. The assumption of independence (i.e. through time) and equal variance (i.e. between factors) were evaluated by adding correlation and variance structures to the models, and evaluating improvements to model fit (based on AICc). Serial dependence between repeated measures was accounted for by using a first-order correlation structure (with time covariate) in the residuals using the `corCAR1` function in the *nlme* package in R. 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.

2.2.1.3 | Model selection framework

To assess the strength of evidence for predation and habitat type driving variation in response variables, Akaike weights (w_i) of alternative candidate models were compared using the same model selection approach as in the observational study described above.

3 | RESULTS

3.1 | Observational study of egg loss

Global instantaneous egg loss rates (Z) across all sites for Pacific herring spawn on BC's central coast were estimated as 0.134 ± 0.028 ,

0.101 ± 0.019 , and 0.116 ± 0.010 for Approaches 1, 2 and 3, respectively (Figures 3, 4), equating to a daily egg loss of 10% to 13%. This corresponds to 88–94% egg loss over a 21 day incubation period, or 50–60% egg loss over a 6.8 day period, the average time lag between spawn deposition and herring egg surveys on the Central Coast (Martell et al., 2012). Global and site-specific estimates of Z were consistent across statistical approaches based on overlapping standard errors (Figure 4). Estimated values based on Approach 1, where the value of 45 was added to all egg numbers as a constant before log transformation, were slightly greater than Approach 2, where all zeros were removed before transformation (except for one out of nine sites). Estimated values based on Approach 2 were consistently lower than Approach 3, where egg loss rate was the response variable. Substantial spatial variation in egg loss rates (maximum egg loss rate values = 0.285, 0.188, 0.205, minimum egg loss rate values = 0.050, 0.029, 0.032, for approaches 1, 2, and 3, respectively) was estimated for all three approaches (Figure 4, Table S4). This variability is illustrated by site-level estimates of loss when included as a fixed effect, with an approximate 5-fold maximum difference in loss rates among sites averaged across modelling approaches (Figures 3 and 4, Table S4).

3.2 | Factors affecting observed egg loss

There was no strong empirical support for one model of egg abundance over another given the ΔAIC_c values of ≤ 2 for the top six models (Table 1). For Approaches 1 and 2, both time and depth were included in all top models. Here, time, depth, and their interaction, account for the greatest variation in egg abundance across the sample period ($RVI = 1$ (depth and time), 0.46 (depth \times time), Figure 5a). Predator abundance, exposure, and spawn area, were also included across top models (Table 1), but were

