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Empirically based models of oceanographic and biological influences on Pacific Herring recruitment in Prince William Sound

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ABSTRACT

Abundances of small pelagic fish can change dramatically over time and are difficult to forecast, partially due to variable numbers of fish that annually mature and recruit to the spawning population. Recruitment strength of age-3 Pacific Herring (*Clupea pallasii*) in Prince William Sound, Alaska, is estimated in an age-structured model framework as a function of spawning stock biomass via a Ricker stock-recruitment model, and forecasted using the 10-year median recruitment estimates. However, stock size has little influence on subsequent numbers of recruits. This study evaluated the usefulness of herring recruitment models that incorporate oceanographic and biological variables. Results indicated herring recruitment estimates were significantly improved by modifying the standard Ricker model to include an index of young-of-the-year (YOY) Walleye Pollock (*Gadus chalcogrammus*) abundance. The positive relationship between herring recruits-per-spawner and YOY pollock abundance has persisted through three decades, including the herring stock crash of the early 1990s. Including sea surface temperature, primary productivity, and additional predator or competitor abundances singly or in combination did not improve model performance. We suggest that synchrony of juvenile herring and pollock survival may be caused by increased abundance of their zooplankton prey, or high juvenile pollock abundance may promote prey switching and satiation of predators. Regardless of the mechanism, the relationship has practical application to herring recruitment forecasting, and serves as an example of incorporating ecosystem components into a stock assessment model.

1. Introduction

Single-species population models commonly used in management of fished stocks have mixed success in predicting future stock size based on past stock size alone. One reason for the difficulty is unaccounted-for ecosystem effects on stock size, yet few examples exist of assessment models incorporating ecosystem variables (Skern-Mauritzen et al., 2016). Ecosystem effects on recruitment are of special interest for herring and other short-lived clupeoid fishes because changes in abundance can be driven largely by variability in the annual number of fish that recruit to the spawning stock (Blaxter and Hunter, 1982).

Pacific Herring (*Clupea pallasii;* hereafter herring), is a vital trophic link between plankton and upper-level predatory fish (Bishop and Powers, 2013), seabirds (Willson and Womble, 2006; Bishop et al., 2015), and mammals (Iverson et al., 1997). In addition to its ecological role, herring in Prince William Sound (PWS) supported an important commercial fishery prior to its population collapse in the early 1990s. The population size has fluctuated widely over time since 1980, when the modern stock assessment time series began (Quinn et al., 2001; Hulson et al., 2008). According to age-structured-assessment (ASA) model estimates, pre-fishery stock biomass has ranged from a peak of 139,298 t (126,369 metric tons [mt]) in 1989, to a low of 10,375 t (9412 mt) in 2001 (Wiese et al., 2015). Identifying the main factors controlling PWS herring recruitment is essential for modeling herring population dynamics and understanding the functioning of this ecosystem.

Recruitment strength for PWS herring, conventionally defined as the annual number of age-3 individuals joining the spawning population (Funk, 1994; Williams and Quinn, 2000), may be determined by multiple factors. Of particular importance are seasonal environmental and biological variables that affect herring survival during their first year (Norcross and Brown, 2001), which begins with spawning in April followed by a three- to four-week egg incubation period (Brown et al., 1996). Survival at the egg stage can be affected by predation pressure from seabirds (Bishop and Green, 2001), invertebrates (Haegele and Schweigert, 1991), other fish (Rooper and Haldorson, 2000), and physical factors such as wave and air exposure (Rooper, 1996). Larvae may be susceptible to high predation mortality (Purcell and Grover,

