

**Causes and Consequences of Pacific Herring
(*Clupea pallasii*) Deep Spawning Behavior**

by

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Abstract

Shifts in the reproductive strategies of marine species can result from ecological disturbance and often lead to either positive or negative population-level effects. Pacific herring (*Clupea pallasii*) can exhibit remarkable plasticity in spawn density and spatial distribution, shifting in response to both climatic and anthropogenic pressure. To test alternative factors leading to recently observed and previously uninvestigated deep spawning events (–30 m, 8 x the preceding 25-year mean), we surveyed spawn sites varying in motorized boat traffic, predator density, and sea surface temperature, and conducted a field experiment to test depth effects (at –3, –15, and –30 meters) on the survival rates of herring eggs exposed and protected from predation. We found herring spawn to –44 m, and strong evidence for a positive relationship between the depth of suitable habitat and maximum spawning depth, which was magnified when spawner density was high. This result is consistent with historical records of fisheries independent survey data collected from 1989 to 2015, showing an increase in maximum spawning depth with greater biomass of spawners. Finally, we found that depth significantly decreased egg survival. Survey observations found that deep spawn was unfertilized, and experimental evidence indicated that fertilized egg survival decreased, on average, by 20 % at –30 m relative to –3 m depths. If declining trends in spawning distribution continue as sea temperatures rise, the prevalence of deep spawning events may expand as herring become further concentrated into deep fjords and smaller geographic areas, adding further risk to already declining stocks.

Keywords: Pacific herring; forage fish; spawn depth; egg survival; central coast; fisheries management

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1. Introduction

Persistent environmental change caused by human activity can alter species' life history strategies causing both positive and negative population-level repercussions (Stenseth et al. 2002). For example, climate-induced changes in the timing of reproduction among birds, butterflies and wild plants have been well documented (Walther et al. 2002; Parmesan & Yohe 2003) as have the effects of habitat loss and degradation on the nesting habitat choice of snakes and lizards (Gibbon et al. 2000). Among these diverse and broad taxonomic cases, the population-level effects have been both beneficial and costly (Stenseth et al. 2002). In marine systems, phenotypic shifts can occur rapidly (Poloczanska et al. 2013) and migratory spawners are highly responsive to shifting oceanographic conditions (Ware & Thomson 2000), the abundance of predators (Lima 1998), and changes in population density (Kuparinen et al. 2014). Here, we investigated the potential causes and consequences of recent deep spawning events by Pacific herring (*Clupea pallasii*) that were discovered exceeding depths of 30 m (8 times the preceding 25-year mean); a shift in spawning behaviour thought to be linked with recent human-induced perturbations. Deciphering the drivers of change to this fundamental reproductive strategy and their effect on demographic rates has generalizable implications for understanding the adaptive capacity of species under persistent anthropogenic stress.

Forage fish species (e.g. sardines, anchovies, and herring) have been shown to possess significant among-population variability in migration lengths and timing, and behavioural adaptations to an extensive range of spawning conditions (Jorgensen et al. 2008). In response to ocean warming from climate change and El Niño Southern Oscillation events, Pacific sardines (*Sardinops sagax*) migrate inshore and aggregate in deeper, colder upwelling water, while Peruvian anchovies (*Engraulis ringens*) move southward and mix with Chilean stocks (Checkley et al. 2017). Pacific herring have adapted to spawn from California to the Bering Sea within a remarkable range of environmental conditions, spanning from 2 to 35 ‰ salinity and from 0 to 15 °C (Blaxter 1985). Such plasticity can allow adaptation to environmental change, but can also be associated with population-level consequences when species are unable to cope with the rate of change or loss of habitat (Shaw & Efterson 2012).

Despite their exceptional plasticity, the past 50 years have marked some atypical and thus concerning trends in Pacific herring population abundance and behavior (Schweigert et al. 2010). In British Columbia (BC), Canada, Herring populations have never fully recovered from unsustainable harvest rates and subsequent stock collapse in the late 1960s, and continue to experience localized declines (Cleary & Taylor 2015). Stock assessments have since measured a decline in weight-at-age (growth) in all major stock areas, from California to Alaska (Cleary & Taylor 2015), and natural mortality estimates have increased since the 1950s, having recently reached record highs in BC (Martel et al. 2012). Spawning behaviors have also shifted. As humans continue to modify habitats, herring have been documented spawning on creosote treated pilings and other anthropogenic substrates (Palsson 1984). The number of spawning areas on the central coast of BC has declined by more than 50 % since the 1940s, and their distribution has contracted from the outer coast, aggregating to inshore fjords, bays, and inlets (Gerrard 2014; Hay & Kronlund 1987). More recently, herring have been observed spawning at depths far beyond their normal range (Mike Reid 2015, personal communication; Cleary & Taylor 2015).

Pacific herring provide immense ecological value as prey for a large diversity of higher trophic level predators, including local indigenous people and commercial fisheries. This value is partially due to their nearshore, shallow water spawning behavior, providing access to an annual energy influx during the spring spawn (Kitasoo/Xai'xais First Nation 2017; Mckechnie et al. 2014; Gauvreau 2015). Spawn areas on the central coast of British Columbia are typically found in inlets, bays, and fjords that are protected from the intense waves and winds found on the outer coast, but still exposed enough to be well circulated with tidal currents and moderate wave energy. Eggs are spawned predominantly in the intertidal and shallow subtidal zones (to roughly -5 m chart datum) on marine algae and sea grass, although a small percentage of spawn can often be found on rock and other hard substrates (Fort et al. 2013; Haegele & Schweigert 1985). Substrate type does not appear to affect egg survival (Hourston et al. 1984; Shelton et al. 2014), as long as water movement provides a clean environment with sufficient aeration and material exchange (Alderdice & Hourston 1985; Griffin et al. 2009).

Since 2013, observations by Heiltsuk Indigenous fishers on the central coast of BC have noted a considerable increase in spawning events at unusual depths (> -30 m), well beyond the typical range (+3 to -5 m) and habitat normally targeted by Pacific herring (Levin et al. 2016; Cleary & Taylor 2015; Mike Reid 2015, personal communication). Heiltsuk fishers postulated that spawning herring could be driven to depth by shifts observed in multiple local abiotic and biotic conditions. For example, in recent years the Heiltsuk have documented the recovery and increase in abundance of herring predators on the central coast, including Steller sea lions (*Eumetopias jubatus*) and humpback whales (*Megaptera novaeangliae*). Coastal locations with significant vessel traffic have also been anecdotally linked with deep spawning events, where herring schools may be exhibiting anti-predator like behaviors to escape acoustic disturbance from engines, sonar, and depth sounders (Robertis & Handegard 2013). Finally, unusually warm water temperatures, driven by climate change and the 2015-2016 El Niño Southern Oscillation (Wang et al. 2017) in the northeast Pacific also appear to be temporally and spatially associated with the recent spike in deep herring spawn observations. To test these alternative yet non mutually exclusive hypotheses we surveyed spawn depths, and biotic and abiotic conditions in four spatially distinct spawning areas differing in history of fishery exploitation, vessel traffic rates, predator abundance, and marine conditions. To test the ecological consequences of these deep spawning events and the magnitude of predation, we transplanted herring eggs at 3 depths, in the presence and absence of predation, and documented their survival rates. We predicted that egg survival would decrease with depth, where developing embryos may be subject to reduced circulation provided by surface currents and wave energy. We then analyzed historical fisheries records of spawn depth, egg density, and spawner biomass to further explore the mechanisms driving changes in herring reproductive strategies.

2. Methods

2.1. Deep Spawn Survey

To determine the factors driving variation in herring spawn depth, we surveyed sites ($n = 3 - 8$) in four spatially distinct spawning areas differing in proximity to coastal communities, commercial fisheries history, vessel traffic, and predator abundance (Fig. 1, Table 1). At each site we quantified spawn characteristics (maximum spawn depth, egg density, egg coverage, and egg survival), abiotic conditions (water temperature and salinity), predator abundance, and marine vessel traffic.