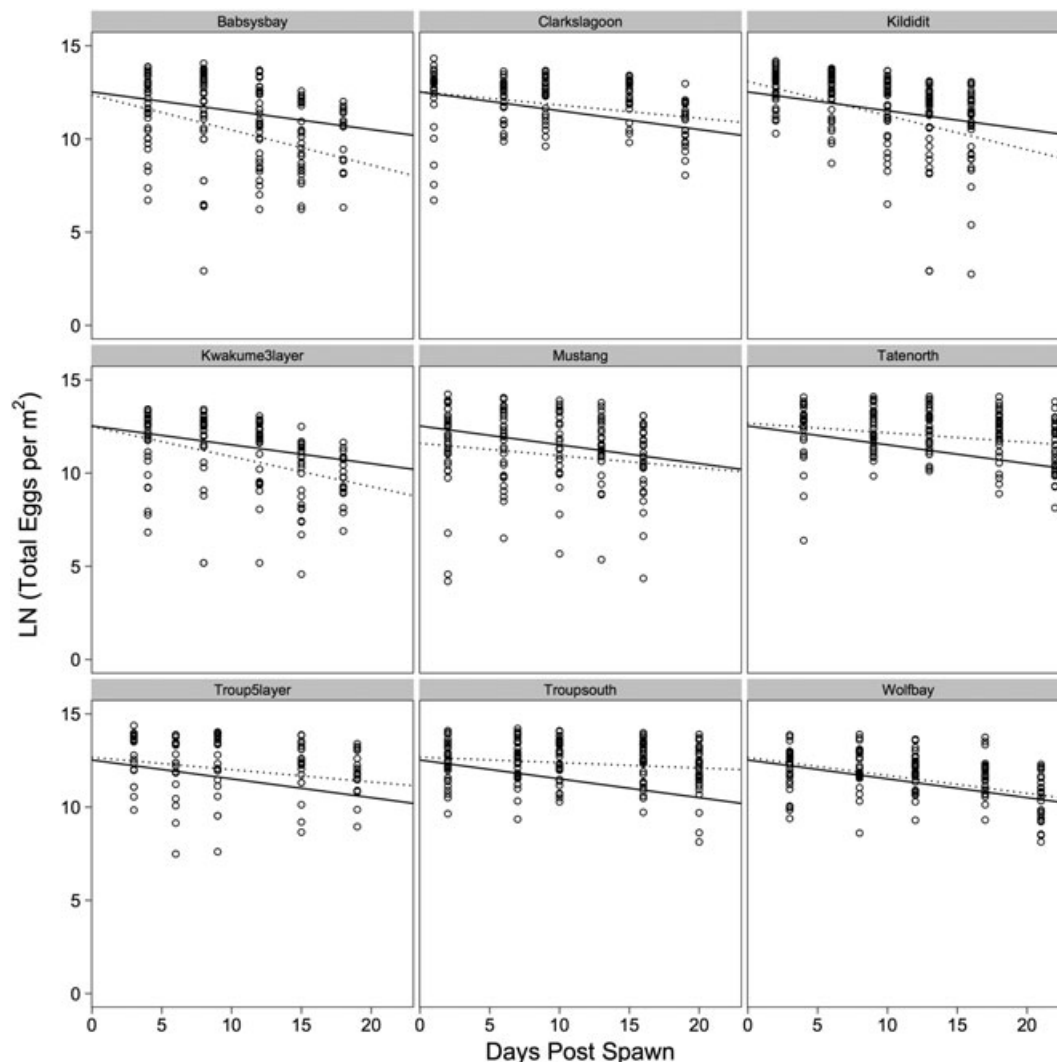


FIGURE 3 Density of Pacific herring eggs, log transformed, as a function of days post spawn at nine sites across British Columbia's central coast. The solid line indicates the global model fit, while the dotted lines indicate site-specific model fits estimated by linear mixed effects models using modelling Approach 2 (all zeros removed from egg abundance data set before log transformation). Slope values are the modelled instantaneous egg loss rate (see Equation 3 & Table S5)

less important overall in predicting egg abundance; their confidence intervals include zero, suggesting that the role of these factors was highly uncertain (Figure 5a). Furthermore, the interactive effects of time with each of predator abundance, exposure and spawn area on egg abundance have an RVI of 0, suggesting these parameters have little influence on egg loss rate, the slope of the model (Figure 5a).

For Approach 3 (with no time), spawn area was the strongest predictor of egg loss (Table 1) and was the most important factor across top models (Figure 5b: RVI = 0.33). However, similar to Approaches 1 and 2, predator abundance (RVI = 0.18), depth (RVI = 0.14) and exposure (RVI = 0.13) were also factors represented across top models (Table 1). Furthermore, averaged across all top models, including spawn area, all factors had large confidence intervals and included zero (Figure 5b).

3.3 | Predator exclusion experiment

The experiment shows strong evidence that both predation and habitat type influence egg loss rates (Figure 6, Table 2). Specifically, both

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

4 | DISCUSSION

This study provides strong empirical evidence that Pacific herring egg loss rates along northwestern Canada's central coast are high, spatially variable, and greatly influenced by predation processes related to habitat, as well as predator abundance, spawn size and physical factors related to depth and exposure. Specifically, 50–60% of eggs spawned by herring were gone from the substrate on which they were

