

Habitat limitation and spatial variation in Pacific herring egg survival

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ABSTRACT: Nearshore habitats play a vital role in the life cycles of many marine fishes. These habitats are particularly important for Pacific herring *Clupea pallasii*, which rely on submerged vegetation in the shallow subtidal for spawning habitat and egg incubation. However, little is known about spatial or temporal variation in egg success or how spawning habitat may affect herring early life history. We estimated herring egg loss rates across multiple spawning vegetations in 5 subpopulations of Pacific herring in Puget Sound (USA), an urbanized estuarine system. We found enormous variation in herring egg loss among subpopulations (range of daily loss rates: 5 to 70 %) and in egg loss of eggs reared under common garden conditions (range of cumulative loss: 20 to 100 %). Egg loss varied by subpopulation but not by spawning vegetation type. Exploratory analyses suggest both wave height and land use patterns may affect hatch success. Using historical survey data, we found that a large proportion of spawning habitat available to Puget Sound herring remains unused each year. Furthermore, we found limited evidence that eggs were deposited disproportionately on particular vegetation types; only the non-indigenous brown algae *Sargassum muticum* was spawned on more than expected by chance. Our results demonstrate that Puget Sound herring are not limited by the amount of available suitable spawning vegetation, and that native vegetation is not preferred over other vegetation types for herring spawning. Rather, it appears that other terrestrial or marine variables are likely determinants of herring egg loss.

KEY WORDS: Puget Sound · Forage fish · Nearshore habitat · Egg loss · Herring · Habitat limitation · *Clupea pallasii* · Eelgrass

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INTRODUCTION

Low trophic level schooling fishes are generally abundant in the world's oceans, and by linking primary production to upper trophic levels these 'forage fish' are vital components of marine ecosystems (Cury et al. 2011, Pikitch et al. 2012). Population collapses of forage species around the world (e.g. clupeoids; Lasker 1985) have spurred interest in understanding the causes of such collapses, how to limit the likelihood of collapses, and how to promote pop-

ulation recovery (Hutchings 2000, Hutchings & Reynolds 2004). Oceanographic conditions can be critically important for recruitment and growth of forage fishes (Jacobson & MacCall 1995, Dickey-Collas et al. 2010, Reum et al. 2011). Additionally, forage species may be particularly vulnerable to fishing pressure (Smith et al. 2011, Pikitch et al. 2012). Consequently, fisheries managers are beginning to adopt more precautionary management strategies, thereby affording additional protection to forage species to buffer against fluctuations in their abundance.

Shallow coastal seas play a crucial role in the life history of many forage fishes (e.g. Hay 1985, Quinn et al. 2012). For example, biogenic habitats such as macroalgae and seagrass provide spawning surfaces and potentially provide refuge from predation (Heck et al. 2003); yet the loss or alteration of these nearshore marine habitats has received scant attention by managers and researchers concerned with forage fishes. With an expected rise in the proportion of urban population living near the coast from 65% to 74% by 2025 (United Nations Human Settlements Programme 2011), coastal ecosystems will likely experience modification of shorelines (e.g. armoring; Toft et al. 2007, Dugan et al. 2008), changes in nutrient and sediment attributes (Bowen & Valiela 2001, Vaalgamaa 2004), and increases in a variety of pollutants (West et al. 2008, Incardona et al. 2012). However, connecting these pressures to their consequences for forage fish and associated marine communities has proven difficult. Thus, while much focus remains on altering fishing pressure to maintain sustainable forage fish populations, the availability and quality of habitat may play an important role for these species.

Here, we focus on the interaction between coastal habitat and one of the primary forage fish of the NE Pacific coastal ecosystem, Pacific herring *Clupea pallasii*. Herring use nearshore marine habitats from California to Alaska to Japan throughout their life cycle (Hay 1985). Herring lay their eggs on nearshore submerged vegetation where the eggs incubate for 8 to >30 d, depending on water temperature (Alderice & Velsen 1971, Palsson 1984, Hay 1985). Following hatching, herring have a short planktonic larval phase after which juveniles appear to remain nearshore (Hay & McCarter 1997, Reum et al. 2011), possibly migrating to deeper water to overwinter as juveniles. Herring older than 1 yr can be found in both nearshore and offshore waters, and they return to nearshore habitats to spawn as adult fish after 2 to 4 yr (Hay 1985). Here we focus on the importance of nearshore habitat characteristics for one life stage, the embryonic stage.

In Washington State, USA, herring exist alongside a growing human population and an altered and changing marine nearshore environment. Washington's population has doubled in the last 40 yr and is predicted to increase by an additional 30% by 2030, with most of that increase centered around Puget Sound (State of Washington Office of Financial Management [WOFM] 2010). At present, approximately 27% of the Puget Sound shoreline has been armored (defined as shoreline that has been 'hardened' in a

variety of ways including rip rap, bulkheads, and seawalls; Pearson et al. 2011, Schlenger et al. 2011), and that armoring may have consequences for herring spawning habitat. One such habitat type, eelgrass *Zostera marina*, shows declining trends: losses have been documented in several major embayments, and since 2000, sites with observed decreases in eelgrass cover outnumber those with increases or no trend (Gaeckle et al. 2011). Concomitantly, trends of Puget Sound herring biomass have been variable but declining overall (Stick & Lindquist 2009, T. Francis unpubl. data), with some subpopulations (i.e. herring biomass associated with a specific spawning location) showing sharp declines in the last 40 yr, while others are increasing or unchanged. One subpopulation at Cherry Point (see Fig. 1) has declined dramatically over the past 30 yr, and was petitioned for listing under the US Endangered Species Act (Gustafson et al. 2006).

Despite these observed changes in nearshore habitat and associated declines in herring, very little work has focused on establishing direct linkages between nearshore habitat and herring, or on understanding what qualities or characteristics are required for herring spawning habitat. Empirical measurements of biologically meaningful rates are required for understanding and projecting any consequences of anthropogenic changes to herring populations and their associated habitat. However, these biological rates are lacking for nearly all Pacific herring populations, including those in Puget Sound.

To this end, it is important to understand the effect of habitat on egg survivorship, a sensitive and highly variable life-history stage in herring, particularly as habitat is increasingly degraded by human activities. Early research suggested that, under optimal conditions, nearly 90% of eggs survived to hatch in British Columbia (Hart & Tester 1934). More recent research has documented survivorship of ~25% (Prince William Sound, Alaska; Rooper et al. 1999), between 22 and 0% (Oregon; Steinfeld 1971), and between ~11 and ~0.01% (Washington State; Palsson 1984). Thus, herring egg survival is likely highly variable in space and over time, motivating empirical measurement of drivers of such variation (Haegele & Schweigert 1990). Furthermore, herring eggs are sensitive to a range of pollutants (Carls et al. 2002, West et al. 2008, Incardona et al. 2012), suggesting that coastal development and shifts in land use could greatly affect herring.

Here we present an empirical examination of the interaction between herring and nearshore habitat across 5 herring subpopulations in Puget Sound. We

combine field observations of naturally spawned herring embryos, a laboratory study of egg hatching rate, and historical data on the presence of nearshore vegetation and herring use of nearshore habitats to ask (1) Does herring egg survivorship vary among spawning vegetation types? (2) Does egg survivorship vary among subpopulations? (3) Does available vegetation for spawning vary among spawning subpopulations? (4) Do herring select certain vegetation types for spawning? and (5) If subpopulations vary in egg survivorship, can we identify plausible environmental drivers of the variation? Addressing these 5 questions provides a first step towards determining if herring populations are influenced by available habitat or habitat quality.

