



Influence of environmental and population factors on Prince William Sound herring spawning phenology

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ABSTRACT: Shifts in spawning phenology may impact the early life stages of small pelagic fishes, affecting their first-year survival and recruitment. In Prince William Sound, Pacific herring is a key forage species that once supported commercial and subsistence fisheries for many decades, but collapsed in 1993 and has yet to recover. Starting in 1980, spawn timing shifted earlier by approximately 2–4 wk over a 27 yr period, then abruptly shifted later by approximately 3 wk over the next 7 yr. We quantified the influence of 15 environmental and population-level covariates on these spawn timing shifts using generalized linear models. Earlier spawn timing was associated with higher biomass in the eastern sound and older mean age in the western sound. Across the entire sound, earlier spawning was associated with weaker downwelling, weaker meridional winds, and the positive phase of the Pacific-North American teleconnection pattern, which is characterized by warmer North Pacific waters. These results are a critical first step towards assessing how changes in spawning phenology impact first-year survival of herring offspring and potentially contribute to persistent poor recruitment that has inhibited the recovery of the Prince William Sound population.

KEY WORDS: Spawn timing · *Clupea pallasii* · Phenology · Forage fish · Small pelagics

1. INTRODUCTION

In nature, timing is everything. For many marine fishes, including temperate small pelagic fishes, shifts in spawn timing may impact larval survival by altering: when larval emergence occurs relative to food availability (the match–mismatch hypothesis; Cushing 1990, Neuheimer et al. 2018), transport of larvae to (and retention in) nursery areas (Sinclair 1988), and exposure of aggregating adults and eggs to potential predators (Sewall et al. 2019). Therefore, examining spawn timing drivers is crucial to understanding how interannual variability in phenology affects first-year survival and recruitment success.

Almost all herring (*Clupea* spp.) populations exhibit large fluctuations in spawning biomass, recruitment and catches (Essington et al. 2015, Trochta et al. 2020), but the causes of these fluctuations remain enigmatic, and a debate as to whether this is due to environment, fisheries, other human-caused impacts or a combination of drivers remains. For example, in our study population, Pacific herring (*Clupea pallasii*, hereafter herring) in Prince William Sound, there have been large shifts in population size over the past 50 yr, including an abrupt collapse in 1993 (Muradian et al. 2017) followed by an anomalously long period of poor recruitment and low biomass (Trochta et al. 2020). The causes of the initial popula-

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tion collapse and lack of recovery are uncertain, with multiple hypotheses attributing the collapse to poor nutrition (Pearson et al. 2012), infectious diseases (Marty et al. 1999, 2003), or the combined effects of the 1989 Exxon Valdez oil spill and overfishing (Thorne & Thomas 2008).

Potential factors that influence the timing and location of spawning among herring populations in the Northeast Pacific have received limited attention. In Prince William Sound, annual peaks in spawn timing shifted earlier by 26 and 15 d in the eastern and western regions of the sound from 1980 to 2006, respectively; then shifted later by 25 (eastern) and 19 d (western) over the next 7 yr (McGowan et al. 2021). Herring population status could be one possible factor driving shifts in the location and timing of spawning in Prince William Sound (McGowan et al. 2021). Following the collapse in 1993, spawning shifted away from historically active areas of the sound to areas that were not widely used in the 1980s, when the population reached peak biomass (McGowan et al. 2021). The spatial differences, previously mentioned, in the rate of change in spawn timing between eastern and western Prince William Sound suggest that local environmental processes may be driving these changes, while the post-collapse contraction of active spawning areas is potentially linked to low spawning biomass levels. Interannual variations in herring spawn timing among herring populations in British Columbia have been primarily attributed to population demographics and temperature (Hay 1985, Ware & Tanasichuk 1989). Processes such as climate and population dynamics have been linked to spawning phenology for a variety of temperate fishes (Clark et al. 2005, Jansen & Gislason 2011, Rogers & Dougherty 2019, Slesinger et al. 2021). However, it is unknown how environmental processes at different spatial scales influence herring spawn timing in Prince William Sound (e.g. regional versus local) or population-level factors (e.g. spawning biomass, age structure, fitness).

To improve our understanding of how population demographics and extrinsic factors influence recruitment dynamics of herring to the Prince William Sound population, we investigated how interannual variability in spawn timing is influenced by population-level and/or environmental processes operating at different spatial scales (within Prince William Sound, ~10s of km; the northern Gulf of Alaska, ~100s of km; the Northeast Pacific, >1000 km). Generalized linear models were used to quantify the influence of 5 population variables, 6 local environmental variables, and 4 climatological variables on

variations in median spawn date (a proxy for spawn timing) for all spawn locations across Prince William Sound and separately for spawning in the eastern and western regions of the sound (Fig. 1).

2. MATERIALS AND METHODS

2.1. Spawning data collection

Herring spawning data were obtained by the Alaska Department of Fish and Game (ADF&G) from aerial surveys conducted over a 40-yr period (1980–2019) across the Prince William Sound (Fig. 1). Aerial surveys are flown between late March and mid May and attempt to account for all spawning within the sound (Shepherd & Haught 2019). Summarized by McGowan et al. (2021), surveys employ a non-random design based on the most recent information regarding herring schools and spawning aggregations reported by boats on the sound and non-survey flight traffic observations. Surveys are flown once or twice per week at the start of the spawning season and then flown more frequently (up to twice a day) when spawning or pre-spawning aggregations are observed. Surveys end when there is no observed spawning or anecdotal reports of spawning in the sound. Flights are conducted along the coastline at approximately 460 m altitude for up to 5 h, covering about 800 km per survey.

During surveys, active spawning events are measured as the total length of milt clouds along the coastline per day, known as mile-days of milt (MDM, 1 mile = 1.609 km), and georeferenced (Brady 1987, Shepherd & Haught 2019, McGowan et al. 2021). The summation of MDM observations per year is used as a key index of relative abundance in the Prince William Sound herring stock assessment (Muradian et al. 2017). Processed spawn and survey effort data (1980–2018) are publicly available through the Alaska Ocean Observing System (<https://portal.aos.org>; Bochenek 2010, Haught & Moffitt 2018) and were combined for this study with survey data from 2019 (see McGowan et al. 2021). Explanatory and response variable time series in the analysis matched the same period as the herring spawning data (1980 to 2019).