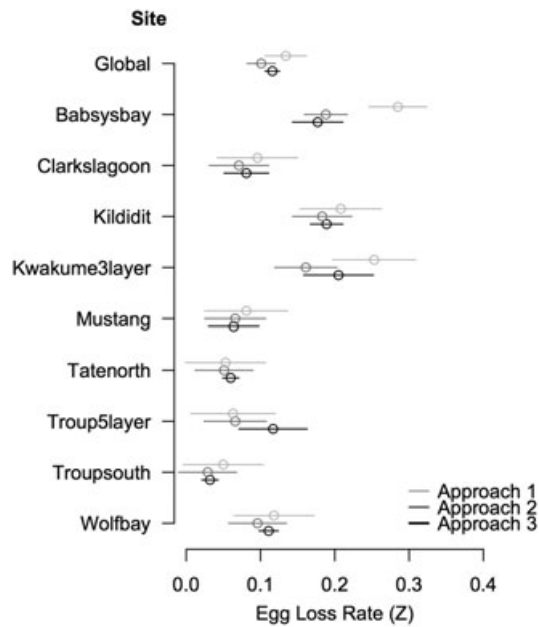
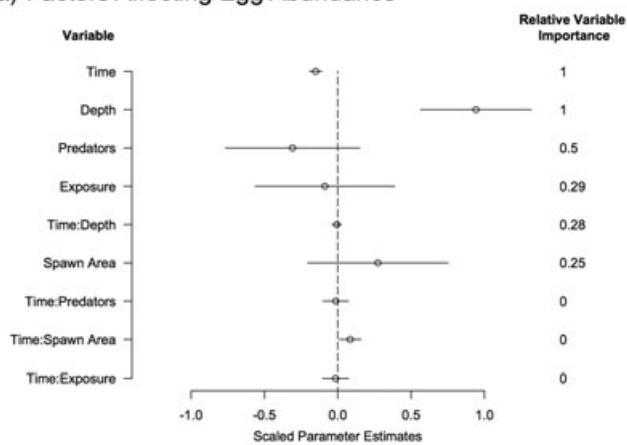


FIGURE 4 Pacific herring egg loss rates (Z , mean \pm standard error) including global mean and 9 site-specific estimates using three comparative modelling approaches. Modelled response variables include Approach 1: $\ln(\text{egg abundance} + 45)$; Approach 2: $\ln(\text{egg abundance})$ with zeros removed before log transformation; Approach 3: egg loss rate calculated using $Z_t + \Delta t = [\ln(N_t) - \ln(N_{t+\Delta t})]/\Delta t$

(a) Factors Affecting Egg Abundance



(b) Factors Affecting Egg Loss Rate

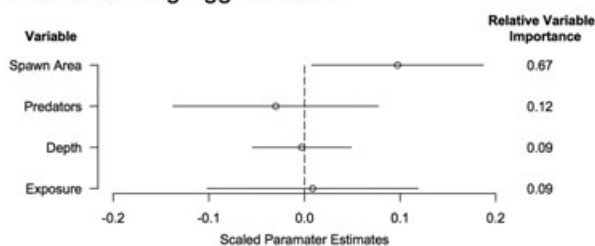


FIGURE 5 Scaled parameter estimates with 95% confidence intervals from averaging multiple linear mixed effects models. (A) Egg abundance using model Approach 2 (response variable: $\ln(\text{egg abundance})$ with zeros removed prior to log transformation). Note: Approach 2 chosen to illustrate trends in panel (A), but Approach 1 and 2 showed consistent, overlapping results. (B) Instantaneous egg loss rate (Z) using model Approach 3. Biological and physical variables thought to drive egg abundance and egg loss rate (on left) are ranked by their relative variable importance (on right)

deposited after 6.8 days, the mean number of days after which spawned eggs are typically surveyed for use in adult spawning population estimates. Moreover, egg loss rates varied from site to site, by a factor of 5 (Figures 3, 4). Field surveys revealed that herring egg survival is density-dependent, such that sites with larger spawn areas had higher egg loss rates (Figure 5b). Furthermore, depth was positively related to egg loss, such that shallower depths resulted in higher egg loss rates (Figure 5a). Experimental evidence revealed that habitat type (i.e. benthic versus pelagic positioning) and predation were strong drivers of Pacific herring egg loss (Table 1). These results have important implications for the conservation of Pacific herring and the social-ecological systems that depend on them.