MATERIALS AND METHODS

Field sampling

We conducted surveys in known herring spawning areas to estimate rates of egg loss under field conditions. The 5 locations (Fig. 1, Table 1) sampled in 2013 are typical spawning grounds for Puget Sound herring stocks, where annual spawning biomass has been monitored since the mid-1970s (Stick & Lindquist 2009). Shorelines of Puget Sound are typified by mixed sand and gravel sediments of glacial origin; bedrock is rare and largely confined to northern Puget Sound (Finlayson 2006, Shipman 2008). Most vegetation used by herring for spawning in Puget Sound is confined to the shallow subtidal and lower half of the intertidal zone, between 0 and -3.0 m mean lower low water (MLLW) (Penttila 2007, Stick & Lindquist 2009). The locations sampled in 2013 occur across a gradient of environmental and biological conditions potentially associated with egg loss rates, including spawn timing, spawning vegetation, historical herring production, and urbanization. Each spawning location has been named by the Washington Department of Fish and Wildlife (WDFW), and a unique herring subpopulation is assumed to be associated with each spawning location: Cherry Point (hereafter, CP), Holmes Harbor (HH), Port Orchard-Port Madison (PM), Quilcene Bay (QB), and Elliot Bay (EB). Spawning events occurred between February and April of 2013 (Table 1).

We monitored egg densities at each subpopulation between 2 and 4 d post spawn at CP, HH, PM, and QB, and 7 d post spawn at EB (Table 1). Shortly after a herring spawn was reported at a particular subpopulation, 2 or 3 fixed transects (33 m) were established

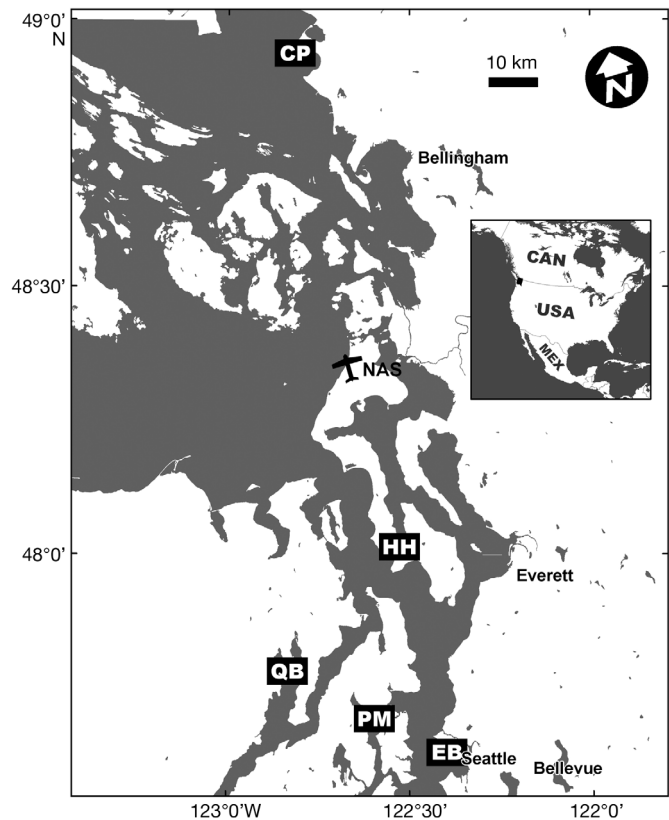


Fig. 1. Study area. Labels show the location of the 5 *Clupea pallasii* spawning sites sampled as well as the location of the weather station for the wind data. CP = Cherry Point, EB = Elliott Bay, HH = Holmes Harbor, PM = Port Madison, QB = Quilcene Bay, NAS = Whidbey Island Naval Air Station (wind data)

in the observed spawning area. Each transect was placed parallel to shore and at a single depth contour (depth varied less than 1.3 m within each transect; Table 1) and, collectively, transect locations were representative of the depth range of spawn observed at each site. Observed herring spawn spanned a narrow depth range that was very consistent among sites; all monitored stations were between -0.1 and -3.1 m below MLLW (Table 1). This distribution of spawn is typical of Puget Sound (Penttila 2007, Stick & Lindquist 2009) and is much narrower than other recorded herring spawn in the north Pacific (e.g. Haegele 1981). While eggs deposited in mid- or high-intertidal habitats are known to experience higher rates of egg mortality (Jones 1972), all transects in this study were subtidal.

Transect locations represented observed spawning depths and vegetation types for each subpopulation. Divers marked 4 sampling stations along each transect, with station locations haphazardly selected

Table 1. Summary of the environmental characteristics and field sampling details for 5 Puget Sound herring *Clupea pallasii* subpopulations sampled in 2013. See 'Materials and methods' for detailed methods for the calculation of expected days from egg deposition to hatch, mean significant wave height, area weighted mean imperiousness, and proportion armored shoreline. Dates are given as mo/d/yr

| Site | Estimated date of spawn | Field sampling dates | Tidal elevation (Transect: water depth relative to MLLW [m]) | Total number of sampling stations | Water temperature (°C; mean and 95% range) | Expected days from spawn to hatch (H) | Mean significant wave height (m) between the first and last sampling dates | Area weighted mean imperiousness | Proportion armored shoreline |
|--------------------------------|-------------------------|---------------------------------------|--|-----------------------------------|--|---------------------------------------|--|----------------------------------|------------------------------|
| Holmes Harbor (HH) | 3/06/13 | 3/08/2013; 3/12/2013; 3/15/2013 | T1: -2.4 to -1.1 T2: -1.5 to -1.2 | 8 | 14.93 (10.04–15.76) | 9.03 | 0.08 | 0.141 | 0.021 |
| Quilcene Bay (QB) | 3/20/13 | 3/22/2013; 3/27/2013; 4/1/2013 | T1: -1.3 to -0.4 T2: -0.8 to -0.5 T3: -0.7 to -0.4 | 15 | 10.12 (9.37–11.81) | 13.64 | 0.12 | 0 | 0 |
| Port Orchard-Port Madison (PM) | 3/24/13 | 3/28/2013; 4/2/2013; 4/5/2013 | T1: -3.1 to -2.2 T2: -1.8 to -1.5 T3: -0.8 to -0.5 | 12 | 9.53 (8.88–10.36) | 14.55 | 0.15 | 0.049 | 0.143 |
| Cherry Point (CP) | 4/30/13 | 5/3/2013; 5/7/2013; 5/10/2013 | T1: -1.1 to -0.2 T2: -0.7 to -0.1 T3: -1.2 to -0.2 | 12 | 12.11 (9.57–14.8) | 11.28 | 0.41 | 0.051 | 0 |
| Elliot Bay (EB) | 4/29/13 | 5/6/2013; 5/9/2013 | T1: -2.3 T2: -0.7 T3: -2.6 | 12 | 10.97 (10.06–12.30) | 12.51 | 0.27 | 0.474 | 0.788 |

based on the presence of vegetation belonging to 6 possible categories: eelgrass *Zostera marina*, *Sargassum muticum*, branched red algae, flat red algae, brown kelp *Laminaria saccharina*, and finely branched brown algae *Desmarestia viridis* (see the Supplement at www.int-res.com/articles/suppl/m514p231_supp.pdf for species included in each category). During each sampling visit, divers collected 4 vegetation samples of the same category from each station, removing an individual eelgrass shoot, a *Sargassum* stipe, a branched red algal stipe, a flat red algal holdfast, or a *Laminaria* stipe randomly from each of four 0.25 m² quadrats arranged in quadrants around a central point (see Fig. S1 in the Supplement). At QB we added additional stations adjacent to 2 transects to include samples from eelgrass habitats. We bagged samples underwater into fine mesh (<0.5 mm) bags, transferred them at the surface to Ziploc® bags containing seawater, and placed them on ice for subsequent quantification. Sampling was repeated at intervals of 3 to 5 d to document changes in herring egg density.