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1990), drifting to unsuitable habitat (Norcross et al., 2001), and starvation (McGurk et al., 1992). Favorable feeding and growing conditions for larval and early juvenile herring in PWS are compressed by the seasonal pattern of productivity typical of high latitude coastal areas. A large spring phytoplankton bloom in April is generally followed three to four weeks later by increased zooplankton abundance in May through June (McRoy et al., 1997; Eslinger et al., 2001). High spring phytoplankton biomass should support high abundances of summer zooplankton prey for juvenile herring (Eslinger et al., 2001; Ware and Thomson, 2005). With sufficient food, herring growth and survival should be promoted by high summer temperatures. Juvenile survival to the end of the first summer can portend relative recruitment strength (e.g., Schweigert et al., 2009), though high variability in the relationship may be due to mortality during the first winter (reviewed in Hurst et al., 2007). Zooplankton abundance declines to winter lows from October or November through March or April, accompanied by a higher proportion of empty stomachs among juvenile herring (Foy and Norcross, 2001). Juvenile herring, like other forage fishes, may experience increased predation risk as hunger and declining condition through winter (Paul and Paul, 1998) suppress predator avoidance behavior (e.g., Robinson and Pitcher, 1989; Sogard and Olla, 1997). Water temperature (Gay and Vaughan, 2001), food availability (Foy and Norcross, 1999), herring condition (Norcross et al., 2001), and predation pressure (Stokesbury et al., 2002) vary among bays in PWS and over time, and this variability likely contributes to differences in survival to recruitment at age 3. Demonstrations of ecosystem effects on herring recruitment are rare, but recruitment variability has been quantitatively linked to summer (July – August) temperature in the herring hatching year and zooplankton biomass in the following spring (April – May) as herring approach age 1 (Brown and Norcross, 2001). Winter sea surface temperature prior to and including spawning has also been shown to influence recruitment (Zebdi and Collie, 1995; Williams and Quinn, 2000); the mechanism is unclear, but it may involve temperature effects on rates of egg and embryonic development and subsequent timing mismatch to the spring phytoplankton bloom.

Changes in the abundances of the main natural predators of herring, including piscivorous fishes, seabirds, and humpback whales (*Megaptera novaeangliae*), likely cause changes in predation mortality and may impact herring abundance and recruitment. For example, herring recruitment in Hecate Strait, British Columbia tended to be low when Pacific Cod (*Gadus macrocephalus*) abundance was high (Walters et al., 1986), though the persistence of that relationship is uncertain (Ahrens et al., 2012). Biomass of predatory Pacific Hake (*Merluccius productus*) during the first year for herring negatively affects recruitment of West Coast Vancouver Island herring (Tanasichuk, 2017). Pacific Cod and Walleye Pollock (*G. chalcogrammus;* hereafter pollock) are likely the primary fish consumers of juvenile herring in PWS, as indicated by their abundance and diet composition (Bishop and Powers, 2013). Predation effects may differ with fish predator age, but their relative importance is often unclear. For example, predation pressure or competition may be greater from juvenile than adult pollock (Sturdevant et al., 2001; Bishop and Powers, 2013) due to greater spatial overlap among juvenile pollock and herring, but adult pollock diets can contain higher proportions of herring (Willette et al., 1999). Hatchery-reared Pink Salmon (*Oncorhynchus gorbuscha*) fry, released in the hundreds of millions annually since the late 1980s, may negatively influence herring recruitment through competition for zooplankton prey or predation (Deriso et al., 2008; Pearson et al., 2012). Adult pink salmon returning to PWS to spawn have also been suggested as important herring predators (Deriso et al., 2008). Seabird predation, predominantly by murres (*Uria* spp.), can remove as much as 10% of the adult herring biomass and even greater biomass of juveniles (Bishop et al., 2015). The abundance of another major herring predator, humpback whales, has increased five-fold since 1978 in PWS (Teerlink et al., 2015), and bioenergetic models indicate they may remove large portions of the herring stock biomass annually (11 – 77%, Rice et al., 2011; 26%, Pearson et al., 2012). It is unclear how much these sources of predation and competition influence herring stock size through reductions in juvenile survival and recruitment.

Some ecosystem factors influencing herring recruitment may also affect other species with similar early life history traits in the same region. Regional synchrony of strong year classes (Hollowed et al., 1987; Hollowed and Wooster, 1995) or recruitment (Mueter et al., 2007) can occur among some North Pacific fish stocks, especially within species groups that are subject to shared forcing factors. Associations between different species have recently been described for the Bering Sea, where age-4 Chum Salmon (*Oncorhynchus keta*) growth, a proxy for ocean conditions, predicts age-1 pollock recruitment the following year (Yasumiishi et al., 2015). Such connectivity has led to expectations that strong herring year classes in PWS may be portended by high juvenile survival of other species, for example, age-0 gadids in PWS (S. Moffitt, ADFG, USA, pers. comm.), PWS pink salmon in their first ocean year (Pegau, 2014), and juvenile pollock in Shelikof Strait (Pegau, 2014). Quantifying linkages among species for PWS or the broader Gulf of Alaska (GOA) could aid in understanding and predicting herring recruitment.