4.1 | Variation in Pacific herring egg survival

Estimates of Pacific herring egg loss rates reported in the literature vary widely. In fact, published egg loss rates used to inform herring population estimates in British Columbia (Martell et al., 2012) vary as much as 2-times, based on those used from sites in Alaska ($Z = 0.076$; 0.042; Rooper et al., 1999), through to north-western Canada's Strait of Georgia ($Z = 0.056$; Haegele & Schweigert, 1989) and west coast of Vancouver Island ($Z = 0.083$; Haegele & Schweigert, 1989). The instantaneous egg loss rates (Z) reported here are substantially higher, ranging between 0.134 ± 0.028 , 0.101 ± 0.019 , and 0.116 ± 0.010 , depending on the quantitative model used (Figure 4). These estimates are consistent across the three modelling approaches, given the overlap in parameter uncertainty (Figure 4). While these rates of loss are higher, and differ substantially from those presented above, the 5-fold range across sites ($Z = 0.05$ to 0.285 ; 0.029 to 0.188 ; 0.032 to 0.205 for Approaches 1, 2 and 3, respectively, Table S4) was comparable with ranges of instantaneous egg loss rates from Puget Sound, Washington ($Z = 0.05$ to 1.29 , Shelton, Francis et al., 2014; $Z = 0.186$ to 0.73 , Palsson, 1984), and Prince William Sound, Alaska ($Z = -0.112$ to 0.263 , Rooper et al., 1999).

4.2 | Factors driving Pacific herring egg survival

The 5-fold difference in egg loss rates across nine sites spanning approximately 100 km of coastline provides strong evidence that herring egg loss is highly context-dependent and influenced by a number of biological and physical factors, including depth, predation, spawn area and wave exposure (Figures 5 and 6). Eggs removed from the substrate on which they were deposited may face mortality; conversely, they could float elsewhere and hatch. Over the entire 21 day incubation period of this critical forage fish, 88 to 94% of the initial eggs deposited were lost across all sites. Field surveys and the experiment point to key factors driving this loss.

Field surveys demonstrate that depth and spawn area were the two factors with positive effects on egg loss rates (Approach 1 and 2 – depth: RVI = 1; spawn area: RVI = 0.22; Approach 3 – spawn area: RVI = 0.33). Shallower depths (positive depth values) resulted in higher egg loss rates. In the experiment, eggs in benthic habitats and exposed to predation suffered greater loss than eggs on vegetation occupying the middle of the water column (Figure 6). This contrast is likely due to differences in sampling design, where eggs in the experiment

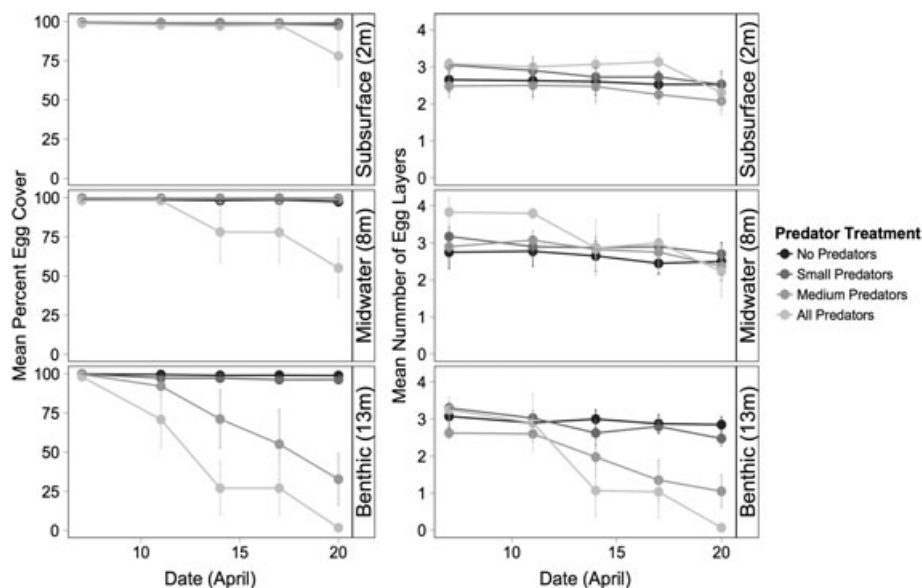


FIGURE 6 Mean percentage egg cover (graphs on left) and mean number of egg layers (graphs on right) through time for pieces of roe on kelp under four different predator treatments and three habitats