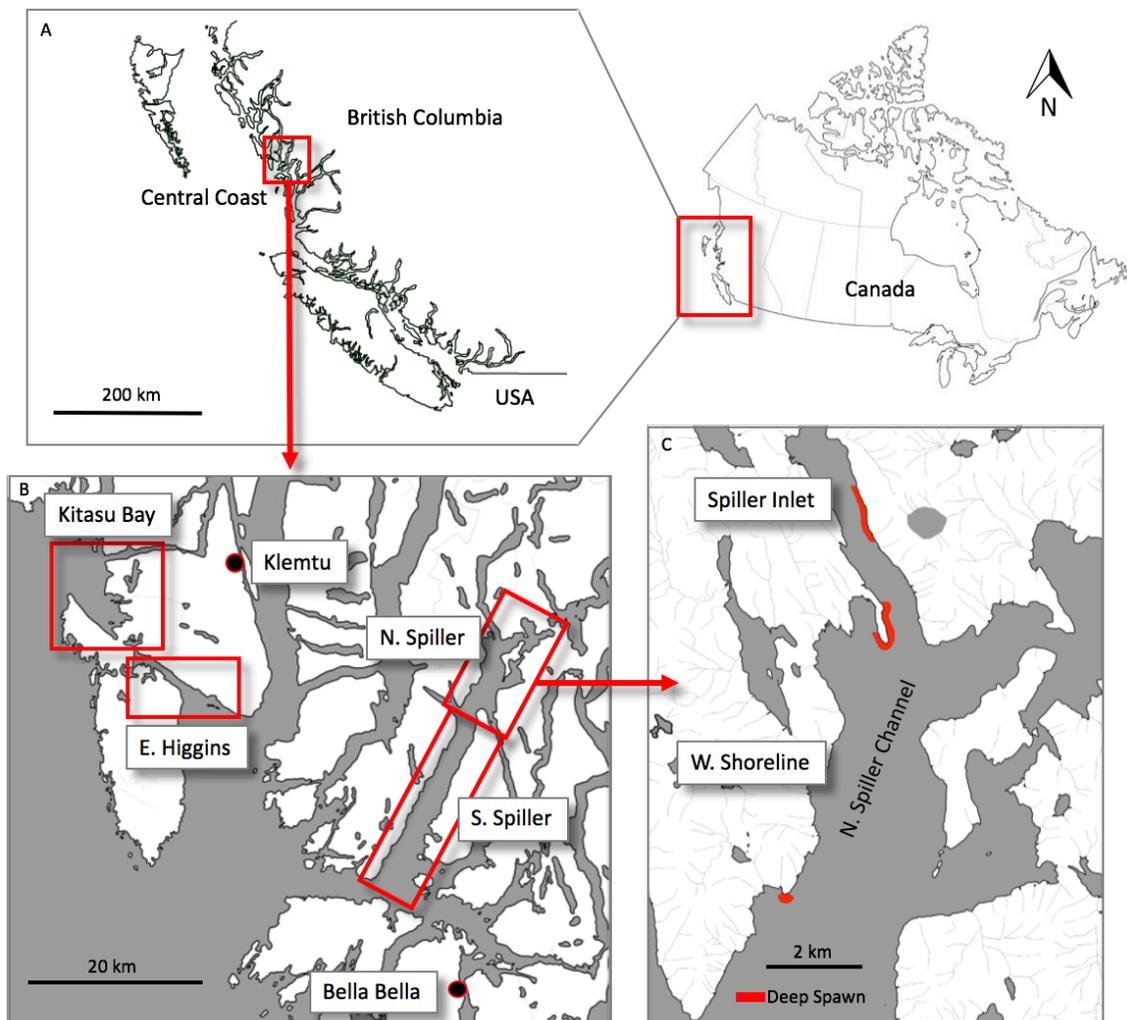


Figure 1. A) On the central coast of British Columbia, Canada we surveyed B) 4 spawning areas in spring 2016: Kitasu Bay, East Higgins Pass, south Spiller Channel, and north Spiller Channel. C) Red outlines show locations where deep spawn was observed in Spiller Inlet and along the west shoreline of north Spiller Channel.

Table 1. Summary of characteristics for spawning areas surveyed during the 2016 herring spawn. The local population in Klemtu was approximately 500, and in Bella Bella approximately 1,400. Commercial roe fisheries include annual openings for both gill net and seine fisheries. Vessel traffic and wildlife abundance refer to amounts observed per km² of shoreline (Appendix D).

Survey site	Distance by water to nearest community	Commercial fisheries openings (1996–2015)	Vessel traffic	Marine mammal abundance
Kitasu Bay	35 km from Klemtu	1	Low	High
E. Higgins Passage	30 km from Klemtu	9	0.1 x Kitasu Bay	0.8 x Kitasu Bay
S. Spiller Channel	15 km from Bella Bella	8	3.9 x Kitasu Bay	0.2 x Kitasu Bay
N. Spiller Channel	38 km from Bella Bella	9	0.5 x Kitasu Bay	0.05 x Kitasu Bay

2.1.1. Field Survey

Site Selection – We searched for deep spawn using a live-feed submersible video camera. Within each spawn area, search sites were systematically selected using a stratified sampling design based on depth and suitable substrate. Sites spanned 100 to 300 m of shoreline, depending on depth and substrate characteristics. We deployed three video camera transects at each site to –30 m. At sites where deep spawn was observed, SCUBA divers surveyed two vertical subtidal transects (surface to –30 m) estimating herring egg percent cover and number of egg layers in stratified 0.5 m² quadrats at depth intervals of 3 m (n= 12 per transect). Divers also collected egg samples from –3, –15 and –30 m; these were preserved in a 5% solution of formaldehyde and examined later with a dissecting microscope to determine survivorship and stages of development.

Spawn Density Estimation – We derived three categories of spawner density based on two variables (Table 2): egg percent coverage, and mean number of egg layers. Herring spawn was observed using binoculars, divers and drop cameras. Total spawn area was estimated using total spawn length and spawn depth, with cameras dropped at 100 m intervals. Minimum spawn length was limited to 150 m – the shortest length of shoreline observed with spawn below –18 m. Egg cover and mean number of layers were documented using visual estimates. The number of spawners was estimated using a standard approximation of 100 eggs per gram of herring (Schweigert 2001).

Table 2. Categories of spawner biomass based on two variables: percent egg coverage and mean number of egg layers. Minimum spawn length was limited to 150 m (the shortest length of shoreline observed with deep spawn). Percent coverage and egg layers were documented with visual estimates at both the surface and along drop camera transects using visually distinct categories (low, medium, and high). Both estimates (coverage, and layers) had to be met or exceeded to satisfy each spawn density category. For example, if a spawn with 80 % coverage (medium) had a mean of 1.5 egg layers (low), it was recorded as a low density spawn.

	Low	Medium	High
Percent Coverage	< 50	50 – 90	> 90
Egg Layers	< 2	2 – 5	> 5

Biotic Factors – We recorded the abundance of herring predators (cetaceans, pinnipeds, and marine birds), the number and types of marine vessels (fishing and recreational), as well as salinity and temperature profiles in each spawn area before, during, and after the herring spawn, from March 21st to April 1st, 2016. Marine predators and vessel traffic were counted and recorded while travelling at a constant speed (~10 knots), approximately 100 m from the shoreline. When necessary (for diving marine mammals and large numbers of birds) the vessel would stop to conduct accurate counts. In situations where wildlife numbered in the hundreds or thousands (typically for gulls and surf scoters), replicate counts were made by multiple observers and averaged.

Abiotic Factors – Temperature and salinity were measured with a conductivity, temperature and depth (CTD) instrument at n = 3 – 8 sites throughout each spawn area, using a 6 Hz sampling rate from the surface to –30 m. CTD drop sites were selected based on bathymetry and geography to capture the variation in temperature within each area, where deep spawn was found, and at our three experiment locations.

2.1.2. Historic Spawn Records

To test whether spawn depth is affected by spawner density, we analyzed historical indices of annual spawn biomass with spawn depths collected from 1989 to 2015 in our four spawn areas by Canada’s federal fisheries agency (Martel et al. 2012). These fisheries-independent indices of herring spawn biomass are calculated by converting total egg density estimates from annual spawn surveys to tonnes of spawning fish, based on an average of 100 eggs per gram of herring (Schweigert 2001).

2.2. Deep Spawn Survival Experiment

2.2.1. Experiment Design

To test if herring egg survival rates varied with depth, we conducted a transplant experiment at three sites in Kitasu Bay (Fig. A1) with similar depth profiles and substrates, and small variations in exposure to marine conditions. Sites were located over sandy substrate in locations where herring had spawned to depths of –15 m on adjacent rocky reefs.

Within 24 hours of a spawn event, herring eggs deposited on kelp blades (*Macrocystis integrifolia*) were harvested from shallow subtidal depths (0 to –3 m). Blade samples were cut to 30 cm lengths and attached at the stipe to 120 x 60 x 40 cm weighted PVC frames (Figs. A2, A3). Twenty samples were haphazardly attached to each frame; 10 samples enclosed in 20 x 30 cm Vexar mesh (2.5 cm) pouches to exclude predators and 10 left exposed to predation. Salinity, temperature, and dissolved oxygen (HOBO) loggers were also attached to each frame. Samples and loggers were collected from depth at two time intervals: T1 = 9 days) midway through egg development – when eye pigments were first visible, and T2 = 15 days) immediately before larvae were predicted to hatch (15 days). Samples were also collected at T1 and T2 from in-situ spawn at –3 and –15 m depths adjacent to each of the experiment sites. Following collection, 8.5 cm circular sections were haphazardly cut from each sample and preserved in 5 % formaldehyde.

For each sample, we determined mean survival rates and developmental stage proportions in the top egg layer with eight field-of-view observations at 20x magnification. Six stage categories of egg development were defined based on the literature (Table A1; Kawakami et al. 2011).

2.3. Statistical Analysis

2.3.1. Model structure for survey data

To test for associations between spawn depth and abiotic and biotic conditions, we fit a series of linear mixed effects models (LMEs) where spawn biomass (Table 2), vessel traffic, predator abundance, temperature, salinity, and the depth extent of bedrock

habitat were treated as fixed effects. Predator abundance for each species was defined as a factor with 6 levels (P0 to P5), where P0 = no predators, and P5 = the highest number observed in all areas. Scores for all species were averaged within spatial blocks (bays, inlets, and shoreline segments). Spawn site, nested within block and area (Kitasu Bay, north, and south Spiller Channel) was treated as a random effect. All models were run in R version 3.3.3 with maximum likelihood using the lme4 package (R Development Core Team 2017; Bates et al. 2017). Significance of model variables was obtained using the R Likelihood Ratio Test. Our model describing spawn depth had the form:

$$y_{hijm} = \beta_0 + \sum_{k=1}^k \beta_k X_{hijmn} + b_{1,h} + b_{2,h,i} + b_{3,h,i,j} + \varepsilon_{ijkm}$$

Where y_{hijm} is the m^{th} observation (spawn depth) at area h , block i , site j , X_{hijmn} is the n^{th} value of the m^{th} independent variable, k is the number of fixed effects (spawn density, rock depth, temperature, predation, traffic), $b_{1,h}$ is the random effect of area h , $b_{2,h,i}$ is the random effect of block i nested in area h , and $b_{3,h,i,j}$ is the random effect of site j , nested in block i , nested in spawn area h .