The numbers of age-3 recruits and other year classes of PWS herring are estimated by managers using an ASA model (described in Hulson et al., 2008). Herring year-class sizes are estimated using a weighted least squares approach that minimizes differences between model estimates and observations of egg densities, mile-days of milt, age composition from commercial seine catches, age composition from fisheries-independent sampling of spawners, hydroacoustic survey biomass, and Ricker stock-recruitment model estimates of age-3 recruits. The Ricker model (Ricker, 1975) is commonly used to estimate recruitment based on stock size and has a number of desirable model attributes: relative simplicity, ease of linearization for parameter estimation, and the ability to account for productivity and density-dependent effects of stock size on recruitment. Density-dependent effects on recruitment may occur in herring through cannibalism on early life stages (Holst, 1992) or mortality of eggs under high density spawning conditions (Taylor, 1971; Hourston et al., 1984). Including stock size in the recruitment models sets boundaries on recruitment at high or low spawning stock sizes (Quinn and Deriso, 1999); for the PWS herring model, it prevents the ASA model from estimating zero or negative recruits (Hulson et al., 2008). Although a Ricker-type relationship is often used in analyses of herring stocks (e.g., Zheng, 1996; Williams and Quinn, 2000), previous work has shown no obvious stock-recruitment relationship for PWS herring over the observed range of stock sizes (Zheng, 1996). Ricker model estimates of recruitment and the observed abundances of age-3 herring in PWS differ widely. The discrepancy reflects the weak relationship between spawning stock biomass and recruitment for PWS herring (Fig. 1), and limits the usefulness of stock size for projecting recruitment. Therefore, median recruitment

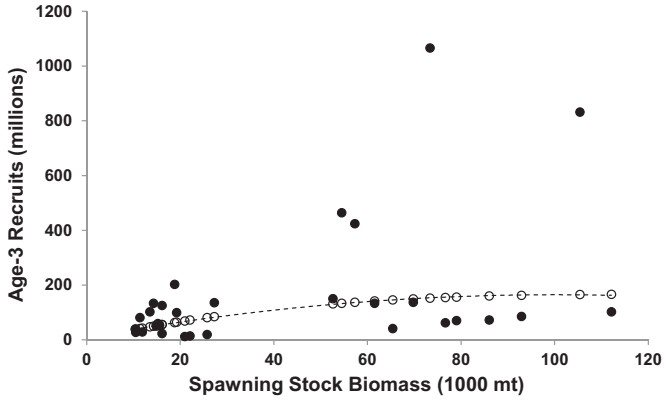

Fig. 1. PWS Pacific Herring age-3 recruits (millions) vs. spawning stock biomass (1000 metric tons), observed (•) and estimated by Ricker stock-recruit model (○, dashed line).

for the previous 10-year period is used by managers to estimate recruitment for the following year in PWS herring stock size forecasts. If the weak stock-recruitment relationship is caused by variable survival to recruitment age, models that incorporate factors that influence survival may improve recruitment estimates.

The objective of this study is to evaluate the usefulness of generalized Ricker stock-recruitment models that incorporate oceanographic and biological variables as predictors of PWS herring recruitment. This is motivated by the premise that ecosystem variability affects juvenile fish survival, especially through their first year, and modifies the relationship between the size of the adult spawning population and the number of their offspring that reach maturity.

2. Methods

2.1. Recruitment data

Time series data for recruitment, defined as the annual number of age-3 herring in millions of individuals entering the PWS population, were available for 30 years from 1980 to 2009 (Appendix Table A1). Recruitment observations were lagged back by three years to match oceanographic and biological conditions in the brood year that herring hatched. That is, the number of age-3 recruits observed in 2012 was used as the 2009 recruitment data point for analysis. Recruitment estimates were generated by the 2012 Alaska Department of Fish and Game (ADFG) ASA model for the PWS herring stock (S. Moffitt, ADFG, USA, unpubl. data).

2.2. Stock size

To predict PWS herring recruitment, the biomass of herring that spawned a given year class was included as a variable in the analyses. Annual spawning stock size for 1980 – 2009, defined as biomass in metric tons of herring age three and older (3+), came from the ASA model that generated the recruitment estimates.