2.2. Spawn timing index

Spawn timing was represented by the day of the year when 50% of total MDM was observed (here-

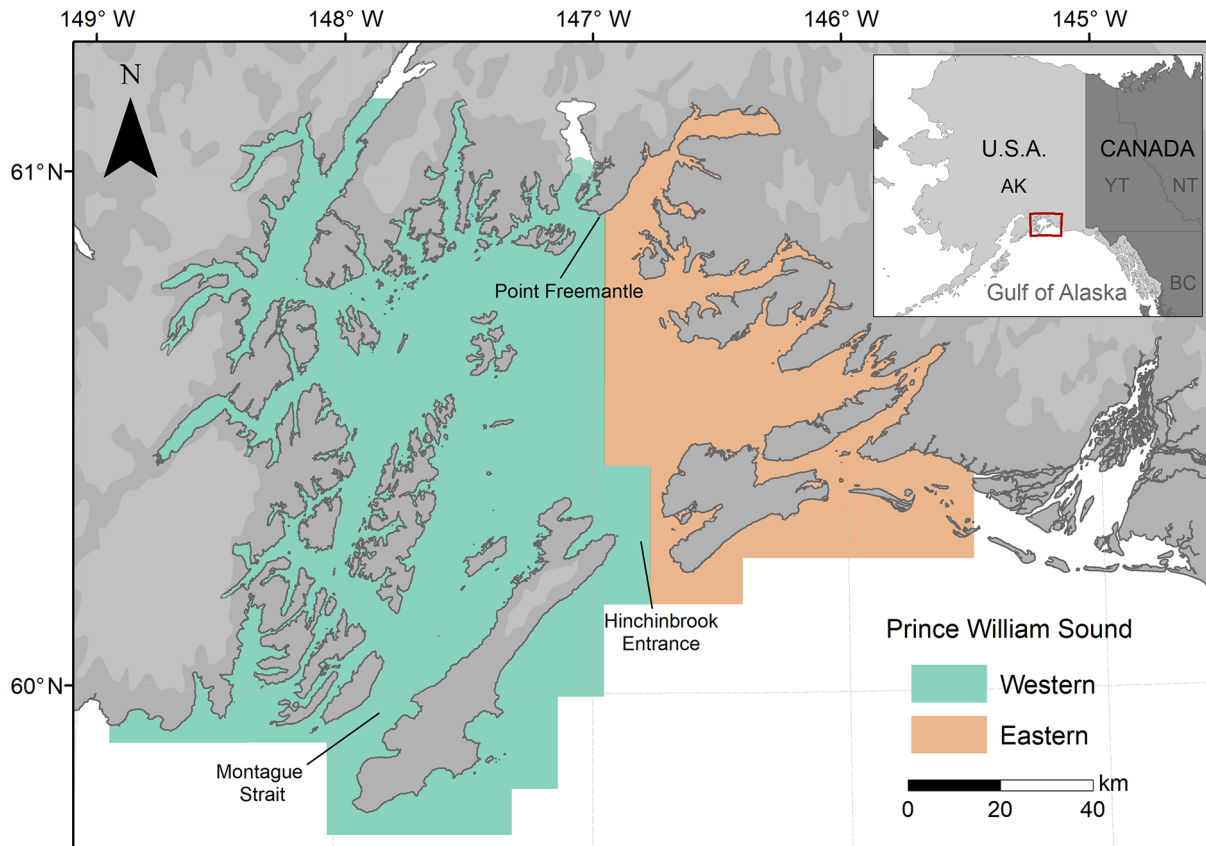


Fig. 1. Prince William Sound area (sum of orange eastern and green western shaded areas), located in the northern Gulf of Alaska (red box in inset)

after median spawn date), which corresponds to the peak of spawning activity in most years throughout the study period (McGowan et al. 2021). Time series of median spawn date were calculated for all of Prince William Sound and separately for the western and eastern areas of the sound, divided north–south from Point Freemantle to Hinchinbrook Entrance (Fig. 1). This spatial delineation is based on previous analyses showing differences in spawn timing trends between these regions (McGowan et al. 2021).

2.3. Explanatory variables

This study only considered explanatory variables that were available in all years of the herring spawn time series (1980–2019). We acknowledge this requirement excluded shorter time series of environmental measurements from within or near the Prince William Sound area that began after the Exxon Valdez oil spill. Nonetheless, we prioritized inclusion of herring spawn data from the 1980s, when the population reached peak biomass, over limiting the study to analyzing spawn timing trends after the

population collapse. We considered 5 population-level variables to examine the potential effects of age structure, condition, and population dynamics, 6 environmental variables representing conditions either within Prince William Sound or over the continental shelf in the northern Gulf of Alaska, and 4 climatological indices representing the effects of physical processes operating at lower frequencies across the Northeast Pacific.

2.3.1. Population-level variables

Biological data (age, length, weight) collected using purse seine or cast net gear by ADF&G following Shepherd & Haught (2019) were used to calculate the mean age and condition factor of age-3+ herring by year for all of Prince William Sound and separately for the western and eastern areas of the sound. The mean condition factor (K) was calculated using the weight–length relationship: $K = W/L^3$, where W is the weight (g) and L is the length (cm) of each herring that was aged (Fulton 1904). Outlier K index values (<0.5th and >99.5th quantiles) were excluded from

the analysis. Median spawning stock biomass (SSB) of age-3+ herring was obtained from the stock assessment model for the entire Prince William Sound region (J. Trochta, University of Washington, pers. comm.). We used the SSB to generate surplus production estimates according to Vert-Pre et al. (2013), where surplus production is defined as the net change of spawning stock biomass plus harvest.

2.3.2. Environmental indices

Time series of mean monthly sea surface temperature (SST) and freshwater input were calculated for all of Prince William Sound and separately for the western and eastern regions of the sound. We used the gridded International Comprehensive Ocean-Atmosphere Data Set (ICOADS; Freeman et al. 2017) to extract mean monthly SST in March and April to represent average thermal conditions experienced by herring at pre-spawning staging areas and spawn sites within the sound just prior to and throughout the peak of spawning. ICOADS data sources include automatic measurement systems including moored buoys and surface drifters (Freeman et al. 2017). Linear interpolation in time was used to replace missing SST values for each given month using the entire time series (1963–present). We used the total yearly freshwater input using 1 km resolution model-based estimates of the combined discharge from precipitation and glacial volume loss (Hill et al. 2015, Beamer et al. 2016). Freshwater input index values ($\text{m}^3 \text{d}^{-1}$) were transformed into total flow input by dividing by 10^9 . Due to data gaps, we excluded Copper River freshwater input.

Separate environmental indices were also included for the northern Gulf of Alaska continental shelf to represent thermal conditions experienced by migrating herring while outside the sound (Bishop & Eiler 2018, Bishop & Bernard 2021) and physical processes that may influence the transport of shelf waters into the sound (Royer 1975, Okkonen et al. 2005, Halverson et al. 2013) 1 to 6 mo prior to the peak of spawning in April (McGowan et al. 2021). Time series of mean SST, and meridional and zonal wind in spring (March, beginning of spawning season), winter (December–February), and fall (October–November) were calculated from the National Centers for Environmental Prediction/National Center for Atmospheric Research (NCEP/NCAR) reanalysis data centered at 60°N , 146.2°W (Kalnay et al. 1996). Indices for the strength of downwelling in spring (March) and prior winter (December–February) and fall

(October–November) were derived from the NOAA Pacific Fisheries Environmental Laboratory monthly upwelling index at 60°N , 146°W (Bakun 1973, 1975, Mason & Bakun 1986, Schwing et al. 1996). The northern Gulf of Alaska continental shelf is predominantly downwelling-favorable from fall through spring (Stabeno et al. 2004), thus upwelling index values are typically negative.