TABLE 2 Strength of evidence for alternative candidate models of the effect of predation (predator exclusion treatment) and habitat type (benthic, midwater, subsurface) using different response variables (Percentage Cover and Egg Layers as measures of egg abundance, and Egg Loss Rate, calculated using Equation 4)

Response and Model	K	Log (L)	AIC _c	Δ _i	w _i
Percentage Cover					
Time*Predation*Habitat	29	-1204.9	2474.3	0	1
Time*Predation	13	-1255.1	2537.7	63.4	0
Time*Habitat	11	-1268.2	2559.4	85.1	0
Time	7	-1282.9	2580.1	105.9	0
Egg Layers					
Time*Predation*Habitat	29	-277.3	621.5	0	0.9
Time*Predation	13	-298.9	627.3	5.8	0.1
Time*Habitat	11	-303.6	632.3	10.8	0
Times	7	-310.7	637.9	16.4	0
Egg Loss Rate (Z)					
Predation*Habitat	10	181.6	-342.2	0	1
Predation + Habitat	7	166.4	-318.2	24.0	0
Predation	6	160.7	-309.0	33.2	0
Habitat	4	156.5	-304.9	37.3	0
Intercept	3	152.3	-298.4	43.8	0

Models showing multiple interaction terms also include all individual interaction and additive terms.

remained subtidal for the duration of the study, while eggs in the observational study deposited in the shallow benthos and located at the intertidal end of the transect, were often exposed to other forms of predation, such as birds, known to account for large proportions of egg loss (30–55% Outram, 1958; 31% Bishop & Green, 2001). Furthermore, sites with larger total spawn areas had higher egg loss rates than those with smaller spawn areas (Figure 5b, Table 1). Multiple alternative hypotheses can be invoked to explain this result. Larger spawns may trigger an aggregative response among predators, such that a greater number of predators concentrate their foraging in areas

of high prey density (Krebs, 2001). However, the results from our observational surveys do not reflect this; it was found that predator abundance, on average, was negatively or neutrally related to egg loss (Figure 5). Alternatively, larger spawns may suffer more proportionally from wind-driven storm events. In Washington State, for instance, wave height was a key factor affecting egg hatch success (Shelton, Francis et al., 2014). In the current study, exposure was an important factor, but varied widely between sites in its effect on egg loss rate (Figure 5). Fortunately, results from the field experiment help disentangle these multiple drivers of egg loss and provide compelling evidence for habitat-mediated predation.

Field experimentation revealed that both subtidal predation and habitat type (water column location) drive herring egg loss. Specifically, eggs deposited on vegetation floating in the middle of the water column had a greater chance of survival than those deposited on vegetation lying on the sea floor (Figure 6). These results imply that marine vegetation with substantial vertical structure in the water column, such as kelp forests, may profoundly benefit herring eggs by decreasing the risk of benthic predation. Consequently, reduction in perennial canopy-forming kelp forests may have long-term indirect effects on herring population dynamics. Conducting a similar experiment within a dense kelp forest would be required to test this hypothesis. In addition, eggs deposited in the middle of the water column, compared with those spawned on the benthos, likely experience increased water flow and reduced sedimentation, both factors known to improve herring egg survival (Alderdice & Hourston, 1985; Griffin, Smith, Vines, & Cherr, 2009). Increasing available mid-water spawning habitat, and therefore surface area, may also allow eggs to be deposited at lower densities (Haegele & Schweigert, 1985a), thereby increasing egg viability through enhanced respiratory exchange within the egg mass (Taylor, 1971) and thus reduced density-dependent mortality. While variation in egg loss rate across substrates was not explicitly considered in this analysis, egg loss has been found to vary by substrate (Haegele & Schweigert, 1989), which combined with differing egg layer thicknesses, will further inform the understanding of

variability in herring egg loss. These findings also emphasize the context dependency of egg loss rates across the Northeast Pacific coastline. In Puget Sound, Washington, an urbanized coastline in this region, physical factors (i.e., wave height) and land use patterns drove spatial heterogeneity in egg survival. However, along the central coast of British Columbia, which currently has low human development, benthic habitat and depth, combined with predation pressure, were the strongest drivers of spatial heterogeneity in herring egg survival.