2.3. Oceanographic influences

To test whether growing conditions for herring in their first year influenced survival to recruitment, indices of sea surface temperature (SST) and chlorophyll-*a* (Chl) levels during their first spring and summer were included in the analysis. Sea surface temperature for PWS from 1982 to 2009 came from NOAA satellite advanced very high resolution radiometer (AVHRR) data, captured monthly at 4-kilometer resolution (Jet Propulsion Laboratory POET data selection tool, http://poet.jpl.nasa.gov, accessed 4/9/2011). To obtain a single data point representing PWS summer SST in one year, temperature readings from 229 pixels across PWS (60.42–60.95°N, 146.10–148.00°W) were spatially averaged by month, and the mean of the monthly averages was computed from June to September. A winter SST index for the same region was computed as the monthly averages from January to April, for comparability with previous studies showing recruitment was affected by SST in the first third of the spawning year (Zebdi and Collie, 1995; Williams and Quinn, 2000). The precise choice of months used would have little effect on model results due to high autocorrelation in SST among adjacent months.

As an index of phytoplankton biomass, Chl measurements for PWS from 1998 to 2009 were obtained from SeaWiFS and MODIS/Aqua satellite data, captured in 8-day successive intervals at 0.25° resolution (NASA Giovanni ocean color radiometry data portal, http://gdata1.sci.gsfc.nasa.gov/daac-bin/G3/gui.cgi?instance_id=ocean_8day, accessed 3/16/2012). To obtain a single data point representing spring Chl, readings from 23 pixels across PWS (60.1–61.3°N, 145.8–148.5°W) were averaged by month, and the mean of the monthly averages taken from April to June to capture peak Chl from April bloom to initial decline in July.

2.4. Biological influences

To address whether adult or YOY Pacific Cod and pollock affect juvenile herring survival, adult biomass and YOY abundance estimates of those species were used in herring recruitment models. Annual stock assessment biomass and abundance estimates for Pacific Cod and pollock in the Gulf of Alaska (GOA) were used as proxies for the PWS stocks, which are not typically assessed as separate stocks by management agencies (Wessel et al., 2014). Adult (age-3+) Pacific Cod stock biomass (1000 mt) from 1980 to 2009 was from the North Pacific Fishery Management Council (NPFMC) GOA Pacific Cod stock assessment model estimates (A'mar, Alaska Fisheries Science Center, unpubl. data), and YOY Pacific Cod abundance (millions) was from the 2014 stock assessment report (A'mar and Palsson, 2014). Adult (age-3+) pollock biomass (1000 mt) from 1980 to 2009 was from the NPFMC GOA pollock stock assessment report (Dorn et al., 2014). Based on a trawl survey of PWS conducted by the state of Alaska in 1999, managers estimate the PWS pollock biomass represents approximately 1% of the total GOA stock (Dorn et al., 2014; Wessel et al., 2014), but the correlation strength between the overall GOA and the PWS stock sizes is unknown. YOY pollock were not directly estimated in the stock assessment, so the reported abundance of age-1 pollock lagged back by one year to the herring brood year served as a proxy for YOY abundance. Age-1 pollock lagged one year are hereafter referred to as "YOY" pollock.

To evaluate the effect of hatchery-reared Pink Salmon fry predation or competition on herring recruitment, PWS hatchery fry releases (millions) in the herring brood year from 1980 to 2009 were included in the analysis (http://mtalab.adfg.alaska.gov/CWT/reports/hatcheryrelease.asp, accessed 12/11/14). Total returns of wild and hatchery Pink Salmon (millions) in the herring brood year from 1980 to 2009 were used as an index of predation by adult Pink Salmon (R. Brenner, ADFG, USA, unpublished data).

To address the potential impact of humpback whale predation on herring recruitment, this study used mark-resight model estimates of summer PWS whale abundance in the herring brood year from 1983 to 2009 (Teerlink et al., 2015).

Data from surveys conducted by the U.S. Fish and Wildlife Service from 1990 to 2007 (McKnight et al., 2008) were used to assess effects of PWS murre predation on herring recruitment. Surveys were conducted in 10 non-contiguous years: 1990, 1991, 1993, 1994, 1996, 1998, 2000, 2004, 2005, and 2007. Murre abundance data were lagged back by one year to the herring brood year because abundances are from March following the brood year, when the murre population has a late winter peak (McKnight et al., 2008; Bishop and Kuletz, 2013) and the herring cohort spawned the previous year approaches age 1.

2.5. Analytical approach

To assess predictors of herring recruitment, generalized Ricker stock-recruitment models that included oceanographic and biological variables were compared using a multiple linear regression approach. Multiple regression models were evaluated in sets with common time frames with no missing data (Table 1). For a group of variables within a time frame, a set of model variants was developed that consisted of a full model containing all variables and simpler models with different variable combinations. All possible variable combinations were generated using the "dredge" function in R ("MuMIn" multimodel inference package, K. Bartoń, 2011) for the two longest time frames, model sets A (30 years) and B (27 years). For the two shortest time frames, model sets C (12 years) and D (10 years), the number of available variables (12) approached or exceeded the number of annual recruitment observations over those periods (12, 10, respectively), so the number of variables included was reduced. For those model sets, some variables were excluded if they were not significant in the full model or in models derived from longer data sets (F-tests), and failed to improve standard Ricker model performance.