During the initial visit to each location, we also collected eggs for common garden incubation in the laboratory (see 'Common garden egg incubation' below). Vegetation with herring eggs was collected from the dominant spawning substrate from each site (see Table S1 in the Supplement). Samples were collected from haphazardly selected locations at each site as above, aggregated into a single Ziploc bag containing seawater, and placed on ice in a cooler for transport to the laboratory.

Laboratory processing

Egg density for each sample was estimated by counting eggs and measuring the surface area of the associated vegetation. Eggs were either counted visually (if few eggs were present) or estimated by volumetric displacement using a graduated cylinder and estimated egg-volume relationships developed for each vegetation type (see the Supplement and Fig. S2). Surface area calculations were driven by vegetation type and morphology, but generally involved a measurement of blade length and width or diameter, and quantification of the number of sub-dominant branches (see the Supplement for details). We developed methods for quantifying surface area of each vegetation type. We preserved a subsam-

ple of eggs from each sampling transect on each collection date in Stockard's solution (see the Supplement) and determined the developmental stage of herring eggs (Moulton & Penttila 2000) to ensure we were not sampling eggs from a secondary spawning event during sequential sampling visits.

Common garden egg incubation

To control for intrinsic differences in egg survivorship among different subpopulations that may influence site variability in observed egg loss, we incubated herring eggs collected at each sampling site under controlled common garden conditions at the NOAA Northwest Fisheries Science Center Mukilteo Field Station to determine hatching rates in the absence of the drivers of egg loss in the field (e.g. predation or physical disturbance). We established 8 replicate egg incubations from each subpopulation. Aggregate spawn-laden vegetation samples collected from each location were divided into 8 subsamples of between 40 and 120 herring eggs, and each subsample was placed into a 2.5 l flow-through, plexiglass tank (Cambro® plastic deep 1/3 hotel trays) piped with single-pass, sand-filtered seawater. Laboratory seawater was drawn from depth (−16 m re. MLLW) and kept at a constant 30 ± 1 psu and a flow of 200 ml min^{-1} . Temperatures were consistent across all treatments and ranged between 9 and 11°C during the incubation period. Larval hatch counts were performed daily (twice daily during peak hatching events). All larvae were removed from tanks post-hatch and daily counts continued until all hatching activity ended. Hatch rates for each tank were calculated by dividing the number of observed hatched larvae by the number of eggs initially introduced into each tank. In subsequent sections, we use the variable Q to designate the proportion of herring that hatched in the common garden experiment.

Egg loss model

We estimated herring egg loss rates for each vegetation type and each subpopulation using a Bayesian state-space model (Clark & Bjørnstad 2004). In brief, this method treats the observations of egg density at each station as very short time series and estimates the density of eggs at each station at each time as well as the egg loss rate for each observed combination of subpopulation and vegetation type. The method accounts for among-station variation in initial egg den-

sity, variation in the rate of egg loss among habitat types, small-scale spatial variation in the density of eggs at each station, and measurement error (see Clark & Bjørnstad 2004). Importantly, these models explicitly model every station and thus avoid conflating spatial variation in egg density with the process of egg loss. Formally, let $x_{ihs}(t)$ be the density of eggs at station i of vegetation type h at subpopulation s at time t . The density of eggs after τ days is then:

$$x_{ihs}(t + \tau) = x_{ihs}(t)e^{-(Z_{hs} + \varepsilon_{ihs})\tau} \quad (1)$$

where Z_{hs} is the daily egg loss rate shared across all stations of a given habitat type at each subpopulation, and the stochasticity in the egg loss process attributable to random forces is $\varepsilon_{ihs} \sim N(0, \sigma_{ihs}^2)$. We also created an observation model where the observed egg density is $y_{ihs}(t)$:

$$y_{ihs}(t) = x_{ihs}(t)e^{\delta_{ij}} \quad (2)$$

with observation stochasticity $\delta_{ij} \sim N(0, \omega_j^2)$. Thus, $x_{ihs}(t)$ represents the true mean density of eggs at station i and $y_{ihs}(t)$ are our observations of the egg density. Generally, we collected 4 samples with eggs at each station at each time, so we have 4 independent observations of $y_{ihs}(t)$. As some of the observation error arises from measurements of vegetation surface area, we estimated a shared observation error based on vegetation morphology type j , recognizing 4 main morphologies: branched brown algae *S. muticum*, eelgrass *Z. marina*, branched algae (including genera such as *Odonthalia* and *Gracillariopsis*, see the Supplement) and a flat, blade-like algal morphology including species such as the brown algae *L. saccharina* and the red algae *Mazaella splendens*. Each category of vegetation contains species with different specific morphologies but they are comparable for the purpose of modeling observation error.

We used diffuse independent normal priors for the egg loss rates for all Z , $p(Z) \sim N(0, 100^2)$, and diffuse inverse-gamma priors for all ω^2 , $p(\omega^2) \sim IG(0.01, 0.01)$. We used an informative prior for the process stochasticity, $p(\sigma^2) \sim \text{Gamma}(2, 10)$. In practice, this set of priors restricts process stochasticity to being small—egg densities cannot increase over time due to stochasticity—but allows observation errors to be large if necessary. Finally, we used diffuse independent normal priors for the initial density of eggs at each station, $\log(x(0)) \sim N(0, 10^2)$. We used Markov chain Monte Carlo (MCMC) methods to estimate the model, with a burn-in of 2000 iterations, 8000 monitored iterations, and 3 replicate MCMC chains from random starting points. We performed standard model convergence checks (Gelman-Rubin Statis-

tics; Gelman et al. 2003). As a small number of observations had 0 eggs, we added a small constant to each observation, $\log(y_{\text{new}}) = \log(y_{\text{obs}} + 0.001)$, and performed all analyses on y_{new} .

To compare estimates of the proportion of eggs that survived from spawning to hatching across all subpopulations and vegetation types, for each sample we combined the loss rate, Z , and the hatching rate of eggs under controlled conditions observed in the common garden incubations, Q . This assumes that egg viability under common garden conditions is representative of viability under field conditions and that egg loss rates in the field are independent of viability. The median density of eggs surviving from deposition (Day 0) to the day of hatching (H) is:

$$x(H) = x(0)Qe^{-ZH} \quad (3)$$

and the proportion of viable eggs surviving from deposition to hatching is

$$\Psi = \frac{x(H)}{x(0)} = Qe^{-ZH} \quad (4)$$

The incubation time for herring eggs is temperature dependent (Alderdice & Velsen 1971, Hay 1985). Therefore, we used published herring egg development curves (Alderdice & Velsen 1971, Jones 1972, Carls et al. 2002) to estimate a relationship between temperature (T) and the number of days after which 50% of individuals have hatched, $H = 159.4491 T^{-1.0622}$, and predict H for each subpopulation (Table 1). To produce uncertainty bounds around ψ , we evaluated Eq. (4) for each subpopulation and habitat type using the 8000 samples of posterior estimates of Z and 8000 independent samples from the method of moments estimator for the distribution of Q (see the Supplement for a description of the method of moments in this case). We refer to ψ as the cumulative probability of hatching hereafter. All analyses were conducted in R (v.3.1.0; R Development Core Team 2013).