2.3.2. Model structure for field experiment data

To quantify the effects from depth on the survival of eggs remaining after losses from predation we constructed a generalized linear model (GLM) with binomial likelihood and a logit link function where depth, predation treatment, site, number of egg layers, and predation amount were treated as fixed effects. We defined survival among eggs collected in the first time interval (T1 = 9 days) as eggs that had reached a development stage where eye pigmentation was visible. Survival in eggs collected from the second time interval (T2 = 15 days) was defined as empty shells (hatched) and eggs that had reached full development (Kawakami et al. 2011). We tested hypotheses of individual effects on egg survival using likelihood ratio tests. All models were run in R version 3.3.3 and fit with Binomial error distribution and logit link function using the lme4 package (R Development Core Team 2017; Bates et al. 2017). Our model describing egg survival had the form:

$$y_{ijkm} = \beta_0 + \sum_{k=1}^k \beta_k X_{ijkmn} + b_{i(j)} + \varepsilon_{ijkmn}$$

Where y_{ijkm} is the m^{th} observation (surviving eggs) at site i , depth j , and treatment k ; X_{ijkmn} is the n^{th} value of the m^{th} independent variable at site i , depth j , and treatment k ; k is the total number of fixed effects (depth, treatment, site, layers, and predation); and $b_{i(j)}$ is the fixed effect of depth j nested within site i .

2.3.3. Model selection

For analyses of survey and field data, we determined the strength of evidence among alternative models using an information-theoretic approach (Burnham & Anderson 2002). To assess the strength of evidence for each explanatory variable in driving 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 (ΔAIC_c) values. 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 using the MuMIn package in R (Barton 2013). Data exploration was carried out following the protocol described by Zuur et al. (2016). All models were tested for linearity, absence of collinearity, homoscedasticity, normality of residuals, and the absence of influential data points.

2.3.4. Historical Analysis

To test whether spawn depth is affected by spawner biomass we constructed linear quantile regression models using the `quantreg` function and `ggplot2` in R to assess the 5th and 95th quantiles for shifts in depth with increasing biomass, and to evaluate shifts in the overall distribution of spawn depths (R Development Core Team 2017; Koenker 2013; Wickham 2009).

Limitations of this analysis include the assumptions of the stock assessment model from which the data themselves were generated, survey observation errors, and the depth restrictions imposed by the survey methods (Cleary & Taylor 2015). Moreover, spawn depth extent below -18 m is recorded only when available dive time and procedures allow (Fort et al. 2013). Considering that an unknown number of spawn events below -18 m have not been recorded, the linear regression estimates are likely conservative.

3. Results

3.1. Deep Spawn Field Survey

The maximum depth of herring spawn in our field surveys was negatively correlated with both the depth of suitable habitat and empirical estimates of spawner biomass (Fig 2, Table 3; $\chi^2 = 91$, $df = 10$). On average, at high spawner densities (> 150 herring/m²) our model estimates that each additional meter of available bedrock depth increased the maximum depth at which herring spawned by 0.32 ± 0.06 m. There was no strength of evidence in the data to support the more complex model, combining the interactive effects of habitat depth and spawner biomass with the effect of temperature ($\Delta t < 2$; Table 3). Deep spawn (below -18 m) was only found in one of our four surveyed spawn areas, where herring had spawned in high densities and in the presence of deep vertical bedrock walls (north Spiller Channel). Note that no suitable habitat for deep spawn was found in East Higgins Passage.

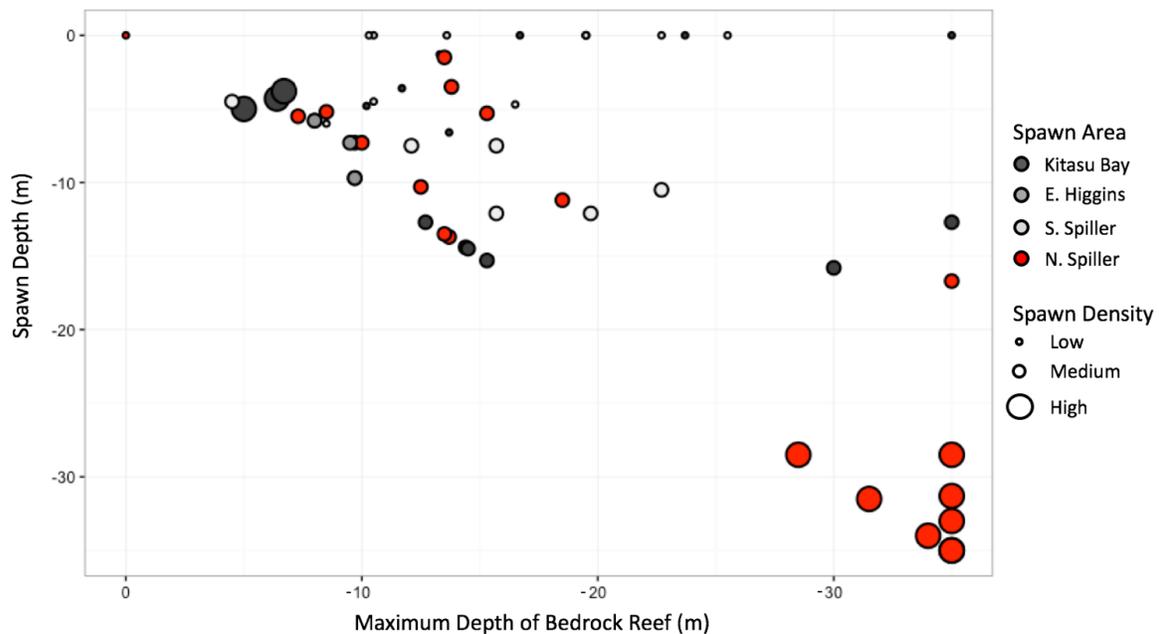


Figure 2. Pacific herring spawn depth in relation to the maximum depth of suitable spawning substrate (bedrock reef) depth. Each point represents a single transect where herring spawn was observed. Estimated spawn density of female fish is represented by increasing point size. Density estimates (Table 2): low density = $< 1,000\text{m}^2$, 50 % substrate coverage, and 1 – 2 egg layers; medium density = $1,000 - 10,000\text{m}^2$, 50 – 90 % coverage, and 3 – 4 egg layers; high density = $> 10,000\text{m}^2$, 90 % substrate coverage, and > 5 egg layers.

Table 3. Strength of evidence for alternative candidate models examining the influence of reef depth, spawn density, and water temperature on spawn depth. Models with varying parameters (K) were compared with differences in Akaike's Information Criterion (AIC_c), log likelihood (Log(L)), and normalized Akaike's weight (w_i) to rank alternate candidate models for best fit. The top 9 models are shown here. R² for Reef Depth * Density = 0.93.

Response and Model	K	Log (L)	AICc	Δt	Wt
Spawn Depth					
Reef Depth * Density	10	-138.0	300.8	0	0.63
Reef Depth * Density + Temperature	11	-137.0	301.9	1.1	0.37
Reef Depth + Density	8	-156.9	332.8	32.0	0
Reef Depth + Density + Temperature	9	-156.2	334.3	33.5	0
Density + Temperature	8	-165.0	349.0	48.2	0
Density	7	-166.6	349.5	48.7	0
Reef Depth + Temperature	7	-172.8	361.9	61.1	0
Reef Depth	6	-174.3	362.3	61.5	0
Temperature	6	-181.6	376.9	76.1	0

Surface water temperatures at this time of year are typically 7 to 8 °C (Fisheries and Oceans Canada 2016). Surface temperatures (9.8 ± 0.25 °C) and temperature gradients from 0 to -30 m (1.40 ± 0.30 °C) were generally highest where deep spawn was observed (north Spiller), while areas with no deep spawn (south Spiller and Kitsu Bay) exhibited comparatively low surface temperatures (9.4 ± 0.77 °C) and gradients (0.76 ± 0.11 °C). Salinities in Kitsu Bay typically fluctuate around 30 parts per thousand (ppt) (Fisheries and Oceans Canada 2016). We found no correlation of spawn depth with variations in either surface temperature or salinity (Appendix C).

Notable differences were found in either predator abundance or marine vessel traffic among the spawn areas (Table 1; Fig. D1). Correcting for shoreline length, Kitsu Bay contained greater than 6 times the density of marine birds (gulls, scoters, and other ducks; 192 ± 278 per km²) observed in south Spiller (25 ± 23 per km²), and 3 times the density observed in north Spiller (56 ± 18 per km²). Marine vessels observed in south Spiller (5.67 ± 0.22 per km²) were nearly four times the amount observed in Kitsu Bay (1.50 ± 0.09 per km²), and eight times the amount observed in north Spiller (0.67 ± 0.07 per km²). Despite significant differences observed in both predator abundance and vessel traffic, inclusion of these variables in our models found no strength of evidence for their effect on herring spawn depth.

Throughout the entire depth range at all three deep spawn sites (Figure 1) the number of egg layers and percent coverage were high, while spawn survival was low (Table B1). The number of egg layers ranged from 1 to 13 (6.2 ± 1.8 layers) and the highest densities were found from -6 to -21 m (8.2 ± 3.1 layers). Percent coverage was greater than 95 % across all deep spawn transects (97.1 ± 2.1 %). All eggs collected from -15 and -30 m depths were dead (opaque white) at the time of collection and fewer than 30 % of eggs collected from -3 m were found alive.