Table 1
Regression model variables with sets of models (A – D) in which they were used indicated by "+." Time series length for each model set is given in parentheses. Years covered by model sets: A (1980–2009), B (1983–2009), C (1998–2009), D (1990–2007, with gaps). Annual data represent conditions in the same year, except where noted as lagged. PWS = Prince William Sound; GOA = Gulf of Alaska; YOY = young-of-the-year.

Variable	Description	A (30 yr)	B (27 yr)	C (12 yr)	D (10 yr)
R	recruits; abundance of age-3 herring in PWS, lagged three years	+	+	+	+
S	spawning stock biomass of PWS herring	+	+	+	+
ln(α)	intercept in linear regressions	+	+	+	+
β1 … β12	variable coefficients in linear regressions	+	+	+	+
SSTSummer	sea surface temp. in PWS (Jun – Sep)		+	+	+
SSTWinter	sea surface temp. in PWS (Jan - Apr)		+	+	+
Chl	chlorophyll-*a* concentration in PWS, spring/summer (Apr – Jun)			+	
Pcod	Pacific Cod age-3+ biomass in the GOA	+	+	+	+
PcodYOY	Pacific Cod YOY abundance in the GOA	+	+		
Pollock	Walleye Pollock age-3+ biomass in the GOA	+	+	+	+
PollockYOY	Walleye Pollock YOY abundance in the GOA (age-1 lagged one year)	+	+	+	+
PinkFry	Pink Salmon hatchery fry releases in PWS	+	+		
Pinks	Pink Salmon total adult returns in PWS	+	+		
Murres	murre abundance in PWS in March, lagged one year				+
Whales	humpback whale attendance in PWS, summer (Apr – Sep)		+		

It is important to note that stock size and other variables used in the models were assumed to be known without error. Measurement error in stock and recruitment data can obscure underlying stock-recruitment relationships (Walters and Ludwig, 1981). Unaccounted for imprecision in the estimates for all variables adds uncertainty to the predictions of herring recruitment. This is true for both the standard Ricker model, which relies solely on spawning stock biomass estimates, and for the more complex models explored here.

2.6. Recruitment models

To model age-3 herring recruitment, this study used a log-transformed version of the Ricker stock-recruitment model:

$$R = \alpha * S * e^{-\beta * S},$$

where R is recruit abundance in millions, α indicates productivity, S is spawning stock biomass in metric tons, and β indicates the level of density dependence (Quinn and Deriso, 1999). The Ricker model was used because it can account for density-dependent influences of stock size on recruitment, and it has often been used in PWS herring stock assessments (Zheng, 1996; Williams and Quinn, 2000; Hulson et al., 2008). The following natural-log transformation is commonly used to normalize recruitment data, linearize the stock-recruitment relationship, and reduce the influence of extreme year classes (e.g., Stocker et al., 1985; Williams and Quinn, 2000):

$$ln(R/S) = ln(\alpha) - \beta * S.$$

The ratio R/S can be regarded as an index of early life stage survival, assuming that egg production is proportional to spawning stock biomass. The Ricker model can be generalized to include other variables that may affect juvenile fish survival to recruitment age (Quinn and Deriso, 1999). The full multiple linear regression model with all oceanographic and biological variables included in this study is

$$\begin{aligned} \ln(R/S) = {} & \ln(\alpha) - \beta_1 S + \beta_2 \text{SSTSummer} + \beta_3 \text{SSTSummer} \\ & + \beta_4 \text{Chl} + \beta_5 \text{Pcod} + \beta_6 \text{PcodYOY} + \beta_7 \text{Pollock} \\ & + \beta_8 \text{PollockYOY} + \beta_9 \text{PinkFry} + \beta_{10} \text{Pinks} \\ & + \beta_{11} \text{Murres} + \beta_{12} \text{Whales} + \epsilon. \end{aligned}$$

To assess the effects of these variables without using the assumed Ricker stock-recruit relationship, alternative models were fit using ln(R) instead of ln(R/S) as the response variable, and tested with and without herring stock size as a variable:

$$\ln(R) = -a + b_1 S + b_2 \text{SST} + \ldots + b_{12} \text{Whales} + \varepsilon.$$