Covariates of egg loss

To evaluate the potential role of environmental drivers on egg loss rates, we used existing data for potential drivers of egg loss: wave action and shoreline urbanization. As wave action has previously been identified as a potential source of egg loss, we modeled the relative exposure of each site to wind and wave action during the sampling period using the waves tool (Rohweder et al. 2008) in ESRI ArcGIS (see the Supplement for details). This model is a first-

order approximation of the wave field, and does not explicitly account for wave dissipation or wave energy refraction as waves propagate over complex and shallow bathymetry (Stevens & Lacy 2012). It integrates the interaction between wind conditions recorded at weather stations and a composite representation of wind fetch at each site. This approach provides a reasonable proxy for wave and wind exposure comparisons over large geographic regions (Mackay et al. 2012, Purkis et al. in press).

Shoreline urbanization degrades the nearshore environment in many ways, and may impact herring spawn. Therefore, we characterized the degree of urbanization in the watershed of each spawning site based on simple measures of anthropogenic modification: degree of imperviousness and proportion of shoreline armoring. Using ArcGIS, we analyzed the terrestrial and shoreline conditions within a 500 m radius circle around each site. The imperviousness data (Homer et al. 2004, Fry et al. 2011) are raster based, at a 30 m resolution, and they are an indicator of the degree of urbanization on land. We summarized the land-based imperviousness at each site by calculating an area-weighted mean imperviousness. The armoring data (Puget Sound Nearshore Ecosystem Restoration Project [PSNERP] 2010) are vector-based linear features, mapped to the Puget Sound shoreline, and are a general indicator of the degree of anthropogenic modification to the interface between land and sea. We characterized armoring by calculating the proportion of the shoreline within the 500 m radius circle that was categorized as armored. We show estimates of both measures of urbanization for each spawning location in Table 1.

Historical spawning habitat use

We used historical records (2006 to 2012) of herring spawn deposition surveys conducted by the WDFW to ask (1) Does the vegetation available for herring spawning vary across space? and (2) Is there evidence that herring prefer to spawn on certain vegetation? Puget Sound herring spawn deposition has been surveyed approximately weekly during the spawning season using a grappling rake deployed from a small boat (1972 to present; Trumble et al. 1977, Stick 1994, Stick & Lindquist 2009). Along with herring spawn density, presence/absence of spawning substrate— together with occurrence and density of spawn on that substrate—is recorded, producing a time series of fine-scale lower intertidal and subtidal vegetation distribution and its use by herring as

spawn substrate. Sampling occurs at all tidal stages and sampled areas represent areas from +1 to -6 m tidal elevation (MLLW is 0 m).

We developed spatially integrated summaries of the vegetation available for spawning habitat at 4 of our 5 sites to determine whether particular vegetation types were disproportionately used as spawning vegetation. We calculated the prevalence of 29 vegetation genera recorded by the WDFW plus 3 additional groups that combine genera into functional categories (branched red algae, flat red algae, flat brown algae; see Table S2 in the Supplement for a list of algal genera). As survey site selection was based on 30 yr of prior survey experience (Stick & Lindquist 2009), we assumed WDFW surveys were representative of vegetation available to receive herring spawn at each site, and that all surveys were conducted where herring spawn was likely to have occurred.

To calculate herring 'preference' for each spawning substrate type, we used the survey observations to estimate the prevalence of each substrate at each spawn site, and the occurrence of spawn deposition on each substrate type. We then used these 2 estimates to determine whether herring spawn occurred on each substrate in the same proportion as it occurred, or less (avoidance), or more (preference). To estimate substrate prevalence at each site, we treated each rake observation as an independent sample of available spawning habitat in each year. The prevalence of vegetation category i in year y , θ_{iy} , given k_{iy} occurrences out of n_y samples, follows a binomial distribution: $\theta_{iy} \sim \text{Bin}(n_y, k_{iy})$. If we assume the prior information for θ_{iy} is $p(\theta_{iy}) \sim \text{Beta}(0.0001, 0.0001)$, i.e. a very diffuse, non-informative prior, then the posterior distribution for θ_{iy} , given the rake survey data, $p(\theta_{iy}|k_{iy}, n_y)$, is (Gelman et al. 2003):

$$p(\theta_{iy}|k_{iy}, n_y) \sim \text{Beta}(0.0001 + k_{iy}, 0.0001 + n_y - k_{iy}) \quad (5)$$

Note that because multiple species can be observed in each rake sample, the proportional occurrence will not sum to 1 across species.

We estimated the occurrence of herring spawn at each site as the proportion of rake samples with herring spawn. We only included the weekly surveys in which at least 1 rake sample contained spawn. Then, the posterior estimate of the prevalence of the spawn, ϕ_y , with m_y total rake points observed, j_y samples having spawn, and a $\text{Beta}(0.0001, 0.0001)$ prior distribution for ϕ_y is:

$$p(\phi_y|j_y, m_y) \sim \text{Beta}(0.0001 + j_y, 0.0001 + m_y - j_y) \quad (6)$$

Finally, we calculated the joint occurrence of vegetation type and spawn, γ_{iy} (i.e. vegetation type i was

observed and it had herring spawn attached to it). Again, we included only data from survey dates when at least 1 rake sample had spawn observed. Let l_{iy} be the number of observations with spawn on vegetation type i , the posterior distribution for γ_{iy} is:

$$p(\gamma_{iy}|l_{iy}, m_y) \sim \text{Beta}(0.0001 + l_{iy}, 0.0001 + m_y - l_{iy}) \quad (7)$$

To determine whether herring selectively use certain vegetation types for spawning, we calculated the expected occurrence of herring eggs on each vegetation type if herring spawn was observed on that vegetation type in proportion to its occurrence, i.e. without preference or avoidance. If the occurrence of a vegetation type (θ_{iy}) and the occurrence of spawn (ϕ_y) are independent, the expected occurrence is $\theta_{iy}\phi_y$. We estimated the product $\theta_{iy}\phi_y$ by drawing 10 000 independent values from the posterior distributions of θ_{iy} and ϕ_y and calculating the mean and 95 % credible intervals. We then compared this independent expectation with the observed joint occurrence, γ_{iy} . Observing $\gamma_{iy} > \theta_{iy}\phi_y$ indicates that spawn is observed on vegetation type i more frequently than expected, while $\gamma_{iy} < \theta_{iy}\phi_y$ indicates the converse. In addition, we calculated the log-ratio of the expected and observed occurrences, $\log(\frac{\gamma}{\theta\phi})$, as a measure of the selectivity of herring for each vegetation type. We calculated credible intervals by taking independent draws from the posterior of each parameter and recalculating the log-ratio. While γ may differ from $\theta\phi$ in any given year due to a random chance, we are interested in patterns of spawn on vegetation that occur across sites and persist among years. Therefore, we calculated a weighted mean for the log-ratio at each site for each vegetation type and asked if there were persistent patterns in spawn on vegetation among sites and years.

RESULTS

In 2013, herring spawned on a variety of vegetation across the 5 sites. We estimated herring egg loss rates on eelgrass (at HH, QB), *Sargassum* (CP, EB, QB), branched red algae (CP, PM), flat red algae (CP), *Laminaria* (EB), and *Desmarestia* (EB) (Fig. 2). Initial egg densities — densities observed on the first day of sampling — ranged dramatically among sites and by vegetation. At QB, we observed very high egg densities on *Sargassum* and eelgrass (mean eggs per cm^2 : 142 and 58, respectively; Table 2). With one notable exception (*Desmarestia* at EB), the other 4 sites had lower egg densities ranging in means from 0.18 to 18.2 eggs per cm^2 (Table 2).