3.1.1. Historical Analysis

Based on historic spawn records collected from 1989 to 2015 (Martel et al. 2012), we found that spawn densities (eggs / m²) increased with spawner biomass (Fig. B1) and spawner biomass had a significant effect on the maximum and mean depths at which herring spawn occurred (Fig. 3, Appendix E). Mean maximum spawn depth on British Columbia's central coast increased by $0.15 \text{ m} \pm 0.05$ for every 1,000 tonne increase in spawning biomass ($p = 0.0032$). This effect increased by an order of magnitude to $1.5 \text{ m} \pm 0.3$ for every 1,000 tonnes when analyzed on an area basis, in locations where herring had spawned on bedrock habitat below -18 m (correlation coefficient = -0.30, Fig. 3).

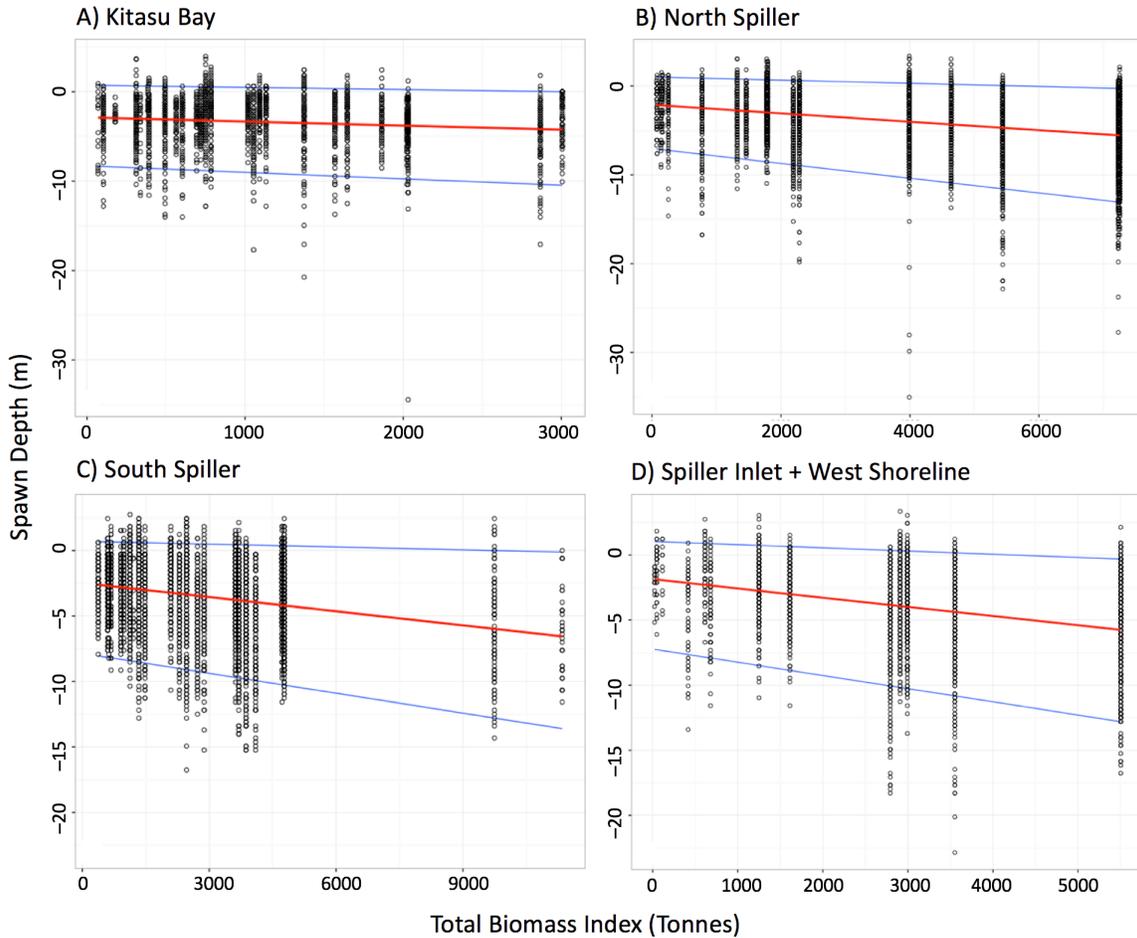


Figure 3. Comparison between historical annual spawn biomass and spawn depths between 1989 and 2015 in 3 of our surveyed spawn areas A) Kitasu Bay, B) North Spiller, C) South Spiller and D) Spiller Inlet and the west shoreline of north Spiller, a subsection B) where we found deep spawn. Each point represents a transect; blue lines are 5 and 95 % quantiles; red lines are the mean. Note differences in the x and y axes scales. Correlation coefficients between depth and biomass: A) Kitasu Bay = 0; C) south Spiller = -0.22 ; B) north Spiller = -0.29 ; D) Spiller Inlet and the west shoreline of north Spiller = -0.30 .

3.2. Deep Spawn Survival Experiment

3.2.1. Egg Survival

Water depth had a significant negative effect on egg survival in our experiment (Tables 3, G1, G2; Fig. 4). Specifically, surviving eggs (averages across $-P$ and $+P$) declined by 10 % between 15 vs 3 m (67 vs 77 %) and by 20 % at 30 vs 3m (57 vs 77 %) after 9 days post-deposition (Fig. 4). After 15 days of development the trend towards decreasing survival with depth held for eggs in the predator exclusion treatment,

declining by 16 % between 15 vs 3 m (27 vs 43 %) and by 20 % at 30 vs 3m (23 vs 43 %) (Fig. 5). Eggs that were exposed to predation, however, improved marginally in survival, remaining unchanged between 15 vs 3 m (36 %), and increasing by 7 % at 30 vs 3 m (43 vs 36 %). Note that predator exposed treatments experienced loss of substantial egg numbers; results for these treatments represent the survival rates of eggs still present after collection.

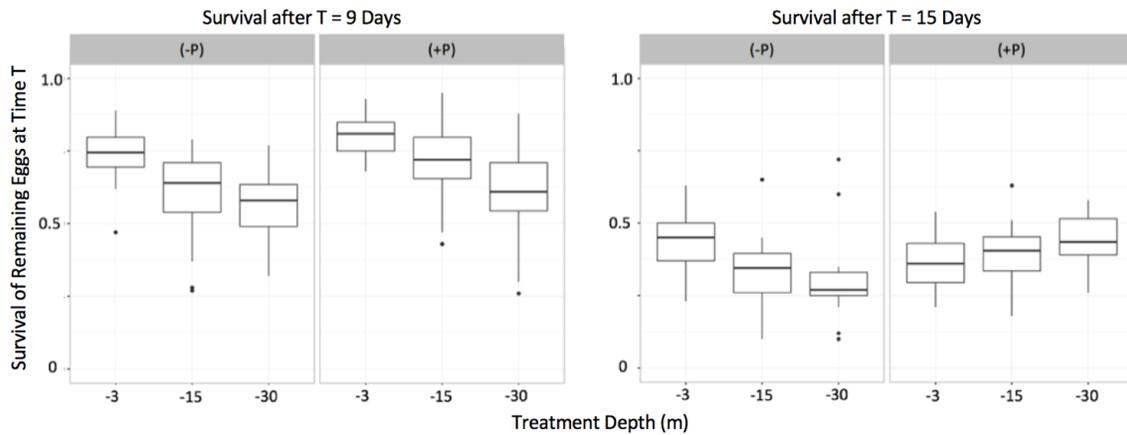


Figure 4. Proportion of herring eggs that survived after T = 9 days (mid-development) and after T = 15 days (complete development) at –3, –15 and –30 m depths for both predation exclusion (–P) and predation exposure (+P) treatments. Note that plots show survival proportion of those eggs present after losses from predation (i.e. estimates do not include eggs that perished from predation).

Table 4. Likelihood ratio tests for generalized linear models of egg survival (proportion) as a function of treatment (+ or – predators), depth, site, egg layers, and predation amount.

Parameter	Surviving Eggs (T = 9 days)			Hatched + Fully Developed Eggs (T = 15 days)		
	χ^2	df	P	χ^2	df	P
Depth	95.1	2	$2.2e^{-16}$	13.3	2	$1.3e^{-03}$
Treatment	59.2	1	$1.4e^{-14}$	58.6	1	$2.0e^{-14}$
Site	126.5	2	$< 2.2e^{-16}$	44	2	$2.8e^{-10}$
Layers	43.9	1	$3.4e^{-11}$	43.6	1	$4.1e^{-11}$
Predation	49.8	3	$8.7e^{-11}$	9.4	3	$2.4e^{-02}$
Depth : Treatment	28.3	2	$7.2e^{-07}$	94.7	2	$< 2.2e^{-16}$
Depth : Site	138.9	4	$< 2.2e^{-16}$	84.7	4	$< 2.2e^{-16}$
Depth : Layers	9.4	2	$9.3e^{-03}$	48.5	2	$3.0e^{-11}$

Table 5. Mean egg survival estimates \pm standard error derived from generalized linear models testing the effects of depth on egg survival (proportion).