For comparison with the 10-year rolling median recruitment used in stock forecasting, annual recruitment using the generalized Ricker model was estimated as

$$\hat{R} = \hat{\alpha} * S * e^{-\hat{\beta}_1 S + \hat{\beta}_2 \text{SST} + \ldots + \hat{\beta}_{12} \text{Whales}}$$

For a given brood year, the generalized Ricker model was fit to data from the start of the time series through the year prior to the brood year. The resulting fitted model was then used to forecast recruitment for the brood year using the values of predictor variables in the brood year. Recruitment for the brood year was also forecast as the median observed recruitment over the 10 prior years. The mean absolute percent differences were then calculated between the Ricker recruitment estimates and observed recruitments, and between the 10-year rolling median and observed recruitments, for brood years 1990–2009.

2.7. Bayesian assessment estimates

Stock assessment methods for PWS herring may be modified in coming years by adopting a Bayesian framework for estimating uncertainty in stock biomass and recruitment, weighting data sets according to likelihoods rather than subjectively weighting sums of squares (Pegau, 2014; Muradian, 2017). To test whether the findings would be similar to those based on current ASA model estimates of stock size and recruitment, models were also fit using stock and recruitment estimates from a Bayesian assessment for 1980–2009 (Muradian, 2017).

2.8. Model selection

Models were evaluated based on their hindcast fits to ASA model estimates of historically observed recruits per spawner, ln(R/S). To determine which model in a given time frame was best, all model variants within a set (A – D) were ranked using the small-sample corrected form of the Akaike Information Criterion (AICc):

$$\text{AICc} = -2\ln(L) + 2K + 2K(K+1)/(n-K-1),$$

where L is the likelihood, K is the number of parameters in the model, and n is the number of observations. Within each set of models being ranked, the model yielding the lowest AICc score was considered best; models scoring 0–2 points higher than the best model had "substantial support," those scoring 4–7 higher had "considerably less support," and those scoring more than 10 higher had "essentially no support" (Burnham and Anderson, 2004).

2.9. Model diagnostics

To check for collinearity among explanatory variables, Spearman

rank-order correlations were calculated for pairwise comparisons of all variables within each time frame. Correlations among explanatory variables should not affect the significance of a multiple regression model, but can obscure which variables are most influential (Graham, 2003). Alternative models were constructed with and without correlated variables to assess their influence individually and in combination.

Linear regression assumptions of normality and homogeneity of variance were verified with Shapiro-Wilk's tests, quantile-quantile (Q-Q) probability plots, and plots of residuals versus fitted values (Shapiro and Wilk, 1965; Zuur et al., 2007). Independence among time series data points was verified by checking for autocorrelation using correlograms, Durbin-Watson tests, and partial correlograms for the full and best models (Durbin and Watson, 1950; Zuur et al., 2007).

High variability in the herring stock and recruitment data created the potential for unusual observations to influence the regression relationships. To check for influential observations, Cook's distances (Cook and Weisberg, 1982) were calculated for each point in the regressions. This study used the convention that a Cook's distance value > 1 or subjectively much larger than all other values indicated an influential point (Zuur et al., 2007) that should be examined further – for example, by repeating the analysis without that data point.

3. Results

3.1. Overview

Survival of Pacific Herring in Prince William Sound to recruitment age showed a strong positive relationship to the abundance of YOY pollock in the Gulf of Alaska (Fig. 2). Accounting for YOY pollock abundance in a Ricker stock-recruitment model increased the explained variability in herring recruitment over the longest time series by more than 50% (Table 2). The association between pollock and herring persisted across three decades, and encompassed the period of high herring biomasses (50,000–120,000 mt) in the 1980s and low biomasses (< 20,000 mt) following the population decline in the early 1990s. Over the four time frames examined, incorporating YOY pollock abundance alone or in combination with any other oceanographic or biological variables, typically yielded the best model fits. For the longest time series, herring stock size appeared to show density-dependent influence on recruits-per-spawner, but results were mixed. Survival was not significantly influenced by SST in summer or winter of the herring brood year, Chl concentrations in spring, or the abundances or biomasses of seven other potential herring predators and competitors, including YOY and adult Pacific Cod, adult pollock, Pink Salmon hatchery fry and total returning adults, murres, and humpback whales. Recruitment estimates from a generalized Ricker model with YOY pollock abundance also matched observed recruitment more closely than the 10-year rolling median used in forecasting, reducing error by half. The YOY pollock-herring association persisted whether using recruitment as a response without stock size, using current ASA model or Bayesian estimates of herring stock size and recruitment, or using pollock recruits-per-spawner as a predictor.