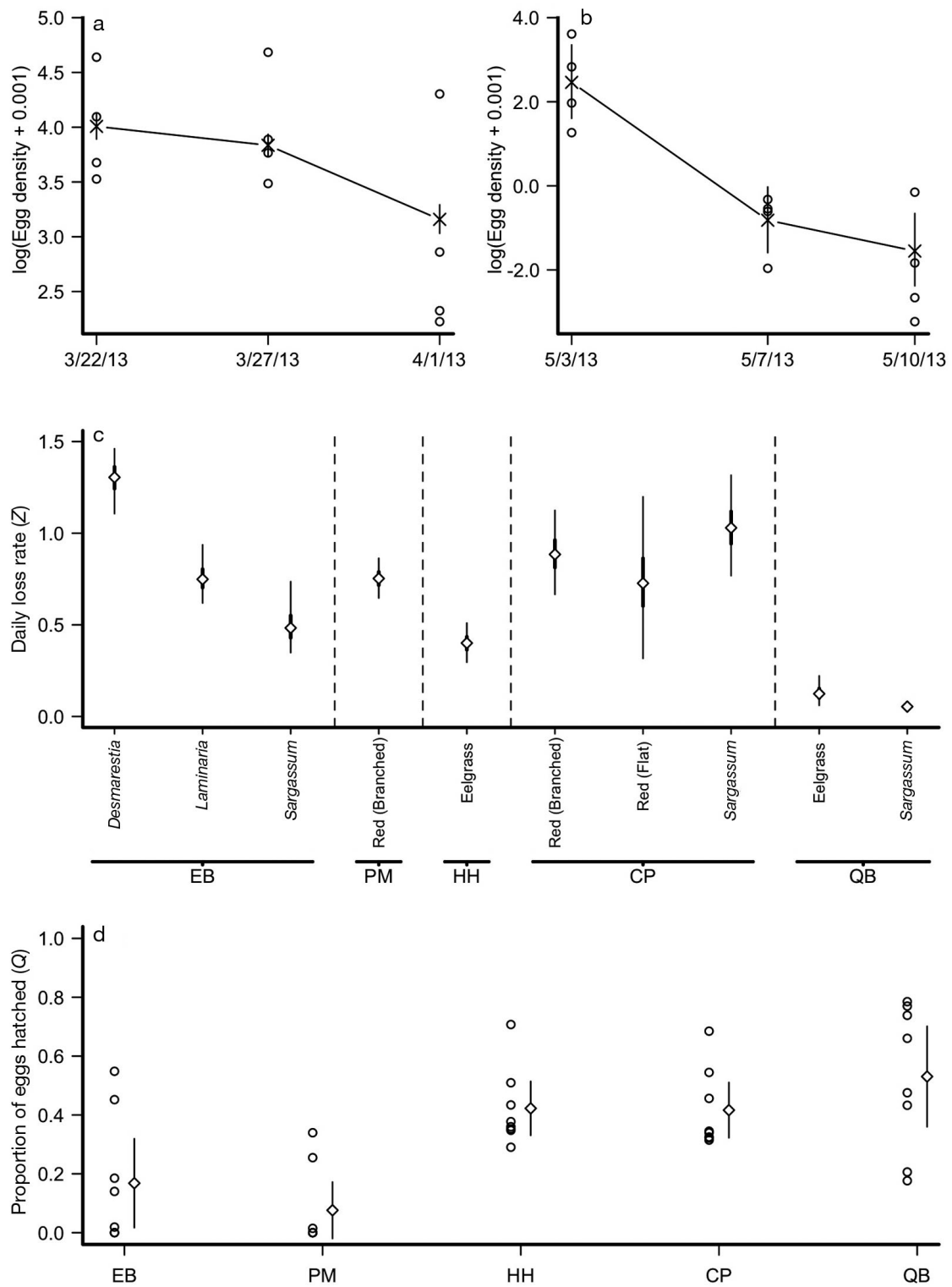


Fig. 2. Example time series of *Clupea pallasii* egg densities at (a) a single station at Quilcene Bay on eelgrass and (b) a station at Cherry Point on *Sargassum*. Observed herring egg densities (o) and posterior estimates of egg densities on each sampling date (x; \pm 95% credible intervals). (c) Posterior estimates of instantaneous daily egg loss rates by vegetation and site. Interquartile and 95% credible intervals are shown. (d) Proportion of eggs hatched under laboratory common garden conditions by site. Observed values for replicate tanks ($n = 8$ for each site) and mean \pm 95% confidence intervals are shown. Dates are given as mo/d/yr. Site abbreviations as in Fig. 1

Egg loss rates

We observed decreases in egg densities on vegetation through time across most sampling stations (Fig. 2, Figs. S3 to S7 in the Supplement at www.int-res.com/articles/suppl/m514p231_supp.pdf). Egg loss rates were highly variable among sites and vegetation types (range of estimated Z : 0.05 to 1.29; Fig. 2c, Table S3 in the Supplement). We saw limited evidence for vegetation-specific differences in egg loss within sites. At sites where herring spawned on multiple vegetation types (EB, CP, and QB), loss rates were lower on *Sargassum* at EB and QB. Herring spawned on a variety of vegetation types across sites so our power to detect vegetation-specific differences in egg loss was low. However, there were site differences in Z , with low loss rates at QB, moderate loss at HH (and possibly on *Sargassum* at EB), and higher rates at CP, EB, and PM. *Desmarestia* at EB had an exceptionally high estimated loss rate (Fig. 2c). The precision of the estimates of Z also varied across sites and vegetation types. As Z was estimated using multiple time-series of egg loss for each site-habitat pair (i.e. from multiple independently sampled stations, see Figs. S3 to S7), differences in precision reflect both the number of time series that contribute to each estimate of Z and the different estimates of process and observation stochasticity associated with these time series.

Egg viability under common garden conditions

Herring hatch rates in individual tanks ranged from 0 to 80%, with an across site mean of 30%. We found differences in hatch rates across sites (Fig. 2d;

Table 2. Initial *Clupea pallasii* egg densities (eggs cm^{-2} of vegetation on Day 0 at each subpopulation). Data are given as mean (SD)

| Subpopulation | Vegetation type | | |
|---------------|--------------------|------------------|--------------------|
| HH | Eelgrass | | |
| | 0.18 (0.17) | | |
| QB | Eelgrass | <i>Sargassum</i> | |
| | 58 (179.9) | 142 (145.2) | |
| PM | Branched red algae | | |
| | 0.69 (0.74) | | |
| CP | Branched red algae | <i>Sargassum</i> | Flat red algae |
| | 4.7 (4.4) | 18.2 (14.4) | 7.8 (5.2) |
| EB | <i>Laminaria</i> | <i>Sargassum</i> | <i>Desmarestia</i> |
| | 9.0 (7.9) | 6.8 (10.2) | 84.1 (87.8) |

$F_{4,35} = 11.34$, $p < 0.001$) and no effect of egg density, which ranged from 41 to 120 per 2.5 l tank ($F_{4,30} = 0.795$, $p = 0.54$). The lowest embryo viability was observed in eggs from EB and PM, and the highest rates were observed in HH, CP, and QB (see also Table S4 in the Supplement). As herring were collected from wild spawn, incubations were conducted over a nearly 3 mo span reflecting the staggered spawning of Puget Sound herring. Incubations from CP and EB, which had the strongest differences in the proportion of eggs hatched, were conducted simultaneously in adjacent containers. Interestingly, in 3 of 8 incubations from EB and 5 of 8 from PM, no embryos survived to hatching. A fungal infection was observed on some eggs collected from EB, and from unfertilized eggs collected from QB.