Depth	9 Days Predator Exclusion	9 Days Predator Exposed	15 Days Predator Exclusion	15 Days Predator Exposed
-3 m	0.74 \pm 0.012	0.81 \pm 0.008	0.43 \pm 0.012	0.36 \pm 0.010
-15 m	0.61 \pm 0.018	0.72 \pm 0.016	0.27 \pm 0.017	0.36 \pm 0.023
-30 m	0.54 \pm 0.009	0.61 \pm 0.016	0.23 \pm 0.019	0.43 \pm 0.031

3.2.2. Experiment Notes

Abiotic conditions – During the experiment, mean temperature, salinity and dissolved oxygen differences from 0 to -30 m ranged from -0.53 to -0.65 °C, +0.68 to +0.95 ppt, and +1.5 to +2.1 mg/L respectively (Table C1, Fig. C2). Temperature, salinity, and dissolved oxygen differences between experiment sites were comparatively negligible.

Predation effects – Predation of exposed samples increased with time and with depth. After 15 days, 53 % of our samples from 30 m were either affected by predation; 27 % were affected at 15 metres, and only 2 % at 3 metres. Exposed eggs collected after 15 days also survived at higher rates with increasing depth (Table 5, Fig 4).

Control survival – Herring in Kitasu Bay spawned to -15 m depths on subtidal algae (*Callophyllis sp.* and *Agarum clathratum*) at each of our experiment sites, providing an in-situ control for comparison against eggs transplanted on kelp blades (*Macrocystis integrifolia*). All eggs at -3 m (in-situ and transplanted) were on kelp blades. Mean survival of in-situ control eggs from -3 m (65 \pm 14 %) was 19 % higher than transplanted eggs (45 \pm 11 %), while mean survival of in-situ control eggs from -15 m (88 \pm 8 %) was 53 % higher than transplanted eggs (35 \pm 9 %).

Assumptions and limitations – Prior to transplant, eggs from our experiment spent the first day of development in comparatively optimal conditions, between 0 and -3 m. Eggs experienced the effects of handling during harvest, setup, and sample collection. During the experiment, sample kelp blades were affected by varying degrees of decomposition. Decomposing blades may have contributed to egg mortality and were consequently removed from the model data set.

4. Discussion

4.1. Density Dependence Across Ecological Scales

Here, we illustrate that spatial and temporal variation in Pacific herring spawn depths correspond with the density of spawners and the depth at which spawning habitat is available. Moreover, the survival of herring eggs declines with depth. We found herring spawn at maximum depths of -33 to -44 m, well beyond the depth range thought to be normally targeted by Pacific herring (Haegele & Schweigert, 1985; Taylor, 1971). These extraordinary spawning events were found exclusively in a deep fjord where herring spawned at high densities ($> 2,000,000$ eggs/m²) on vertical bedrock slopes (Fig 2, Table B1). Using these survey data our quantitative analyses provide strong evidence that herring spawn deeper as suitable habitat increases in depth, and that this effect is magnified when spawner density is high (Table 3). These results are consistent with historical records of fisheries independent survey data (1989 – 2015; Martel 2012) that show an increase in maximum spawn depths with increasing spawner biomass (where deep spawning habitat is present), while minimum depths remain unchanged (Fig 3; correlation = -0.22 to -0.30). In addition to these findings, evidence from our experiment indicates that egg survival decreased, on average, by 20 % when transplanted to -30 m, relative to -3 m (Fig 4, Table 5; $\chi^2 = 20.7$).

The observations that depth of spawn exhibits density dependence and egg survival declines with depth suggests that spawn concentration may, in part, be responsible for compensatory stock-recruit dynamics in Pacific herring. Small-scale local conditions, such as population density and spawn habitat, have been shown to have significant influence on recruitment success in migratory spawners (Milner et al. 2003; Zheng 1996). At high spawner concentrations, increases in both the depth and density of Pacific herring egg deposition are likely to act as limitations that moderate recruitment success (Alderdice & Hourston 1985). These dynamics may be magnified in deep fjords and other environments that allow for deep spawning events. In addition to exceptional depths, our observations from three separate deep spawning events found high densities (6.2 ± 3.4 layers) and low fertilization rates (< 10 %). In our surveys, no herring eggs were found fertilized below -15 m, and it is likely that more than 100 billion eggs were left unfertilized in total (approximately 2/3 of the entire estimated spawn for north

Spiller). Combined with the decrease in survival with depth found on our experiment, we can infer that high density spawning events resulting in spawn depths beyond the shallow subtidal severely reduce the likelihood of egg survival due to cumulative effects from depth, high egg densities, and a narrowed chance of fertilization.

4.2. Factors Influencing Egg Survival at Depth

The effects from depth on egg survival are likely determined by complex dynamics, including interactions between multiple abiotic and biotic factors. Even under optimal conditions, egg survival is highly variable across differing experiments and environments (Shelton et al. 2014; Keeling et al. 2017). This context-dependence should be kept in mind when comparing the results from our experiment (transplanted eggs on kelp blades) with deep spawn found on our survey (spawned in-situ on vertical bedrock). There are, however, depth effects that may be inferred across differing environments. Substrate type has comparatively small effects on egg survival (Hourston et al. 1984; Shelton et al. 2014), as long as water movement provides a clean environment with sufficient aeration and material exchange (Alderdice & Hourston 1985; Griffin et al. 2009). Atlantic herring, for example, typically spawn on gravel at depths much deeper than Pacific herring (–20 to –80 m); these spawning habitats are high energy environments with tidal currents that run up to 3 knots (Reid et al. 1999). In contrast, Pacific herring typically spawn in intertidal and shallow subtidal habitats on algae and seagrass (Haegele & Schweigert 1985) where eggs are kept aerated and free of sedimentation with surface currents and wave energy. As circulation from the surface decreases with depth, whether on vertical rock or blades of kelp, oxygen transport and the removal of metabolites will diminish, likely contributing to a decrease in egg survival (Alderdice & Hourston 1985).

4.3. Factors Influencing Spawn Depth

Where spawning habitat is deep and spawner densities are high, spawn depth may be driven by competition for space. In deep fjords composed of vertical bedrock shorelines the spatial constraints on spawning habitat extend far deeper than most other coastal locations, allowing for the occurrence of deep spawning events, given the right conditions. Typical shorelines on the central coast drop off gradually, moving from bedrock to cobble, sand, and sediment in the shallow subtidal (from –12 to –18 m). The

absence of deep spawn habitat in these locations spatially constrains the spawn, forcing it to spread laterally along the shoreline. Where we found deep spawn (north Spiller) there was no shortage of historical shallow spawning habitat (> 60 km of bedrock and algae), but herring have spawned in this same fjord to -30 m or deeper every year since 2013 (Cleary & Taylor 2015). Herring spawn at our three deep survey sites cumulatively covered 2.4 km of shoreline at mean densities exceeding 2,000,000 eggs/m². At typical central coast spawn depths (-5.0 m) and densities (< 650,000 eggs/m²) a spawn of this size would cover more than 30 km of shoreline. Along these deep bedrock walls, herring have the freedom to move to greater depths in search of preferred conditions and available habitat, and it's plausible that competition for space amongst millions of herring may be pushing them to spawn deeper, wherever suitable habitat can be found. Despite this hypothetical explanation, densities of spawners have historically been much higher, consequently, this begs the question 'why now'? Perhaps this is normal behavior that occurs when and where conditions permit deeper spawn, and we haven't noticed until recently simply because we haven't thought to look.

If the depth and frequency of deep spawning events have increased (as recent observations suggest) this may indicate an additional possibility, that we are observing a localized phenotypic shift in spawning behaviour in response to effects from climate change and the recent El Niño Southern Oscillation. Our models do not provide evidence for a potential link between increasing spawn depth and temperature (where high spawner densities and deep habitat were present) (Table 3, Fig C5), but convergent trends in rising sea surface temperatures and deep spawn observations suggest that more investigation is warranted here. Deep spawn observations by fisheries survey divers and indigenous fishermen on the central coast have coincided with recent and unusual temperature increases across the eastern Pacific (Peterson et al. 2016). Eighty percent of all deep spawn observations (below -18 m) recorded by Canada's fisheries agency have occurred since 2013, and mean surface temperatures (9.8 – 10.5 °C), recorded on the central coast during herring spawn seasons have increased above the previous 20 year mean by 3.3 °C in 2015, and 2.5 °C in 2016 (Fisheries and Oceans Canada 2016). Climate change has altered migrations, habitat selection, and reproduction timing in many species worldwide (Walther et al. 2002) and it remains plausible here that rapidly increasing temperatures have disturbed the ecological

synchrony between migration timing and optimal spawning conditions, causing herring to dive deeper in search preferred conditions.

There are several concurrent trends in the status of Pacific herring populations on the central coast of BC that should also be considered in relation to deep spawning events. Herring populations have never fully recovered from unsustainable harvest rates and subsequent stock collapse in the 1960s, and continue to experience localized declines (Cleary & Taylor 2015) resulting in the closure of the commercial sac-roe fishery for seven of the past ten years, including 2016. Throughout this period of instability there has been a concurrent spatial contraction and aggregation in the distribution of spawning areas, equating to an 8 % decline per decade (Gerrard 2014). Remaining spawning grounds are now further from the outer coast, and often up deep fjords and inlets, where deep spawning events appear to be increasing in prevalence. Combined with these shifts in both abundance and spawning behaviour, climate change is predicted to add yet further shifts in species ranges and uncertainty in their resilience and productivity (Weatherdon et al. 2016).