2.3.3. Climatology variables

We considered large-scale climate indices that represented processes that influence exchange between the Gulf of Alaska and Prince William Sound. The sound straddles the longitudinal boundary (147°W) of 2 distinct ecoregions, the western and eastern Gulf of Alaska (Ferriss & Zador 2021); therefore, we considered indices that are influential in either ecoregion during 2 periods to allow for potential lagged effects on herring spawn timing. Four climatological indices were included for the winter (November–March) and summer (June–September) prior to each spawning season to allow for delayed effects of large-scale processes represented by these indices to influence conditions within Prince William Sound that herring potentially use as spawning cues. The Pacific Decadal Oscillation (PDO) is a year-round North Pacific SST variability pattern (Mantua et al. 1997), and a key indicator of climatological variability for the Gulf of Alaska west of 147°W (Ferriss & Zador 2021). The Multivariate El Niño/Southern Oscillation index (MEI.v2) integrates the effects of sea-level pressure, SST, zonal and meridional surface wind, and outgoing long-wave radiation (Zhang et al. 2019); this index is identified as one important climatic component for the Gulf of Alaska east of east of 147°W (Ferriss & Zador 2021). The North Pacific Gyre Oscillation is a climate pattern derived from the second dominant mode of sea surface height anomaly in the North-east Pacific that is highly correlated with changes in salinity, nutrients, and chlorophyll (Di Lorenzo et al. 2008), the latter of which are important indicators for the Gulf of Alaska. The Pacific-North American teleconnection pattern (PNA) represents atmospheric variability in the North Pacific that consists of the geopotential height fluctuation between Hawaii and Alberta and North Pacific and the Gulf of Mexico coast (Wallace & Gutzler 1981, Feldstein 2002, Chen et al. 2018). The PNA affects the Gulf of Alaska by affecting the location and intensity of the Aleutian Low (Wu & Johnson 2010).

2.4. Regime shift analysis

The Northeast Pacific has experienced a series of environmental and species-level regime shifts (Yati et al. 2020). Due to fluctuations in herring biomass during the study period (1980–2019), we wanted to test the hypothesis of different biological regimes based on SSB and surplus production (described above). We used the sequential *t*-test analysis of regime shifts (STARS) approach (Rodionov 2004, Rodionov & Overland 2005, Stirnimann et al. 2019) applied to SSB and surplus production across the whole population (Vert-Pre et al. 2013), as different regimes were not identified for the different parts of the sound. The cut-off period for minimum regime lengths was set at 5 and 10 yr, with a significance level of 0.1 (Vert-Pre et al. 2013).

2.5. Modeling approach

Data diagnostics, analysis, and model development were conducted in R version 4.0.2 (R Core Team 2020). Candidate models composed of independent covariates were created using variance inflation factor (VIF) values to assess collinearity among the population, environmental, and climatological variables using the *olsrr* package (Hebbali 2020). VIF is calculated as: $VIF = 1/(1 - R^2)$. Predictors with a VIF value >2 were incrementally dropped one at a time from the analysis, after which the VIF was recalculated until values were <2 for all remaining covariates (Zuur et al. 2010).

Generalized linear models (GLMs; Nelder & Wedderburn 1972) with a Gaussian link function were used to quantify covariate influence on herring spawn timing. Preliminary analyses that fit generalized additive models (GAMs) to the data identified linear relationships, justifying our choice of GLMs for the modeling framework. Candidate models were analyzed using 3 modeling approaches: (1) a single model for the entire Prince William Sound; (2) separate models for the western and eastern sound; and (3) a single model that included spatial (western and eastern sound) and temporal (population-level regimes) factors. Model selection was performed using Akaike's information criterion corrected for small sample size (AICc; Burnham & Anderson 2002) with the *AICcmodavg* package version 2.3-1 (Mazerolle 2020). The most parsimonious model had the lowest AICc value, and models with $\Delta AICc < 2$ were considered statistically similar (Burnham & Anderson

2002, Burnham et al. 2011). We calculated AIC weights, which are the relative probability each model is the best, given the available data and set of models (Burnham & Anderson 2002).

Deviance explained was also used to estimate the explanatory power of each model (Guisan & Zimmermann 2000): $D^2 = \text{null deviance} - \text{residual deviance} / \text{null deviance}$, where null deviance is deviance of the model at the intercept only, and residual deviance is unexplained deviance that remained in the model after all variables have been included. Final plots were generated with the R packages *visreg* (Breheny & Burchett 2017), *ggplot2* (Wickham 2016), and *patchwork* (Pedersen 2020). Diagnostics were used to assess independence among the variables. Kurtosis and skewness (Cullen & Frey 1999) of the response variable distribution were computed using the function *descdist* from the *fitdistrplus* package (Delignette-Muller & Dutang 2015) to assess model fit.

3. RESULTS

There were divergent trends in median spawn timing between the western and eastern sound that play important roles in the temporal variability of spawning phenology. By 2019, spawn timing in the western sound shifted later by 2 wk relative to the long-term mean, while herring in the eastern sound spawned 2 wk earlier (Fig. 2). Among the population-level covariates, mean age showed spatial differences in trends (Fig. 3). While condition factor was included in some candidate models, it was not retained in any of the respective final models. Younger fish spawned earlier in the Prince William Sound model ($t = 2.073$, $p < 0.05$; Tables 1 and 2, Fig. 3); however, older herring spawned earlier in the western sound model ($t = -2.948$, $p < 0.01$; Tables 3 and 4, Fig. 3) while mean age covariate was not among the variables for the best model in the eastern sound (Tables 5 and 6, Fig. 4). Model diagnostics showed no kurtosis or skewness of the data and supported our model choice (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m696p103_supp.pdf). All models passed the diagnostics, and covariates used in the models were independent (Figs. S2–S4). The following covariates were not retained in the final model candidates for any of the models due to lack of support during the backward selection: condition factor, spring meridional winds, fall zonal winds, spring upwelling index, and PDO index.