Cumulative probability of egg survival

We integrated estimates of egg loss, egg viability, and temperature-dependent development rates to produce a cumulative probability of eggs surviving from deposition to hatching (Fig. 3). The cumulative probability of survivorship (ψ) ranged over nearly 7 orders of magnitude across all sites. Estimated survival was highest at QB (median: 0.10 and 0.25 for eelgrass and *Sargassum*, respectively), intermediate at HH (median: 0.012), and less than 0.001 at all other sites and vegetation types (Fig. 3). Differences in cumulative survival reflect variation in the egg loss rate, Z , egg viability, Q , and differences in time to hatching among sites (range: 9.0 to 14.5 d, Table 1). In particular, we observed very low survival probability on brown alga.

Drivers of egg loss

We explored potential drivers of egg loss by comparing (1) field estimates of egg loss against estimates of wave height, and (2) laboratory estimates of egg viability from the common garden experiment against proxies of urban development. CP experienced dramatically higher significant wave height during the egg development period than any other site (Fig. 4, Table 1), providing a potential explanation for high rates of egg loss at that site. There was a trend toward a negative relationship between both shoreline armoring and upland development and hatching rate; areas with lower levels of armoring and impervious surfaces tended toward higher survivorship under common garden conditions.

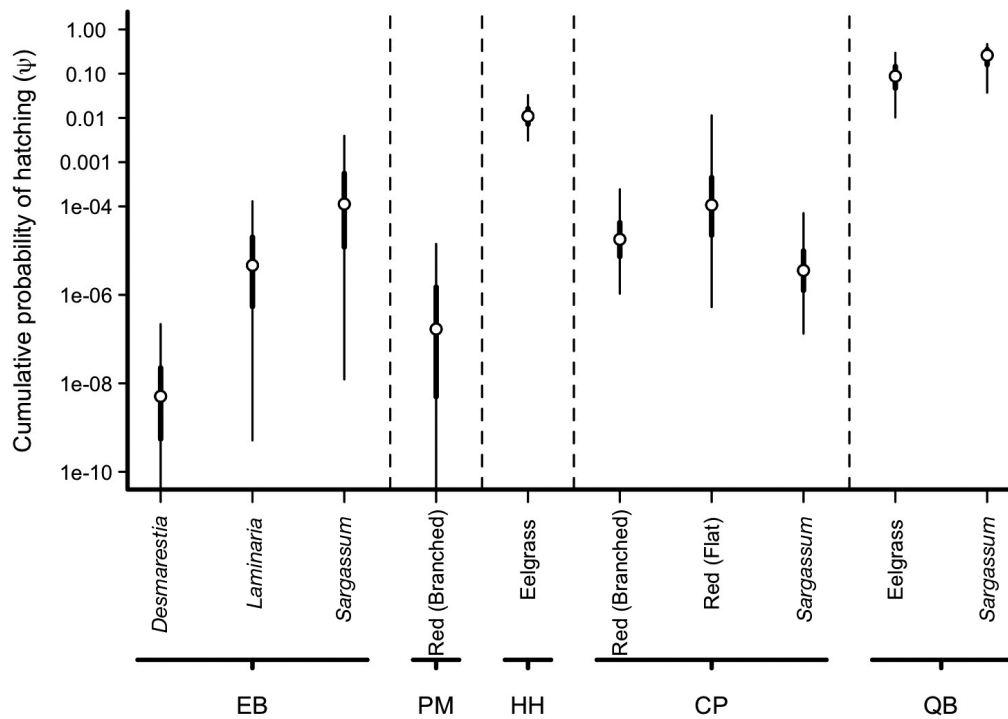


Fig. 3. Cumulative probability of *Clupea pallasii* eggs surviving to hatch by site and spawning vegetation. Median probability, interquartile range, and 95 % credible interval are shown. Note the logarithmic scale on the y-axis. Site abbreviations as in Fig. 1

Spawning habitat availability and use

Between 2006 and 2012, there was variation in the composition of vegetation available for herring spawn across sites (Fig. 5). HH was dominated by eelgrass beds (>97 % of rake samples contained eelgrass) with all other vegetation categories rarely observed. Eelgrass was also abundant at QB (~60 %) with *Sargassum* and branched red algae commonly observed and the remaining groups relatively rare. Branched red algae predominated at PM (63 %) followed by eelgrass, brown algae, and polychaete worm tubes (*Phyllochaetopterus* sp.; Penttila 2007). CP had the most even distribution of vegetation types with eelgrass, branched red algae, brown algae and terrestrial debris (e.g. sunken logs and wood) each occurring in approximately 40 % of rake samples, and *Sargassum*, flat red algae and *Desmarestia* occurring in approximately 20 % of rake samples. The diversity of vegetation observed at CP may reflect the larger geographic area sampled, resulting in greater diversity of habitats (Table S5).

In any given year, we estimated the proportion of available spawning habitat receiving spawn, ϕ , to be relatively low. Across the 7 yr of data, $\phi = 0.093$ (0.061–0.141) for CP (across year mean and range of annual values), $\phi = 0.273$ (0.170–0.476) for HH, $\phi =$

0.099 (0.051–0.159) for PM, and $\phi = 0.287$ (0.212–0.363) for QB.

In almost all cases, the observed joint occurrence of vegetation type and spawn closely matched the rate of co-occurrence expected by chance (Fig. 6), suggesting little evidence of habitat selection. In most cases, the frequency of eggs on individual vegetation types either did not differ from that expected by chance (e.g. eelgrass; Fig. 6a,d), or showed variation among sites, (e.g. branched red algae; Fig. 6c,f). Importantly, however, there was some evidence of disproportionate occurrence of spawn on non-indigenous *Sargassum* (Fig. 6b,e).

DISCUSSION

In recent years, concern has been mounting over the status of forage fish and the ecosystem services they provide (Pikitch et al. 2012). In Puget Sound, where fishing pressure is currently low, efforts to maintain resilience in herring stocks must be focused on non-fisheries pressures, i.e. on spawning habitat, nearshore water quality, disease, and trophic interactions. Our results demonstrate enormous spatial variation in the survival of Puget Sound herring embryos but suggest populations are not limited by the