4.4. Implication for Fisheries Management

Our analysis provides evidence that herring tend to spawn deeper in the presence of deep bedrock walls, and that this effect is magnified at high spawner densities. Although our models do not provided an explanation for why these deep spawning events are occurring, there are several possibilities that warrant further investigation. It remains possible that what we have observed is typical behaviour that occurs occasionally where conditions permit deeper spawn, and has only just been noticed in recent years. There may, however, be effects caused by climate change that we were unable to detect, or effects from shifts in population structure that have yet to be explored. Notwithstanding the cause, we have found strong evidence that deep spawn has harmful effects on egg survival. Moreover, prior research has shown that herring spawn areas appear to be disappearing from the outer coast, and a greater proportion of herring are now spawning up inland fjords (Gerrard 2014). If the spatial contraction in spawning areas continues as sea temperatures rise, the prevalence of deep spawning events may expand as herring become further concentrated into deep fjords and smaller geographic areas, adding further risk to already declining stocks. This threat can be managed with risk-based harvest policies that protect forage fish from fisheries when they are susceptible to

collapse, providing substantial ecological benefit to the rest of the food web that relies on herring (Essington et al. 2015; Pikitch et al. 2014). Support for these kinds of integrated risk-based approaches could enable transitions towards improved management of forage fish and the social-ecological systems in which they are embedded.

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Appendices.

Appendix A. Deep transplant experiment

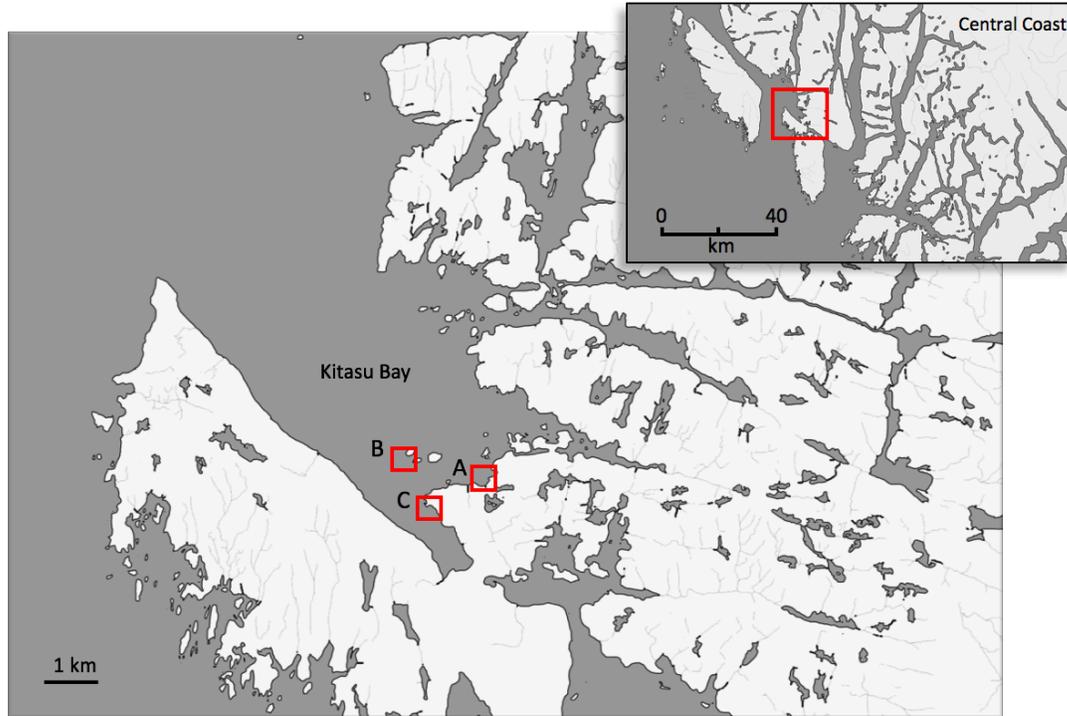


Figure A1. Experiment site locations in Kitasu Bay.

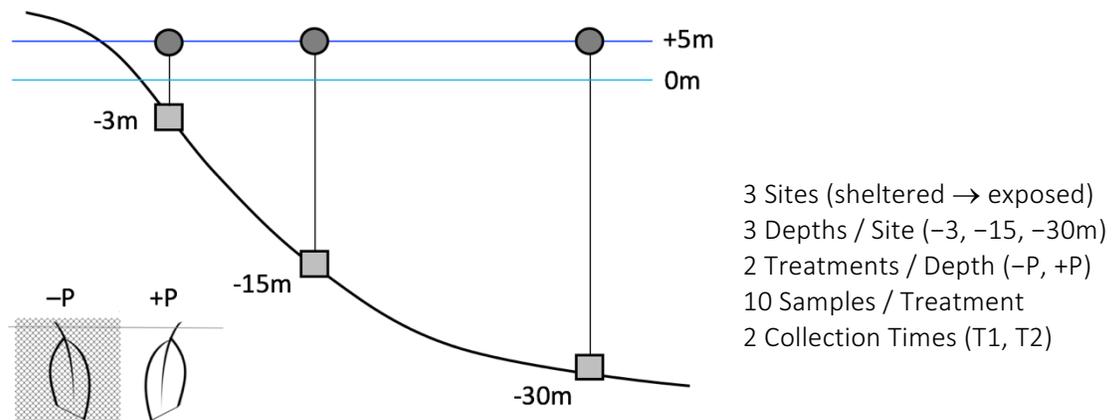


Figure A2. Experiment design. Herring eggs harvested on kelp blades from the shallow subtidal (0 to -3m CD) were attached to weighted frames and transplanted to 3 depths (-3, -15, and -30 m CD). Samples were treated for predator exclusion or predator exposure; predator exclusion samples were placed in 2.5cm Vexar mesh pouches. Transplants were completed at 3 sites, each with differing exposure to marine weather. Sample collection took place at two time intervals: T1 (9 days) midway through egg development (when eye pigments were first visible) and T2 (15 days) shortly before larvae were predicted to hatch.

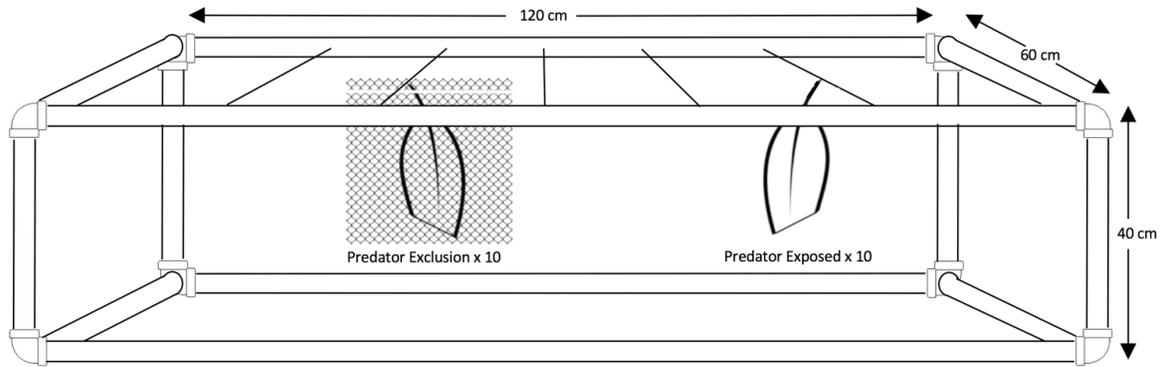


Figure A3. Herring egg transplant frame. Twenty samples (eggs on kelp blades) were haphazardly attached to each frame; 10 from each treatment (predator exclusion and predator exposed); predator exclusion samples were placed in 20 x 30 cm Vexar mesh (2.5 cm) pouches.

Table A1. Six categories defined to document relative frequencies of survival and different stages of development (Kawakami et al. 2011):

1. Dead: opaque (typically white) or damaged
2. Fertilization to epiboly
3. Segmentation to pharyngula
4. Eye pigmentation to melanophore appearance
5. Full development
6. Empty (hatched or predation loss)

Appendix B. Deep spawn characteristics

Table B1. Deep spawn observations for locations shown in Figure 1. Layer and % cover values for each depth are averaged from multiple transects at each location. Survival estimates determined from samples collected at -3, -15, and -30 m along each transect.

Depth (m)	Spiller Inlet		Cheenis Point		Spiller Inlet Point	
	Layers	% Cover	Layers	% Cover	Layers	% Cover
3	4	100	6	100	4	100
0	5	100	5	100	7	100
-3	5	100	8	100	5.5	100
-6	3.5	70	10	100	8	90
-9	6	100	13	100	13	100
-12	8	100	12	100	10	100
-15	6	100	8	100	12	100
-18	4	100	6.5	100	8.5	80
-21	3.5	100	6	100	10	100
-24	2	100	3	100	7	100
-27	1.5	90	2.5	100	5	95
-30	1	80	1.5	90	1.5	100
Mean:	4.1	95.0	6.8	99.2	7.6	97.1
* Survival:	-3 m: 19 %		-3 m: 19 %		-3 m: 66 %	
Max Depth:	-33.3		-39.8		-44	

* No eggs from -15 and -30 m depths were alive when collected

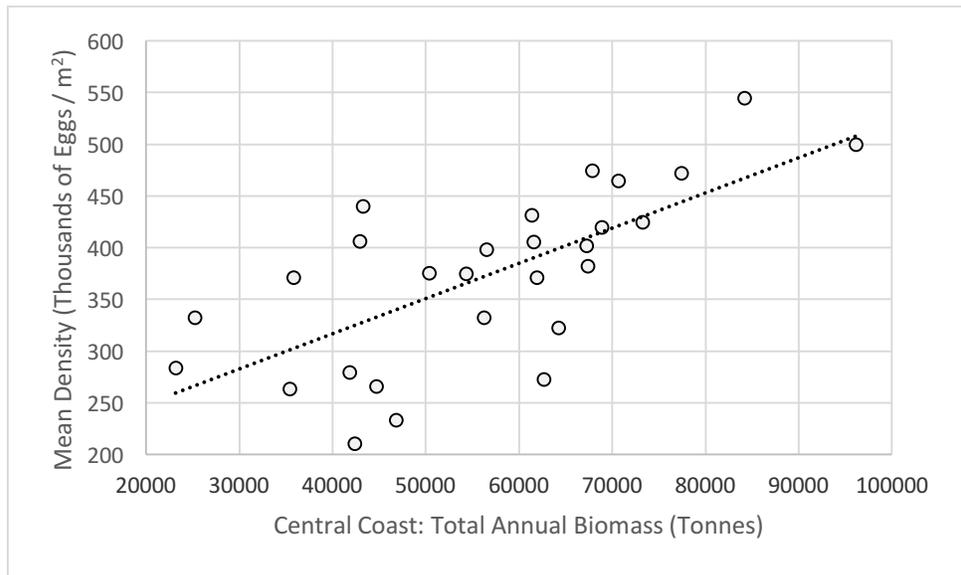


Figure B1. Mean density of herring eggs (thousands of eggs/m²) compared with total annual biomass estimates (tonnes) using linear regression. Data retrieved from Fisheries and Oceans Canada spawn surveys (1989 – 2015).