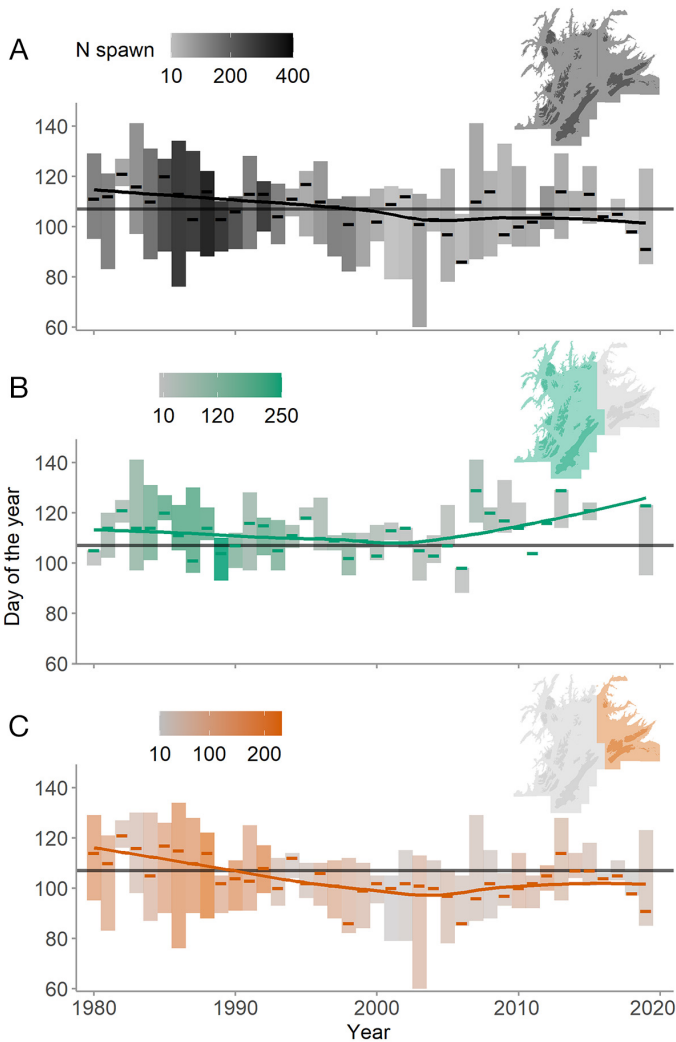


Fig. 2. Spawn timing patterns of Pacific herring (A) across Prince William Sound and in the (B) western and (C) eastern regions of the sound. Bars indicate the first and last day of observed spawning by aerial surveys, and the color scales the number of observed spawning events (N spawn). Dashes: median day of spawning in each year, curvilinear line: loess fit, horizontal straight line: mean across all years

3.1. Prince William Sound

Variations in spawn timing across Prince William Sound were best explained by a model that included covariates for mean age, April SST ($t = -2.084, p < 0.05$), winter upwelling index ($t = -1.999, p < 0.1$), fall meridional winds ($t = 2.250, p < 0.05$), and summer PNA ($t = -3.468, p < 0.01$), accounting for 52.1% of observed variability in spawn timing (Tables 1, 2, and Table S1). Spawning was predicted to occur earlier in Prince William Sound when the population mean age was younger, April SST in the sound was warmer, there was a relaxation of downwelling over the northern Gulf of Alaska shelf during the prior winter, meridional winds in the northern Gulf of Alaska during the prior fall were negative (i.e. blowing north to south), and the PNA was in a positive phase the prior summer (Fig. 4).

3.2. Western sound

The best model for the western sound included mean age ($t = -2.948, p < 0.01$), modeled freshwater input ($t = -3.099, p < 0.001$), and summer PNA ($t = -2.165, p < 0.05$), accounting for 37.5% of observed variability in spawn timing (Tables 3, 4, and Table S2). Spawning was predicted to occur earlier in the western sound when the population mean age was older, total annual freshwater input in the western sound was higher, and the PNA was in a positive phase the prior summer (Fig. 4).

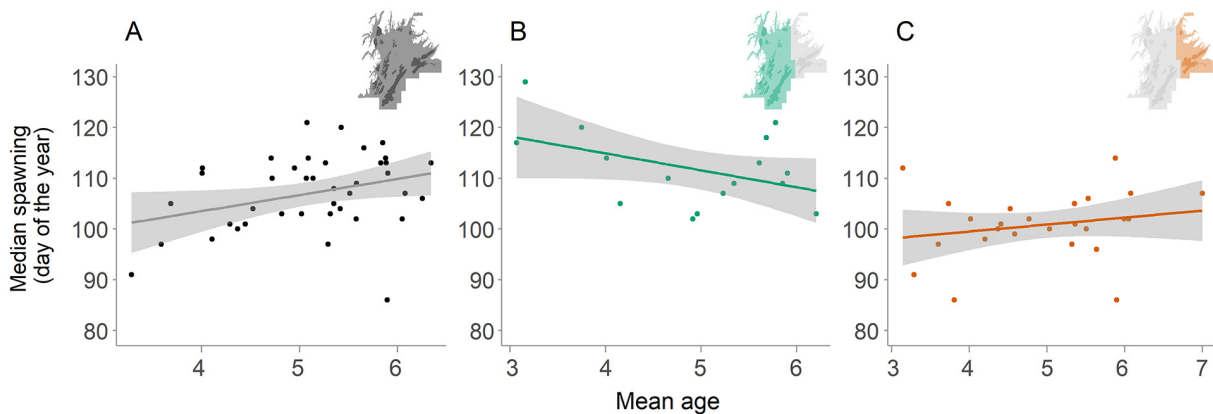


Fig. 3. Median herring spawn date relative to mean age for (A) Prince William Sound, (B) western and (C) eastern regions, including annual observations (dots), linear fit (solid line), and 95% confidence intervals (shaded)

Table 1. Model performance of the best models ($\Delta AICc < 10$) for Prince William Sound as a whole based on Akaike's information criterion corrected for small sample size (AICc). Response variable is the median spawn date. SST: sea surface temperature; PNA: Pacific-North American teleconnection pattern; SSB: spawning stock biomass; NLL: negative log-likelihood; k : model parameter; $\Delta AICc$: difference between AICc best model value, in parentheses, and the given model; AICc wt: weighting from AIC for each model; D^2 : deviance explained

Model	NLL	k	$\Delta AICc$	AICc wt	D^2
~Mean age + April SST + Winter upwelling + Fall meridional winds + summer PNA	-121.96	7	0 (261.4)	0.517	0.52
~Mean age + April SST + Winter upwelling + Summer PNA	-124.74	6	2.59	0.141	0.45
~SSB + Mean age + April SST + Winter upwelling + Fall meridional winds + Summer PNA	-121.69	8	2.60	0.140	0.53
~April SST + Winter upwelling + Summer PNA	-126.47	5	3.27	0.100	0.40
~Mean age + March SST + Winter upwelling A + Fall meridional winds + Summer PN	-123.64	7	3.36	0.095	0.48