Notably, the strong effect of predation that was clearly revealed by the manipulative experiment was only weakly detected in our consideration of predator abundance in the observational field surveys (Table 1, 2; Figure 5). This could be because the surveys of subtidal predator abundance did not include avian predators, as discussed above. In addition, during the underwater visual transects, fish and other marine mammal predators may have avoided divers and escaped observation, resulting in diver detection bias (Sale & Douglas, 1981). Observational research conducted elsewhere attribute up to 30% of herring egg loss to subtidal predation by fish and invertebrates (Haegele, 1993; Haegele & Schweigert, 1989; Rooper, 1996), corroborating the role of predation as an important driver of herring egg loss and emphasizing that herring-derived biomass is a major player in ecosystem-level processes. Regardless of the source of loss, the magnitude and spatial variability in egg loss rates can have major implications for estimating and projecting Pacific herring populations.

4.3 | Implications for estimating and projecting Pacific herring populations

Estimates of spawning stock abundance and productivity are highly sensitive to assumptions of survey bias. In this context, such biases are known as 'catchability', a measure that relates 'true' biomass abundance to observations (Arreguín-Sánchez, 1996; Quinn & Deriso, 1999). For Pacific herring in the north-eastern Pacific Ocean, egg loss rates are a direct measurement of the bias associated with egg surveys, which are used to estimate spawning stock abundance (Washington: Stick, Lindquist, & Lowry, 2012, British Columbia: DFO, 2015, Alaska: Hebert, 2014). The estimated spawning stock abundance, typically measured in biomass, is directly proportional to egg 'catchability', given by $q = e^{-Zt}$, which is controlled by egg loss rates (Z) and the time elapsed between egg deposition and the survey (t). As a consequence, employing a higher or lower egg loss rate than the 'true' value can result in erroneously high or low spawning stock biomass estimates, meaning estimates may provide overly optimistic or pessimistic estimates of stock status (DFO, 2015). Inaccurately high estimates of spawning stock biomass can result in overexploitation. The observed egg loss rates from this study ($Z = 0.101$ to $Z = 0.134$; Figure 4) could have substantial effects on biomass estimates, as they were up to 3.6 times higher than the estimate ($Z = 0.0642 \pm 0.0187$) used in the past to inform Canada's Pacific herring population assessment model (Martell et al., 2012). Importantly, estimates of egg loss rates (Z) can also have substantial effects on other stock assessment properties, beyond bias, that also contribute to estimating spawning biomass.

Incorrect specification or biased estimation of Z , and the corollary effects on biomass estimates, can also affect estimates of spawning stock productivity (i.e. spawner–recruit 'steepness') from which

estimates of important equilibria, such as 'unfished spawning stock biomass' [B0] and maximum sustainable yield [MSY], are derived to produce catch quotas and metrics for conservation thresholds (Brooks, Powers, & Cortés, 2010; Lee, Maunder, Piner, & Methot, 2012; Martell et al., 2012; Rose & Cowan, 2003; Walters & Martell, 2004). Here, low estimates of spawning stock biomass can lead to erroneously high estimates of overall population productivity (i.e. 'steepness'). This can be especially problematic for highly productive fish (e.g. forage fish), where estimating a spawner–recruit relationship (and thus productivity) within a stock assessment framework has been questioned (Lee et al., 2012; Magnusson & Hilborn, 2007). For Pacific herring, the degree to which estimates of productivity exhibit sensitivity to Z depends upon several possible factors. Stock assessments that include additional data sources beyond egg deposition surveys (i.e. surveys of juvenile fish recruitment, acoustic telemetry of population abundance, and fisheries catch data) may provide independent inferences that can, in some cases, buffer against estimation bias in Z . In contrast, severe bias in Z may ensue when additional data sources do not agree, either in time or in type of demographic information. Furthermore, these effects will be increasingly complicated if Z in fact varies in time and space, as reported here.