Appendix C. Temperature, salinity, and dissolved oxygen results

Table C1. Mean dissolved oxygen (mg/L) levels during the depth experiment

	-3 m	-15 m	-30 m
Site 1 (sheltered)	7.1	8.7	9.6
Site 3 (exposed)	8.1	9.3	10.2

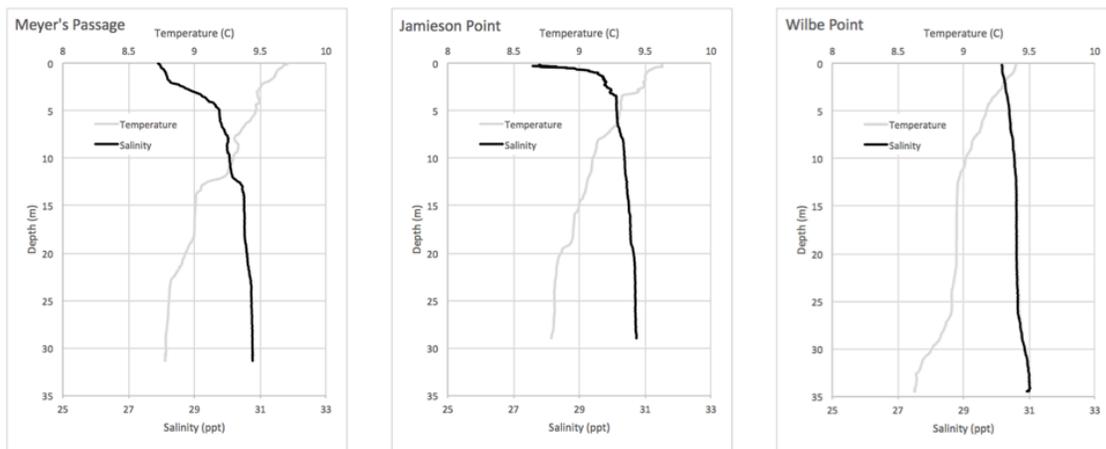


Figure C1. Temperature and salinity results from CTD drops in Kitasu Bay

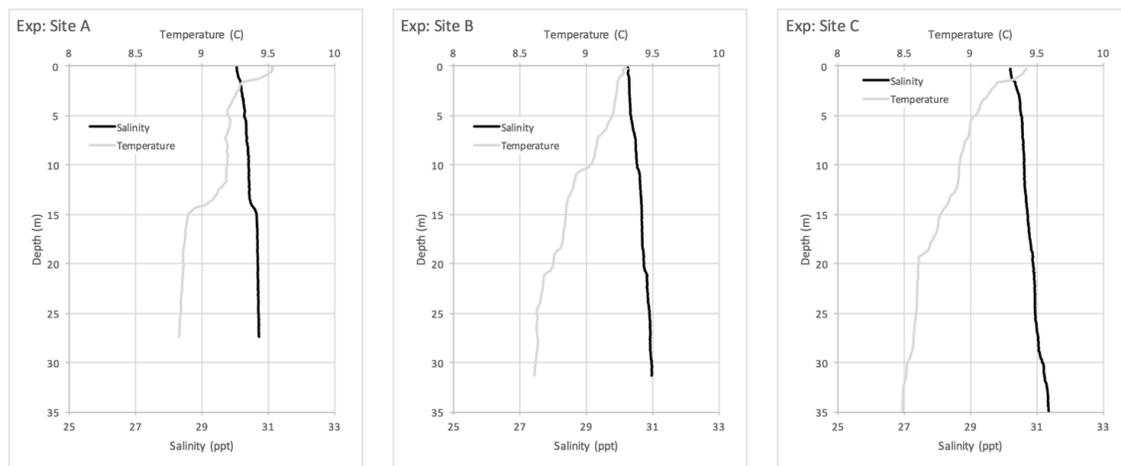


Figure C2. CTD Temperature and salinity results from experiment sites (A, B, and C) in Kitasu Bay

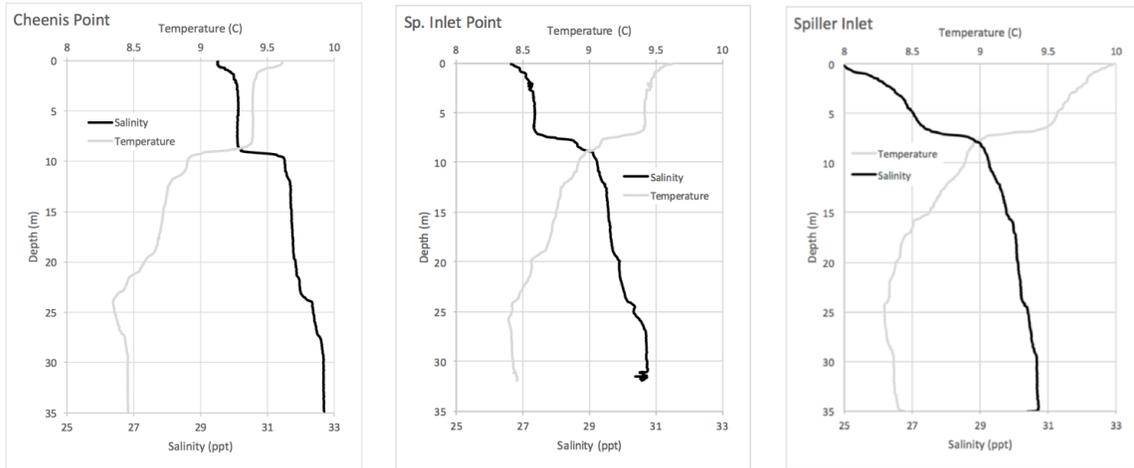


Figure C3. Temperature and salinity results from CTD drops in north Spiller Channel.

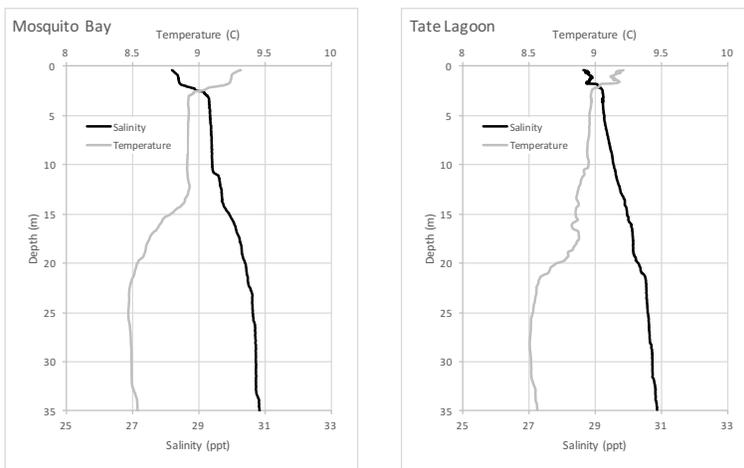


Figure C4. Temperature and salinity results from CTD drops in south Spiller Channel

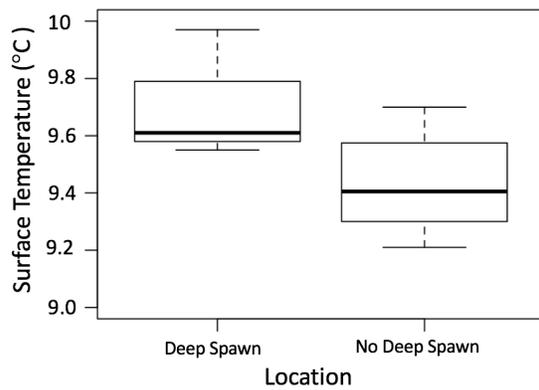


Figure C5. Surface temperature comparison between spawn areas with and without deep spawn.