3.3. Eastern sound

The best model for the eastern sound included the MDM index ($t = 1.959$, $p < 0.1$), winter meridional winds ($t = 2.607$, $p < 0.05$), winter upwelling index ($t = -2.747$, $p < 0.01$), and summer PNA ($t = -1.806$, $p < 0.1$), accounting for 49.5% of observed variability in spawn timing (Tables 5, 6, and Table S3). Spawning was predicted to occur earlier in the eastern sound when total spawn (MDM index) was lower, meridional winds in the northern Gulf of Alaska were neg-

Table 2. Details of the best model for Prince William Sound in Table 1. Significance codes: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; $\cdot p < 0.1$. Abbreviations as in Table 1

	Estimate	SE	t	$p (> t)$
p-value	107.10	10.90	9.82	<0.001***
Mean age	2.44	1.18	2.07	0.046*
April SST	-2.62	1.26	-2.08	0.045*
Winter upwelling	-0.01	0.01	-1.99	0.054 \cdot
Fall meridional wind	1.38	0.61	2.25	0.031*
Summer PNA	-5.46	1.57	-3.46	0.001**

Table 3. Model performance of the best models ($\Delta AICc < 10$) for the western sound based AICc. Response variable is the median spawn date. MEI.v2: Multivariate El Niño/Southern Oscillation index. Other abbreviations as in Table 1

Model	NLL	k	$\Delta AICc$	AICc wt	D^2
~Mean age + Freshwater input + Summer PNA	-92.63	5	0 (197.75)	0.740	0.375
~Mean age + Freshwater input+ April SST	-94.70	5	4.15	0.093	0.283
~Mean Age + Freshwater input + Summer MEI.v2	-95.11	5	4.96	0.060	0.263
~Mean age	-98.23	3	5.63	0.044	0.092
~Mean age + Winter meridional winds + Modeled freshwater input + April SST	-94.64	6	7.17	0.021	0.286
~MDM + Mean age + Freshwater input + April SST	-94.70	6	7.30	0.019	0.283
~Mean age + Freshwater input + April SST + Winter upwelling + Fall meridional winds + Summer PNA	-91.38	8	7.87	0.015	0.425

ative (i.e. north wind) or weakly positive, there was a relaxation of downwelling over the northern Gulf of Alaska shelf the prior winter, and the PNA was in a positive phase the prior summer (Fig. 4). In contrast to model results for Prince William Sound and the western sound, candidate models that included mean age had lower explanatory power than the best model for the eastern sound ($\Delta AICc \geq 3.38$, Table 5 and Table S3).

Table 4. Details of the best model for the western sound in Table 3. Significance codes: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$. Abbreviations as in Table 1

	Estimate	SE	t	$p (> t)$
p-value	162.80	13.76	11.83	<0.001***
Mean age	-3.89	1.32	-2.95	0.007**
Freshwater input	-8.22	2.65	-3.10	0.004**
Summer PNA	-4.07	1.87	-2.16	0.039*

Table 5. Model performance of the best models ($\Delta\text{AICc} < 10$) for the eastern sound based on AICc. Response variable is the median spawn date. MDM: mile-days of milt. Other abbreviations as in Table 1

Model	NLL	k	ΔAICc	AICc wt	D^2
~MDM + Winter meridional winds + Winter upwelling + Summer PNA	-124.54	6	0 (263.6)	0.537	0.495
~MDM + Mean age + Winter meridional winds + Winter upwelling	-126.23	6	3.38	0.099	0.45
~MDM + Winter meridional winds + Winter upwelling + Winter PNA	-126.29	6	3.49	0.093	0.449
~SSB + Winter meridional winds + Winter upwelling	-128.48	5	5.09	0.042	0.385
~Mean age + Winter meridional winds + Winter upwelling	-128.51	5	5.16	0.041	0.384
~MDM + Fall meridional winds + Winter upwelling + Summer PNA	-127.13	6	5.18	0.040	0.425
~ Winter meridional wind	-131.39	3	5.81	0.029	0.288
~MDM + Mean age + April SST + Winter meridional winds + Winter upwelling + Summer PNA	-124.43	8	5.86	0.028	0.498
~SSB + Winter meridional winds + Winter zonal wind + Winter upwelling + Summer PNA	-126.18	7	6.23	0.023	0.452

3.4. Regime shifts

The STARS analysis identified 3 regimes with a 5 yr moving window, but the models including 3 regimes always had ΔAICc greater than 10 and were excluded from further analysis. Two regimes were identified with a 10 yr moving window (Fig. 5), although even these models had a low AICc weight of less than 0.05 (Table 7).

3.5. Effects of spatial and temporal factors on spawning timing

The last set of models jointly fit the western and eastern sound indices to candidate models that expanded upon the earlier models by including spatial factors (western and eastern sound) and temporal factors (regime shifts corresponding to shifts in SSB and surplus production; Fig. 5) and interaction terms with population covariates. The model that best explained variation in spawn timing in both the western and eastern sound included the region factor and interaction terms with the MDM index and mean age, along with multiple environmental covariates (winter meridional winds, winter upwelling, freshwater input, summer PNA) retained in the earlier models (Tables 2, 4, 6), and accounted for 57% of the observed variability (Tables 7, 8, and Table S4). Inclusion of the region factor and interaction terms allowed the model to account for spatial differences in how the total amount of spawn (MDM index) and mean age were related to spawn timing. The MDM index was positively related to spawn timing in the eastern sound, but explained a minimal amount of

Table 6. Details of the best model for the eastern sound in Table 5. Significance codes: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; $\cdot p < 0.1$. MDM: mile-days of milt; other abbreviations as in Table 1

	Estimate	SE	t	$p (> t)$
p-value	94.73	2.53	37.43	<0.001***
MDM	0.07	0.04	1.96	0.058 \cdot
Winter meridional winds	1.72	0.66	2.60	0.013*
Winter upwelling	-0.02	0.01	-2.75	0.009**
Summer PNA	-3.02	1.67	-1.80	0.079 \cdot

variation in spawn timing in the western sound. In contrast, increases in population mean age were strongly related to earlier spawning in the western sound, but weakly related to later spawning in the eastern sound (Table 8, Fig. 6). The remainder of the environmental and climatological covariates presented similar relationships across all the best models (Figs. 4 and 6).