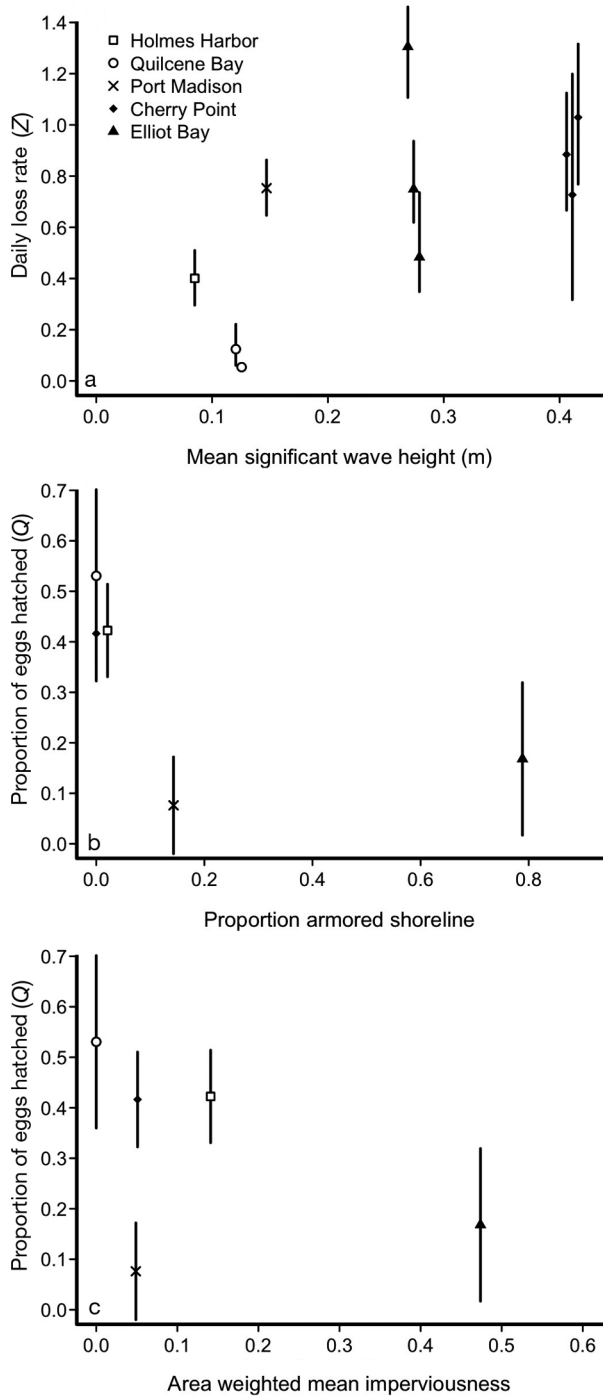


Fig. 4. Potential drivers of herring *Clupea pallasii* egg loss. (a) Significant wave height experienced at each site during herring incubation and field estimates of egg loss. Each point represents egg loss for distinct vegetation types (see Fig. 2). (b) Egg hatching rate and the proportion of shoreline with armoring within a 500 m radius of each sampling location. (c) Egg hatching rate and the area weighted mean imperviousness of the terrestrial region within a 500 m radius of each sampling location. Lines show 95% credible intervals in all panels

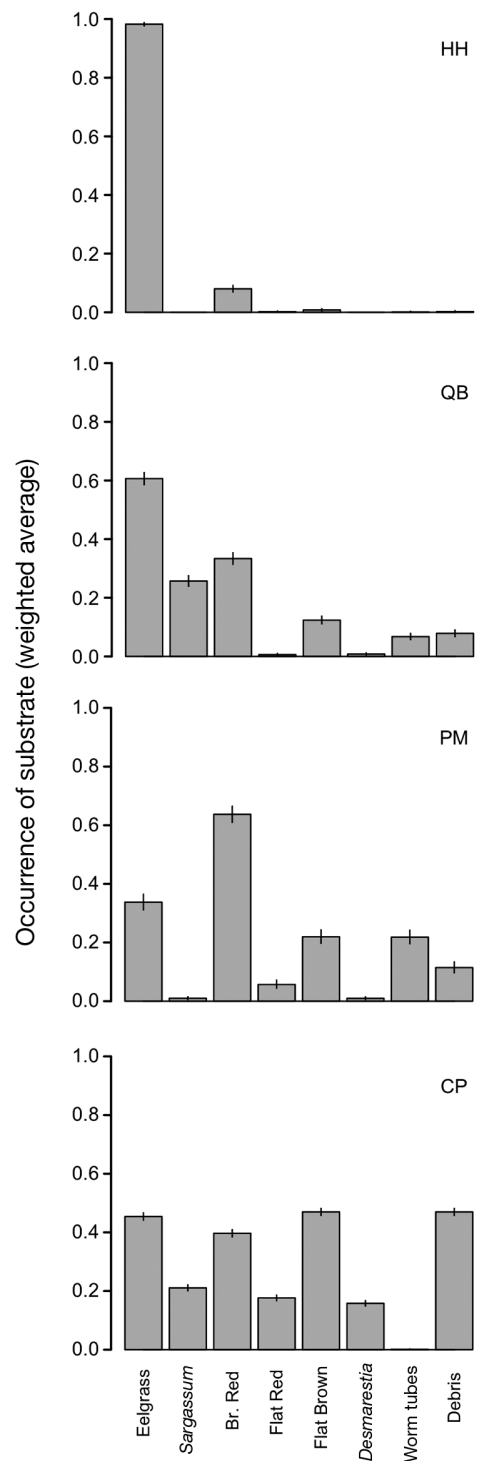


Fig. 5. Occurrence of major vegetation types at 4 Puget Sound herring *Clupea pallasii* spawn locations from 2006 to 2012. Bars show weighted average ($\pm 95\%$ credible interval from weighted variance) from 7 yr of survey data. Note that because multiple vegetation types can be observed in a single rake sample, the occurrence will not sum to 1 across groups. Site abbreviations as in Fig. 1