Appendix D. Survey observations

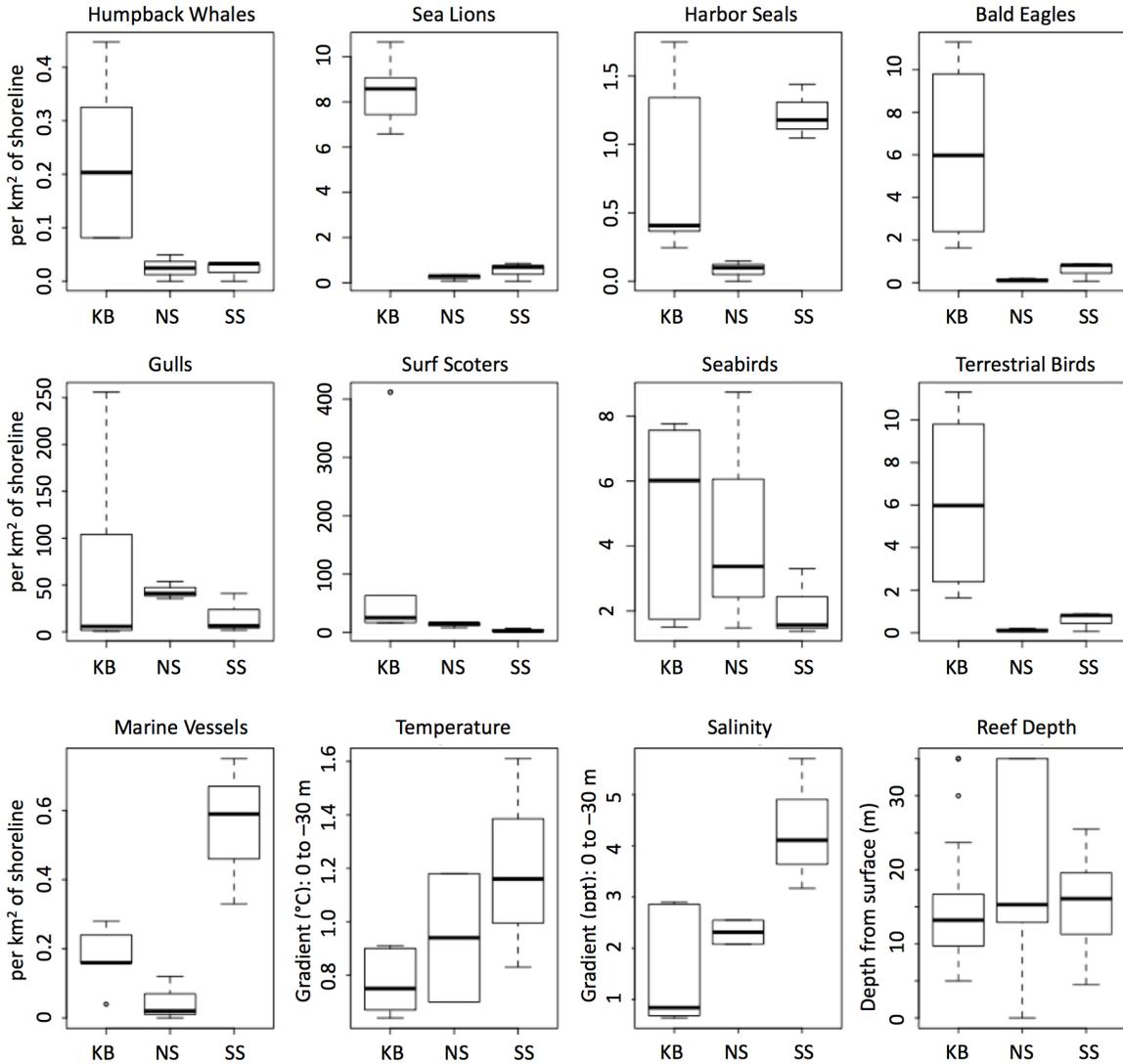


Figure D1. Survey observation comparisons between Kitsu Bay (KB), north Spiller Channel (NS), and north Spiller Channel (SS). Wildlife and vessel traffic observations were recorded while travelling at a constant speed, approximately 100 metres from the shoreline. Temperature and salinity measurements were taken using a CTD at a 6 Hertz sampling rate. Reef depth is a measure of the uninterrupted presence of bedrock from the surface to its maximum depth. Reef depth was obtained using a submersible camera system. Higgins Passage has been omitted here for simplicity, as reef depth did not allow for the possibility of deep spawn.

Tables D1 and D2. Mean and maximum daily predator abundance in Kitasu Bay, Higgins Passage, and Spiller Channel before, during, and after the 2016 herring spawn.

Table D1 A – Predator Abundance Observed in Kitasu Bay

Species	Highest Daily Abundance	Mean Daily Abundance
Humpback Whales	8	4
Steller Sea Lions	262	220
Harbour Seals	43	23
Bald Eagles	278	181
Gulls	6,297	2,251
Surf Scoters	10,135	3,180
Other Seabirds	191	142
Terrestrial + Shorebirds	85	33

Wildlife was observed in Kitasu Bay on March 24, 25, 27 and 31. Kitasu Bay = 24.6 km of shoreline. Herring spawned from March 27 to April 1.

Table D1 B – Predator Abundance Observed in Higgins Passage

Species	Highest Daily Abundance	Mean Daily Abundance
Humpback Whales	2	1
Steller Sea Lions	22	11
Harbour Seals	7	3
Bald Eagles	34	14
Gulls	992	342
Surf Scoters	3,502	2,139
Other Seabirds	77	35
Terrestrial + Shorebirds	18	5

Wildlife was observed in Higgins Passage on March 24, 25, 27 and 31. Higgins Passage = 8.1 km of shoreline. Herring spawned from March 27 to April 1.

Table D1 C – Predator Abundance Observed in Spiller Channel

Species	Highest Daily Abundance	Mean Daily Abundance
Humpback Whales	11	4
Steller Sea Lions	33	220
Harbour Seals	44	41
Bald Eagles	30	23
Gulls	2,320	2,028
Surf Scoters	791	663
Other Seabirds	397	248
Terrestrial + Shorebirds	120	85

Wildlife was observed in Spiller Channel on March 26, 28 and April 1. Spiller Channel = 71.2 km of shoreline. Herring spawned from March 23 to April 4.

Table D2 – Species List

Common Name	Latin Name
Birds	
Bald Eagle	<i>Haliaeetus leucocephalus</i>
Belted Kingfisher	<i>Megasceryle alcyon</i>
Bonaparte's Gull	<i>Chroicocephalus philadelphia</i>
Bufflehead	<i>Bucephala albeola</i>
Brandt's Cormorant	<i>Phalacrocorax penicillatus</i>
California Gull	<i>Larus californicus</i>
Common Goldeneye	<i>Bucephala clangula</i>
Common Merganser	<i>Mergus merganser</i>
Common Murre	<i>Uria aalge</i>
Common Raven	<i>Corvus corax</i>
Great Blue Heron	<i>Ardea herodias</i>
Mallard	<i>Anas platyrhynchos</i>
Northwestern Crow	<i>Corvus caurinus</i>
Pacific Loon	<i>Gavia pacifica</i>
Pelagic Cormorant	<i>Phalacrocorax pelagicus</i>
Rhinoceros Auklet	<i>Cerorhinca monocerata</i>
Surf Scoter	<i>Melanitta perspicillata</i>
Western Grebe	<i>Aechmophorus occidentalis</i>
Pinnipeds	
California Sea Lion	<i>Zalophus californianus</i>
Harbour Seal	<i>Phoca vitulina</i>
Steller Sea Lion	<i>Eumetopias jubatus</i>
Cetaceans	
Harbour Porpoise	<i>Phocena phocena</i>
Humpback Whale	<i>Megaptera noveangliae</i>
Killer Whale	<i>Orcinus orca</i>

Appendix E. Spawn density observations

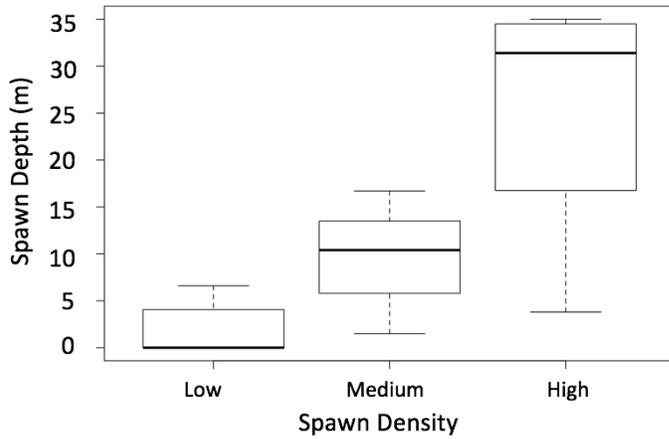


Figure E1. Spawn depths observed on our survey between spawning events with differing estimated spawn densities. In general, density estimates were made using the following guidelines: low density = $< 1,000\text{m}^2$, 50% substrate coverage, and 1 – 2 egg layers; medium density = $1,000 - 10,000\text{m}^2$, 50 – 90% coverage, and 3 – 4 egg layers; high density = $> 10,000\text{m}^2$, 90% substrate coverage, and > 5 egg layers.

Appendix F. Predation of exposed experiment samples

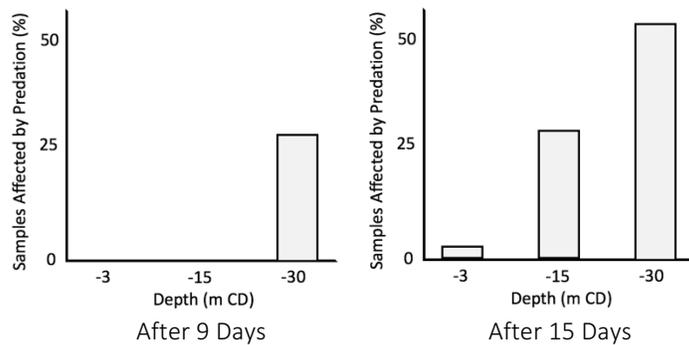


Figure F1. Percent of exposed samples affected by predation (either total or partial consumption).