4. DISCUSSION

Interannual variability in spawn timing of North-east Pacific herring populations has previously been attributed to population and environmental factors, such as age and temperature (Hay 1985, Ware & Tanasichuk 1989). In Prince William Sound, we showed that spatial variability also plays a significant role in herring spawning phenology. There are distinct differences in spawning phenology trajectories between the eastern and western sound (McGowan et al. 2021). In this study, we demonstrated how accounting for such spatial differences is necessary

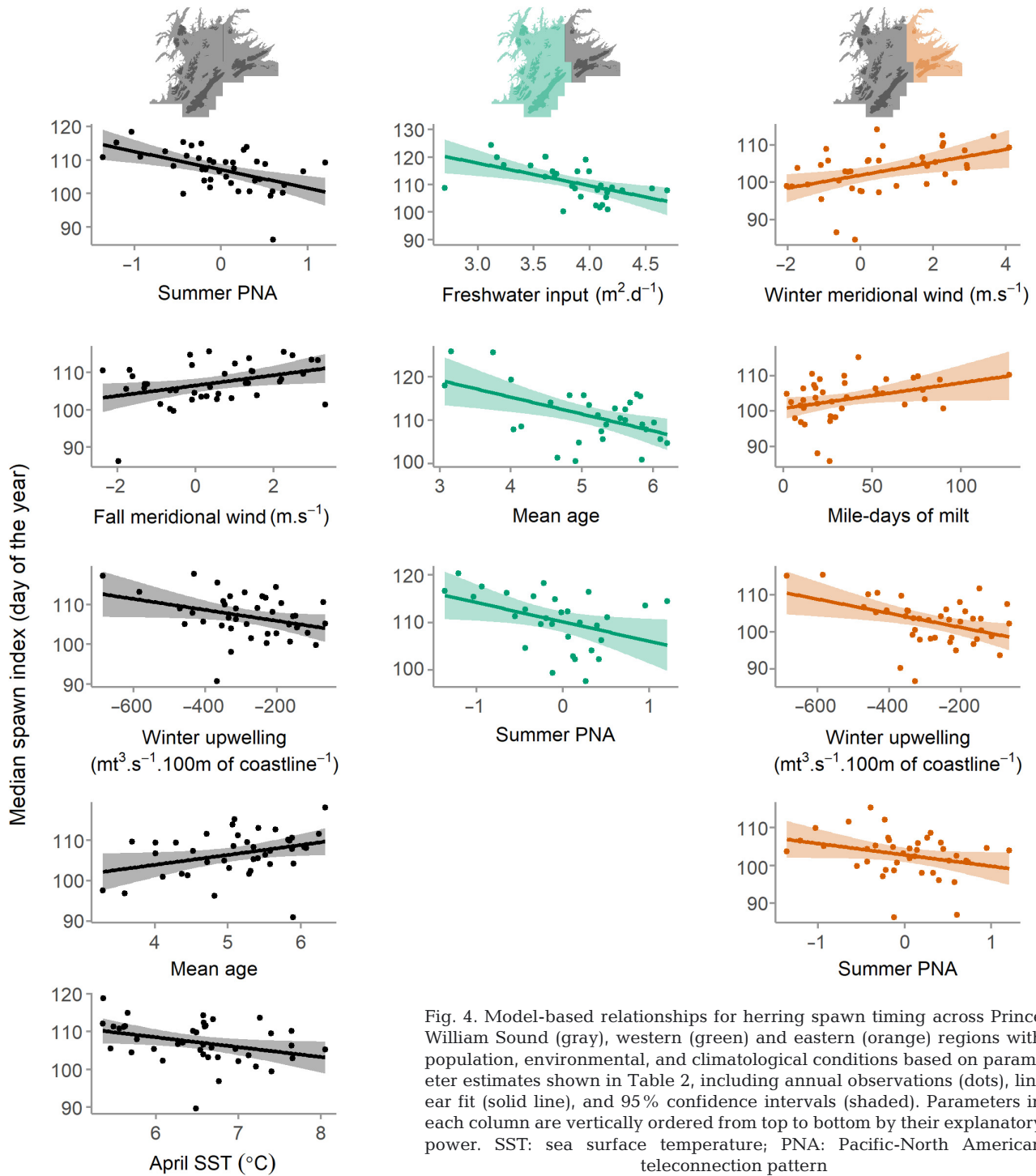


Fig. 4. Model-based relationships for herring spawn timing across Prince William Sound (gray), western (green) and eastern (orange) regions with population, environmental, and climatological conditions based on parameter estimates shown in Table 2, including annual observations (dots), linear fit (solid line), and 95% confidence intervals (shaded). Parameters in each column are vertically ordered from top to bottom by their explanatory power. SST: sea surface temperature; PNA: Pacific-North American teleconnection pattern

to understand mechanistic relationships between predictors and the biological response variables. The relationship between spawn timing and population mean age showed a counterintuitive trend, in which older fish spawned later in the season for Prince William Sound overall, but this relationship only occurred when the location of spawning was ignored

(eastern versus western sound). Models that either included region as a factor or limited observations to a geographic area showed older fish spawned earlier in the western sound while mean age did not explain spawn timing variations in the eastern sound. Previous studies have shown that in populations with multiple cohorts and staggered spawning, older fish typ-

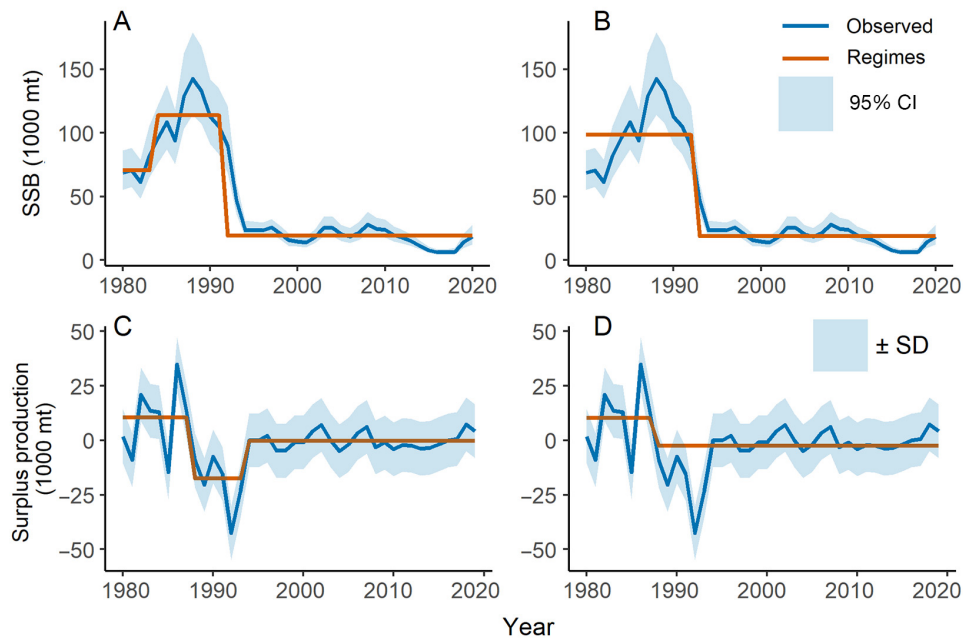


Fig. 5. Regime shifts identified from (A,B) spawning stock biomass (SSB) and (C,D) surplus production estimates from the Prince William Sound herring stock assessment. (A,C) 5-yr moving window, (B,D) 10-yr moving window

ically spawn earlier (Hay 1985, Ware & Tanasichuk 1989). New, naive recruits are hypothesized to adopt the behavior of older, experienced spawners, where first-time spawners initially follow older fish to spawning areas and return to these general areas in subsequent years (McQuinn 1997, Corten 2002, MacCall et al. 2019). In addition, gonadal maturation

rate is influenced by fish weight and daily temperature, resulting in earlier spawning by larger fish during warm years (Ware & Tanasichuk 1989). When the age structure of a population is truncated (e.g. decline of older age classes), spawning grounds may no longer be used due to the potential loss of leadership from older fish, resulting in fewer active spawning