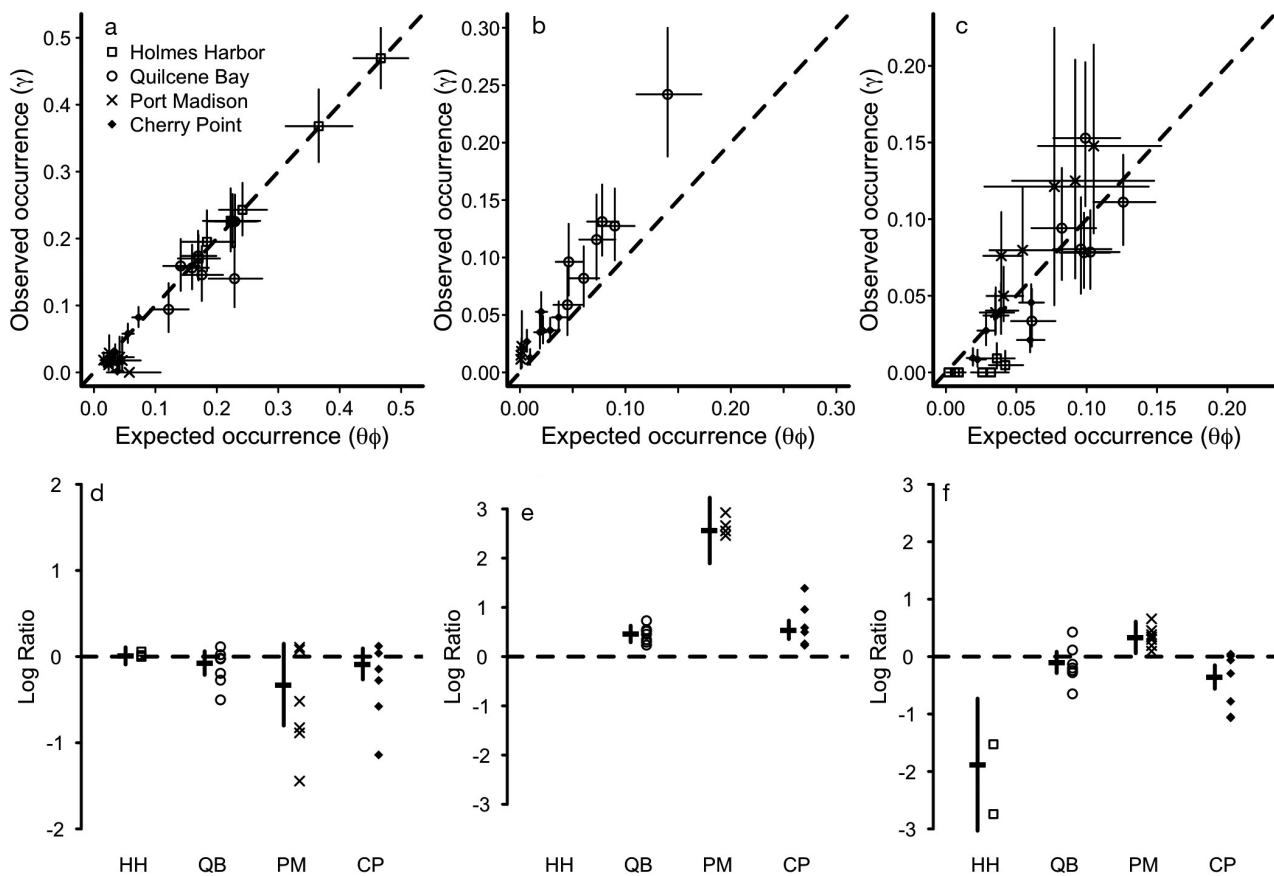


Fig. 6. Habitat use by herring *Clupea pallasii* at 4 sites in Puget Sound. Top row: Expected versus observed occurrence of spawn for (a) eelgrass, (b) *Sargassum*; and (c) branched red algae. Each point represents a single year at a site (posterior mean $\pm 95\%$ CI). Points that fall on the dashed line indicate the vegetation type was utilized as spawning habitat in proportion to its abundance, points above the line indicate that the habitat was spawned on more frequently than expected by chance, and points below the line indicate the vegetation was selected less frequently than expected by chance. Bottom row: The log-ratio of observed to expected occurrence (i.e. $\log[\frac{\gamma}{\theta\phi}]$). Each point represents the log-ratio for a single year for (d) eelgrass, (e) *Sargassum*, and (f) branched red algae. Horizontal bar represents the weighted among-year mean ($\pm 95\%$ weighted CI). Dashed line corresponds to random chance. *Sargassum* has not been observed at HH. Site abbreviations as in Fig. 1

amount of suitable spawning vegetation. Rather, it appears that other land-based or oceanographic variables are more important for determining herring success in Puget Sound.

The rates of egg loss we observed fall within the range of rates estimated in geographically proximate locations. Palsson (1984) estimated egg loss rates in 2 additional sites in Puget Sound ranging from 89.3% ($Z = 0.186$ at Quartermaster Harbor, on Vashon Island in Central Puget Sound) to 99.9% ($Z = 0.726$ at Birch Bay, near our Cherry Point study site). The Quartermaster rate is close to the lowest loss rate we observed, while the rate observed at Birch Bay is close to the median rate we observed (Fig. 2). In Georgia Strait, Canada, herring had a substantially lower egg loss rate, averaging 58% (Haegel & Schweigert 1990).

We observed substantial variation in the vegetation available for spawning, but saw no evidence suggesting that herring selected specific spawning substrates, except non-native *Sargassum*. This observation is particularly relevant given the concern over the contraction of some native eelgrass meadows in Puget Sound (Gaeckle et al. 2011, Puget Sound Partnership 2012) and the regional expansion of several introduced eelgrass species (Britton-Simmons 2004). Moreover, our results show that vegetation type does not dramatically affect egg loss. Overall, we found no evidence indicating that eelgrass is limiting for embryonic Puget Sound herring. However, we note that the local disappearance of some eelgrass meadows has led to the cessation of herring spawning activity in particular areas (Mumford 2007, Gaeckle et al. 2011).

Our results contrast with previous studies (e.g. Haegele & Schweigert 1990) that have found variation in egg loss rates across vegetation type. Divergence between the present results and others may result from variation in herring spawn depth in different systems. For example, in other systems, herring spawn on *Fucus* spp., a predominantly intertidal species group that results in higher egg loss rates than other species. We did not observe intertidal spawn on *Fucus* or any other intertidal algae in Puget Sound in 2013, eliminating desiccation as a major contributor to egg loss (Hay 1985, Rooper et al. 1999), and eliminating this vegetation-specific effect. We did observe vegetation-specific effects on egg loss rates that may be driven by intrinsic algal characteristics. Specifically, we observed the lowest egg survival rates on *Desmarestia viridis*, a species of brown algae known to accumulate extremely high levels of sulfuric acid (McClintock et al. 1982). This observation has been made previously, where low Atlantic herring egg survival occurs on filamentous brown algae, owing to algal exudates (Aneer 1987).

Our results suggest that site-specific characteristics drive egg survivorship, and that these site differences are unlikely to be explained simply by the habitat available at each site. However, other factors may also determine herring spawning habitat quality, and it is likely that some combination of these factors may be driving the across-site variability in egg loss. Egg loss rates appear to be positively associated with the wave environment experienced during egg development (Fig. 4a; Rooper et al. 1999). Furthermore, the laboratory hatching rate shows a trend toward a negative relationship with both shoreline armoring and the amount of impervious surfaces on land adjacent to the sampled spawning grounds (Fig. 4b,c). As field-collected eggs were removed from the spawning grounds after only a few days in the water, this suggests that the environment experienced in the first days of egg development may influence herring hatching. With data from only 5 sites, we lack the statistical power to formally test for relationships between egg hatching and metrics of development, but our results certainly warrant further investigation.

Egg predation may also be affecting variation in egg loss. Anecdotally, we observed elevated egg predation by birds at CP and QB, increased densities of benthic meso-predators at PM, and fungal infections at EB. Many organisms have been observed to consume substantial portions of herring spawn on the Pacific coast and elsewhere. Highly mobile predators may capitalize on the resources provided by herring

spawn events, and adjust their habitat use to take advantage of the presence of eggs. For example, surf scoters, gulls, and other birds were commonly present during herring spawning events and in the days after, and their diets include herring eggs (Haegele 1993a, Bishop & Green 2001, Žydelis & Esler 2005). In addition, invertebrate predators, such as crabs and sea stars, can consume up to 3–4% of the herring spawn at a given site (Haegele 1993b). While we did observe both avian and invertebrate predators at our sampling sites, we did not quantify predator abundance or egg predation. This is an area that warrants further consideration in the context of identifying causes of observed variation in egg loss rates across Puget Sound.

We estimated that the probability of herring eggs surviving to hatching varied over more than 5 orders of magnitude among sites. While our study was not designed to determine the exact mechanism underlying spatial differences in loss rates, the magnitude of differences in egg loss we document here is profound for the density of larval herring produced at these sites and, potentially, for subsequent life stages. The success of recently hatched herring in Puget Sound, like many other species, is tied to nearshore conditions during their first summer (e.g. Reum et al. 2011, Schweigert et al. 2013). Peak spawn times, and the total spawning window, vary among Puget Sound herring subpopulations, which may result in a range of vulnerabilities of larvae and juveniles to seasonal environmental variation (especially the spring plankton bloom and associated zooplankton prey availability). If egg hatch rates are low at sites that have relatively high vulnerability, it could affect the abundance of young-of-the-year herring and subsequent year class strength for those cohorts. Rigorously connecting observed variability in egg survival rates to subpopulation growth rates will require additional research. Nonetheless, we note that the 2 subpopulations with the highest egg survival (QB and HH) have increased in recent years, while the 2 subpopulations with lower egg survival rates (CP and PM) have decreased over the past 30 yr (Stick & Lindquist 2009). No time-series data exist for EB.

We caution that there are limitations to our historical habitat-use data. For example, it is inappropriate to directly compare the proportion of area used by herring for spawn (ϕ) among sites for a variety of sampling reasons. And while exact values of ϕ should be interpreted cautiously, all estimates of ϕ were much less than 1, indicating that there were extensive areas where vegetation was present but did not receive spawn. As annual surveys were only con-

ducted in areas that have previously received spawn, or, in which there is a credible report of a new herring spawn, this suggests that abundant suitable habitat is available for herring spawn. However, some surveyed areas may be unsuitable for herring spawn for reasons that are not apparent to us.

This research provides a step towards determining if herring populations are limited or inhibited by available habitat or habitat quality. It is among the first to investigate the role different vegetation types may play in determining herring survival, and is a vital step toward understanding how spatial and habitat variation may drive population level changes in herring. Clearly more research is needed to understand the interaction between nearshore biogenic habitat and herring populations, but our work shows that there is biologically significant spatial variation in the success of herring eggs across our study sites and avenues for understanding the drivers of this variation.

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