In this study, egg loss rates do vary dynamically in space and time. Between 50 and 60% of herring eggs were lost over a 6.8 day period (Figure 3). This arises, in part, from variation in predation (Figures 5, 6). Because predation rates vary in time, and across space, the assumptions of a constant and density-independent Z in time (between years) and space (between management regions or between spawn locations) have strong potential to be flawed. Time-varying catchability is a common feature in fisheries data (Wilberg, Thorson, Linton, & Berkson, 2009) that can impose severe bias in trends and estimates of productivity if left unaccounted for. Because Z (egg loss) directly affects survey bias, assuming a constant Z in time and space will yield erroneous estimates of spawner biomass and productivity even if the mean value for Z (i.e. the single estimated value used across years in the assessment) is unbiased. For Pacific herring in the central coast of British Columbia, even estimating a fixed catchability has proven challenging as sensitivity analyses suggest catchability is driven largely by the Bayesian prior chosen in the model (DFO, 2015). These considerations highlight the need to consider the sensitivity of Pacific herring stock assessment output when Z in fact varies in time and space, and whether it is even possible to estimate Z under such circumstances. Here, catchability has been shown to vary in time and space from a mechanistic empirical standpoint. Consequently, future studies should ask: can time-varying Z be integrated into Pacific herring stock assessments, and if not, what are the consequences for Pacific herring abundance estimates?

Beyond Pacific herring, this research highlights the importance of quantifying measurement error and environmental heterogeneity for all species whose adult populations are estimated from early life-history stages that are prone to significant loss. For example, estimates of frog and salamander populations are typically based on annual surveys of egg masses found in breeding ponds because they are spatially discrete, and eggs, as well as tadpoles, can be accurately counted (Crouch & Paton, 2000; Loman & Andersson, 2007; Petranksa, Harp, Holbrook, & Hamel, 2007). Planktonic egg and larval surveys can provide an

estimate of spawning population abundance independent of commercial catch data for marine fish such as cod, Baltic sprat, Australasian snapper and sole (Armstrong et al., 2001; Haslob et al., 2012; Stratoudakis, Bernal, Ganas, & Uriarte, 2006), as well as for marine invertebrates such as the Norway lobster (Briggs et al., 2002). In addition to Pacific herring, population estimates for many pelagic forage fish such as mackerel, sardine, and anchovy, are informed by surveying spawned eggs (Stratoudakis et al., 2006). Yet, variability and uncertainty exist in early life-stage counts for many of these species, with profound implications for their population assessments and management.

4.4 | Conservation implications

The results have profound implications for the conservation of Pacific herring and the ecosystems and social systems that depend on them. Erroneously low estimates of egg loss rates can lead to underestimates of spawning stock biomass and erroneously high estimates of overall population productivity can in turn lead to the overexploitation of Pacific herring. The underlying assumption that there exists a single stock–recruit relationship with lognormal recruitment deviations (the standard assumption) is likely flawed given the large spatial variation documented here, and the range of factors leading to this variability. We expect this finding to apply to many fisheries, and other managed populations, where spatial variation below the scale of management is not adequately represented in population-level models. Improved estimates of herring population abundance and productivity, in addition to a better understanding of the factors driving their dynamics, will improve our ability to conserve this forage fish and thus the diversity of predators, including humans, that prey on herring throughout their various life stages, from eggs to larvae, juveniles and adults.

A diversity of conservation interventions could reduce the risk of overfishing herring along Canada's Pacific coast and strengthen the resilience of this coupled human–ocean system. For example, higher conservation thresholds, spatial closures on vulnerable spawning aggregations, shifting towards stage-specific harvest practices that minimize the risk of fishery closures and drawing from multiple knowledge systems are several practices that could support the sustained use of this forage fish by both people and nonhuman predators.