Table 7. Model performance of the best models ($\Delta AICc < 10$) for the Prince William Sound, with western and eastern sound (region) as factors, based on AICc. MDM: mile-days of milt; other abbreviations as in Table 1

Model	NLL	<i>k</i>	$\Delta AICc$	AICc wt	D^2
-Region + MDM × region + Mean age × region + Winter meridional winds + Winter upwelling + Freshwater input + Summer PNA	-217.13	11	0 (460.82)	0.495	0.570
-Region + MDM × region + Mean age × region+ Winter meridional winds + March SST + Winter upwelling + Freshwater input + Summer PNA	-216.72	12	2.09	0.174	0.575
-Region + MDM × region + Mean age × region + Winter meridional winds + April SST + Winter upwelling + Modeled freshwater + Summer PNA	-217.07	12	2.79	0.122	0.571
-MDM × region + Mean age × region + Winter meridional winds + Winter upwelling + Freshwater input × region + Summer PNA	-217.11	12	2.88	0.117	0.570
-Region + MDM × region + Mean age × region + Winter meridional winds + April SST + March SST + Winter upwelling + Freshwater input + Summer PNA	-216.70	13	5.08	0.039	0.576
-Region + Surplus production 10-yr regime shift + MDM × surplus production 10-yr regime shift + Mean age × surplus production 10-yr regime shift + Winter meridional winds + Winter upwelling + Freshwater input + Summer PNA	-214.11	15	6.28	0.021	0.606
-Region + MDM × region × SSB 10-yr regime shift + Mean age × region + Winter meridional winds + Winter upwelling + Freshwater input + Summer PNA	-214.40	15	6.87	0.016	0.602
-Region + MDM × region + Winter meridional winds + Winter upwelling + Modeled freshwater + Summer PNA	-222.53	10	7.98	0.009	0.498

Table 8. Summary table of the best model for Prince William Sound with region as factor. Significance codes: *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; $\cdot p < 0.1$. MDM: mile-days of milt; other abbreviations as in Table 1

	Estimate	SE	<i>t</i>	<i>p</i> ($> t $)
p-value	152.7	12.46	12.26	5.56e-18***
Regions	-49.03	10.65	-4.61	2.19e-05***
MDM	-0.027	0.03	-0.96	0.339
Mean age	-4.428	1.41	-3.14	0.002**
Winter meridional wind	1.006	0.53	1.91	0.061·
Winter upwelling index	-0.016	0.01	-3.04	0.003**
Modeled freshwater input	-6.158	2.28	-2.70	0.009**
Summer PNA	-3.894	1.27	-3.07	0.003**
Region: mile-days of milt	0.130	0.04	3.07	0.003**
Region: mean age	4.962	1.75	2.84	0.006**

sites and decreasing the likelihood of reproductive success (McQuinn 1997, Corten 2002, MacCall et al. 2019). Truncation of population age structure can also influence spawn timing if the ‘go with the older fish’ hypothesis is considered (MacCall et al. 2019). Older spawners reach gonadal maturation earlier than younger fish (Lambert 1987).

Although temperature has been shown to be an important cue for spawning in herring and other pelagic fishes (Hay 1985, Carscadden et al. 1997, Jansen & Gislason 2011, Lombardo et al. 2020), we could not directly corroborate this hypothesis. That might be attributed to the coarse temporal resolution of available data due to a lack of finer-resolution measurements over the full study period, as well as a lack of continuous temperature time series for specific spawning sites. A future, more in-depth examination of the role of temperature on herring spawn timing in the sound could entail a separate analysis that quantifies the relationship between continuous temperature measurements from a pair of moorings located within the sound operating since the mid-1990s with spawn timing at weekly or daily intervals. However, our best model that included regions as factors shows the value of incorporating climatological indices such as the PNA. Positive phases of PNA were associated with warmer North Pacific temperatures. Positive summer PNA increases

Arctic ice melt and promotes circulation of warm air masses in the North Pacific and Arctic regions, and also influences the directionality of heat fluxes in the northern Gulf of Alaska (Liu et al. 2021).

Weaker meridional winds and downwelling over the northern Gulf of Alaska shelf in winter were also correlated with earlier spawning, consistent with the winter condition river–lake hypothesis of Cooney et al. (2001) and extended for juvenile herring by Gorman et al. (2018). It has been suggested that in years with relaxed downwelling, there is less connectivity between