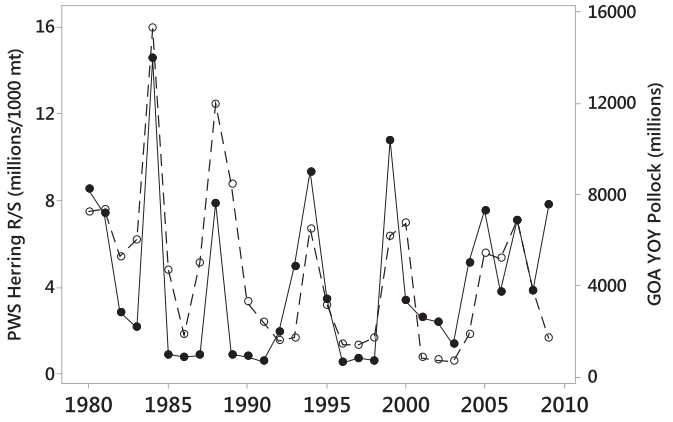

Fig. 2. PWS Pacific Herring age-3 recruits (R; millions) per spawning stock biomass (S; 1000 metric tons) by brood year (•); GOA YOY Walleye Pollock (millions), estimated as age-1 pollock lagged back 1 year to the herring brood year (○).

Table 2
Multiple linear regression terms and results for select alternative models from model set A (full model, 5 lowest AICc scores, and simplest models with and without herring stock size, S), using data from 1980 to 2009. F-test statistics (F), coefficients of determination (R^2), and significance values (p) are given for F-tests comparing each model with the null model, and differences relative to the lowest corrected Akaike Information Criterion score (ΔAICc). See Table 1 for descriptions of variables.

Model terms: ln(R/S) ~ …	F	R^2	p	ΔAICc
Full model:				
S + Pcod + PcodYOY + Pollock + PollockYOY + PinkFry + Pinks	6.09	0.659	< 0.001	13.21
Five lowest-scoring models:				
S + PollockYOY	20.97	0.608	< 0.001	0
S + PollockYOY + Pinks	15.34	0.639	< 0.001	0.46
S + PollockYOY + Pollock	15.01	0.634	< 0.001	0.87
S + PollockYOY + Pcod	13.74	0.613	< 0.001	2.52
S + PollockYOY + PcodYOY	13.7	0.613	< 0.001	2.58
Simplest models, with and without S:				
S + Pcod	2.27	0.144	0.123	23.46
S + PcodYOY	2.53	0.158	0.098	22.96
S + Pollock	2.15	0.138	0.136	23.68
S + PinkFry	2.34	0.148	0.116	23.33
S + Pinks	1.17	0.079	0.327	25.64
S	2.42	0.079	0.131	22.96
Pcod	0.02	0.001	0.881	25.42
PcodYOY	0.97	0.034	0.332	24.42
Pollock	0.01	< 0.001	0.912	25.43
PollockYOY	11.02	0.282	0.003	15.49
PinkFry	0.17	0.006	0.684	25.26
Pinks	0.26	0.009	0.612	25.16

3.2. Model set A – fish populations, 1980–2009

For model set A, containing the longest time series (Table 1), 1980–2009, the strongest influence on PWS herring recruits-per-spawner was GOA YOY pollock abundance. The correlation between herring ln(R/S) and YOY pollock abundance was positive and significant (Spearman's rho = 0.557, p = 0.001). For regression analysis, linear regression model assumptions were met, and no influential outliers were identified. In the full model, the only significant terms at the 95% confidence level were herring spawning stock size and YOY pollock abundance (*t*-test, $p < 0.001$). Herring stock size negatively influenced recruits-per-spawner in the full model, consistent with a density-dependent effect of S on R, but the effect was confounded by correlations with other predictors. Stock size and YOY pollock abundance were present in all five of the best, lowest-scoring models (Table 2; ΔAICc ≤ 2.58) out of 128 possible variable combinations. Stock size alone in the standard Ricker model explained less than 8% of the variability in ln(R/S), and was not significant. By comparison, the model with S and YOY pollock terms was highly significant and accounted for 61% of recruitment variability.