4.4.1 | Higher conservation thresholds

A recent meta-analysis on forage fish management and conservation worldwide recommends that existing uncertainties and knowledge gaps be explicitly addressed by adjusting conservation thresholds and harvest rates based on the quality and quantity of information on population status and key ecosystem linkages (Pikitch et al., 2012). Given the variability and uncertainty in Pacific herring egg loss rates (Figure 4), a key parameter used to estimate herring populations, and the ecological importance of herring to higher order predators such as Steller sea lion, black bear, and sea ducks such as surf scoters (Anderson et al., 2009; Fox et al., 2014, 2015; Lok et al., 2012; Willson & Womble, 2006; Womble et al., 2009), current conservation thresholds for Pacific herring (which equate to 25% of the estimated unfished biomass) need to be re-evaluated in light of

these global recommendations. Moreover, the uncertainty and variability in egg loss rates presented here have broad implications for uncertainty around reference points for forage fish management in general.

4.4.2 | Spatial closures on vulnerable spawning aggregations

While the spatial structure of Pacific herring populations is not known with certainty, recent work has revealed independent dynamics among spawning subpopulations in Puget Sound (USA), suggesting that variation in herring production is partially driven by local effects at or near spawning grounds (Siple & Francis, 2016). This independence and asynchrony at the subpopulation level confers stability at the larger regional population level (i.e. a 'portfolio' effect; Schindler et al., 2010). Consequently, harvest rates tailored to regional population estimates, but imposed on local subpopulations, could lead to serial collapse of localized subpopulations and reduced overall regional population stability if vulnerable spawning aggregations are targeted. Local spatial closures, nested scales of herring management and improved understanding of the spatial structure of herring metapopulations will advance strategies aimed at conserving this species. While these population-level 'portfolio effects' have been found for other fishery species (i.e. salmonids), regional scales of management have been slow to embrace heterogeneity in sub-population dynamics, across a wide range of species.

4.4.3 | Stage-specific harvest practices that minimize risk of ecosystem overfishing

Recent work assessing the interactions between Pacific herring populations, herring-dependent predators and two herring fisheries, one that targets adults and the other that targets spawned eggs, showed that herring stocks can withstand higher levels of egg harvest relative to adult harvest before becoming depleted (Shelton, Samhoury et al., 2014). Moreover, ecosystem thresholds designed to maintain the persistence of herring predators did not constrain fisheries any more than conventional harvest rules (Shelton, Samhoury et al., 2014).

Among fisheries worldwide, there is an increasing need to balance issues of social equity, conservation and use. Unfortunately, the livelihood and lifestyle objectives of indigenous communities are often overlooked (Plagányi et al., 2013). In the case of Pacific herring, a pressing need exists to evaluate the trade-offs among alternative harvest scenarios and the extent to which they meet the ecological, socio-cultural and economic objectives of all actors in this social–ecological system. This will require explicit consideration of the asymmetry in the population implications of all herring fisheries, those that harvest eggs and those that harvest adult fish (Shelton, Samhoury et al., 2014), and the ripple effects to ecological and social systems.

4.4.4 | Drawing from multiple knowledge systems

Understanding these complex systems, and developing conservation strategies that support their resilience can be enhanced through collaboration with coastal communities and the use of multiple sources of knowledge (Adams et al., 2014; Housty et al., 2014). Here, partnering with indigenous knowledge holders catalysed our main

research question, informed our hypotheses and improved the design of a field experiment that tested them. Specifically, this experiment, based on a First Nations traditional spawn-on-kelp fishery, illustrates how the incorporation of indigenous knowledge and manipulative experiments can offer novel contributions to our understanding of habitat-mediated predator–prey interactions, and in this case, Pacific herring population estimates. Broadly, this work showcases that the co-production of knowledge can provide innovative and scientifically rigorous insights into management and conservation solutions.

In summary, by combining observational surveys with field experiments, local traditional knowledge, and contemporary quantitative modelling techniques, this study revealed the degree of, and the factors driving, heterogeneity in Pacific herring egg survival. These results can be used to improve Pacific herring population estimates, and thereby advance the conservation of this critical forage fish and the ecosystems and social systems in which it is embedded.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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