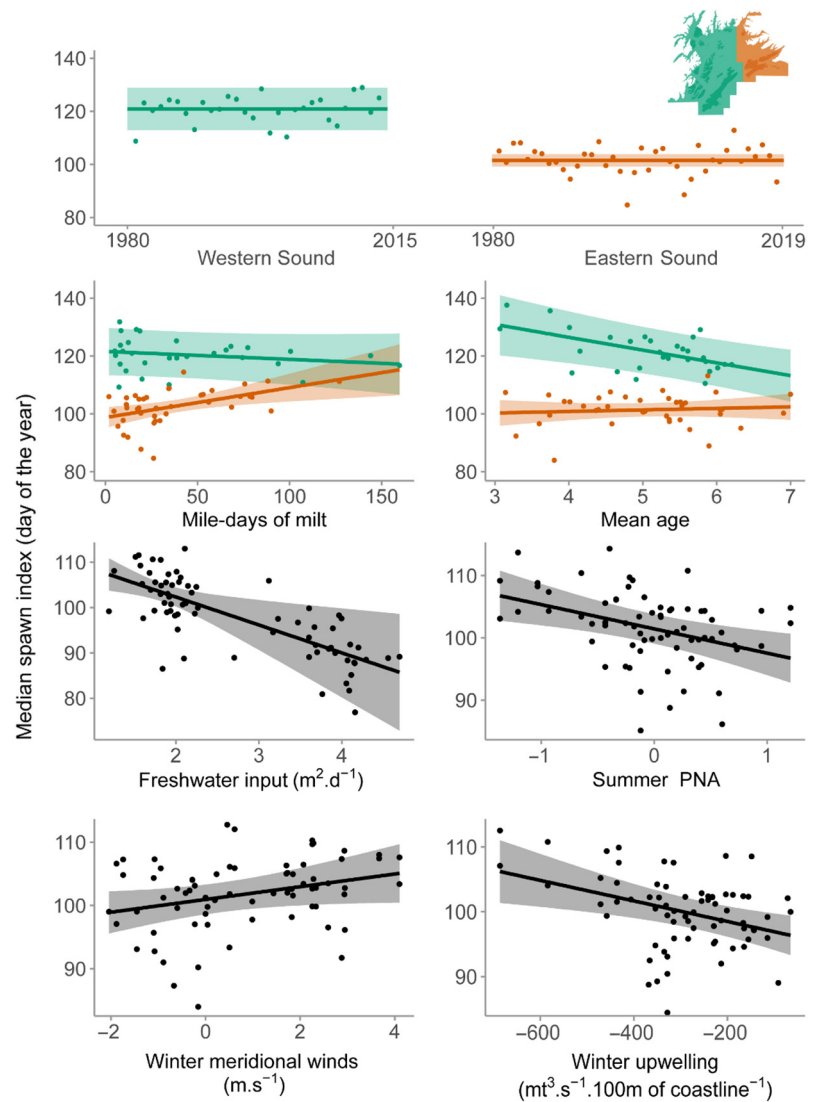


Fig. 6. Observed trends in aerial survey data and population, environmental, and climatological conditions for the best model using regions as a factor, including annual observations (dots), linear fit (solid line), and 95% confidence intervals (shaded). PNA: Pacific-North American teleconnection pattern

the shelf waters adjacent to Prince William Sound ('lake-like'), while the Alaska Coastal Current predominates when downwelling is strong ('river-like'). Strong downwelling in winter leads to influxes of cooler, low-salinity water over the shelf that will be transported into the sound (Royer 1975, Halverson et al. 2013); years with stronger downwelling can thus be expected to be cooler than average during spring spawning periods, which could lead to later spawning times under the assumption that spawning is influenced by temperature (Haegerle & Schweigert 1985, Hay 1985).

Interannual fluctuations in total freshwater input were also shown to explain variations in spawn timing in the western sound. Ringed by glacially fed fjords, the western sound is generally cooler and fresher than other parts of the sound (Campbell 2018). Thus, increased freshwater input in the western sound could result in cooler temperatures and delayed spawning. For example, in the Bering Sea, migration of herring to spawning grounds is highly correlated with ice melt, as herring likely use thermoclines to orientate themselves (Tojo et al. 2007). Ward et al. (2017) showed that herring productivity is negatively correlated with freshwater discharge in the Prince William Sound region. Although they proposed that freshwater impacts to lower trophic level productivity could be the root cause, our results suggest another potential impact earlier in the life history, as changes in spawn timing (as well as the phenology of the annual productivity cycle) could result in match–mismatch situations for larval herring post-hatch.

The results of this study are potentially affected by our choice of using a single median value to indicate spawn timing each year and the design of the aerial survey. In most years, the day of year when 50% of total spawn was observed coincided with a single mode of peak spawning (see Fig. S2 in McGowan et al. 2021), but this metric would not accurately represent spawn timing in years when multiple spawning waves resulted in multiple modes of total spawn (e.g. Haegerle & Schweigert 1985). Early examination of aerial survey data showed this was a rare occurrence over the 40-yr study period; years in which it occurred were primarily due to spawning waves migrating to different regions of the sound (see Fig. 9 in McGowan et al. 2021), supporting our use of separate indices for the western and eastern sound. The number of flights and consistency of spatial coverage by the aerial survey have fluctuated over the study period due to overall declines in spawning, weather, and periodic budget constraints, potentially resulting

in spawning events going unobserved. Although this bias has not been quantified, spatial and temporal coverage of the survey is adequate within the sound (see Table S1 and Fig. S1 in McGowan et al. 2021), and we believe the date of peak spawning is a metric that is robust to potentially missing early spawn events compared to other measures of spawn timing (e.g. date of first observed spawning). Further, it should be noted that the survey estimate is interpreted as a census of all spawning activity and continues to be relied upon as a key input as an index of relative abundance in the stock assessment (Murdian et al. 2017).

4.1. Regime shifts

Although spawning phenology is linked to demographic and environmental variables, models that included biological regime shifts did not improve model fits and are not included in the model selection tables. Even the 40-yr time series in our data may not have been long enough to capture all biological regime shifts, including the key shift before 1980, when the Prince William Sound herring population increased (Funk & Sandone 1990).

4.2. Match–mismatch hypothesis

Timing is the essence of biological processes. For herring spawning to lead to successful recruitment to the Prince William Sound population, eggs need to be deposited in the right location and at the right time for larval herring to later be transported and retained in areas with sufficient resources and refuge for young-of-the-year herring to endure their first winter (Norcross & Brown 2001, Norcross et al. 2001, Gorman et al. 2018). Correspondence between changes in herring spawning phenology and intra-annual and interannual shifts in circulation patterns within the sound that influence transport trajectories of post-hatch larvae (Pegau 2013), along with variations in the timing, magnitude, and duration of the spring plankton bloom (Henson 2007), will ultimately determine the fate of herring during early larval stages. Our study provides a mechanistic explanation behind herring spawning phenology that can inform future examination of coherence between spawn timing and spring phytoplankton blooms within Prince William Sound and subsequent effects on herring mortality during early life stages (i.e. match–mismatch hypothesis; Cushing 1990). This would

improve our understanding of factors influencing first-year survival of herring under different environmental conditions.

The Prince William Sound herring population has experienced persistent poor recruitment for an extended period following its collapse in the early 1990s (Trochta et al. 2020), and improving our understanding of factors influencing first-year mortality rates and subsequent recruitment is needed for their assessment and management. Future research could examine linkages between spawn timing, first-year survival, and recruitment to identify covariates that improve estimates of natural mortality estimates and recruitment strength in the assessment model (Trochta & Branch 2021). As an example, Sewall et al. (2019) suggested that overwinter survival models could be improved with estimates of young-of-the-year herring size and food consumption estimates. Tracking the factors that would affect spawn timing can provide more information to predict young-of-the-year fall fitness and future recruitment trends. Recent studies have shown that during the 2014–2016 marine heat wave, there was a decline in the nutritional value of key forage species (von Biela et al. 2019, Arimitsu et al. 2021). Marine heat wave events are becoming more predominant (Oliver et al. 2018, Laufkötter et al. 2020); therefore, knowing how these events would affect forage fish populations is crucial for managing the population in the future.

Phenological responses are changing across several species and populations (Staudinger et al. 2019). Therefore, it is crucial to detect what variables are associated with spatiotemporal changes to identify future research opportunities and better inform management actions. Here, we identified some key variables associated with distinct spawning trends for western and eastern Prince William Sound, which may provide insight into the ongoing mystery of persistent low recruitment in this population.

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