Other fish population variables did not appear to influence herring recruitment, though some model variants had similar AICc scores and slightly higher R^2 values than the model with S and YOY pollock. The influence of the other variables was confounded by strong correlations among them and with herring stock size. Herring stock size was positively correlated with Pacific Cod biomass and pollock biomass (Spearman's rho, $p < 0.001$), and negatively correlated with Pink Salmon fry (p = 0.003) and Pink Salmon, marginally (p = 0.058). These non-herring variables were not significant in the full model, and yielded non-significant model fits when each variable was added to the Ricker model individually.

3.3. Model set B – including SST and whales, 1983–2009

For model set B, which included SST (winter and summer) and whales in addition to the fish population variables, the strongest influence on herring recruitment was YOY pollock abundance. In the full regression model spanning 1983 – 2009, the only significant terms were S ($p = 0.013$) and YOY pollock ($p < 0.001$). Stock size and YOY pollock abundance were present in all five of the best, lowest-scoring model variants ($\Delta AICc \leq 3.51$) out of 1024 possible variable combinations. The model with S and YOY pollock yielded the second lowest AICc score ($\Delta AICc \leq 2.81$); the lowest score was obtained for the model that included adult Pacific Cod and pollock biomasses in addition to S and YOY pollock. Comparisons of the simplest model variants that contained only each term individually showed that YOY pollock was the only term significantly related to recruitment. S was marginally non-significant to significant when tested in combination with other terms. The most parsimonious low-scoring model included only herring S and YOY pollock abundance. This model outperformed ($R^2 = 0.612$, $p < 0.001$) the standard Ricker model ($R^2 = 0.111$, $p = 0.090$) in predicting herring recruits-*per*-spawner.

3.4. Model set C – including primary production, 1998 – 2009

For model set C, which included Chl data as a primary production index for 1998–2009, none of the variables examined significantly influenced herring recruitment. GOA YOY pollock was still the best, though not significant, predictor of herring recruitment over this time frame. The lack of significance was likely due to small sample size rather than a weakening of the pollock-herring relationship over time. The divergence in data points at the end of the time series plot of YOY pollock abundance and herring recruits-per-spawner was not unusual compared to prior years (Fig. 2). For this time frame, the number of potential explanatory variables equaled the number of data points, so a reduction in model terms was necessary. Several variables were excluded based on results with model sets A and B: winter SST, YOY Pacific Cod abundance, pink salmon hatchery fry releases, abundance of adult pink salmon, and abundance of whales. Spring Chl and summer SST also did not interact, despite the expectation that increased food and temperatures are both needed to promote growth and survival, so no interaction term was included. For all 64 resulting variable combinations, the lowest-scoring model contained only the YOY pollock term. Among models with S, the standard Ricker model yielded the lowest AICc score, but explained only 6% of recruitment variability and was not significant ($p = 0.455$). Adding YOY pollock to the Ricker model increased explained variability to 34%, with a similarly low AICc score ($\Delta AICc = 0.49$), but also was not significant ($p = 0.157$). Adding Chl to the model with S and YOY pollock increased explained variability by only 8%, increased overall model p to 0.205, and yielded a substantially higher AICc score ($\Delta AICc = 5.20$).

3.5. Model set D – including murres, 1990 -//- 2007

For model set D, which included 10 years of murre abundance data, no variables significantly influenced herring recruitment. Variables in this set included all from model set C except Chl, which was replaced with murres. No terms were significant in the full model, and no model variants explained significant variation in herring recruitment, likely due to small sample size. The standard Ricker model yielded the lowest AICc score and accounted for 35.3% of the variability in herring ln(R/S), though was not significant ($p = 0.070$). Adding murres to the Ricker model explained similar variability (35.6%; $p = 0.214$; $\Delta AICc = 5.96$). Adding YOY pollock to the Ricker model produced an AICc score similarly low to the Ricker model ($\Delta AICc = 3.39$), and increased explained variance by ~ 15%, but the fit was also not significant ($p = 0.087$). Murre abundance was highly variable, so analyses were also conducted on log-transformed abundances without one influential year of anomalously high abundance, 1992. The results were similar; no model explained significant variability in herring recruitment, and the standard Ricker model yielded the lowest AICc score.

3.6. Using ln(R) as response

Using ln(R) as the response variable, independent of stock size, yielded similar overall results: the strongest influence on herring recruitment was clearly YOY pollock abundance. Results differed slightly in that the model with the lowest AICc score included both adult and YOY pollock without S. While this model explained 69% of the variability in recruitment, most of that explanatory power came from the YOY pollock term; the model with only YOY pollock accounted for 60% of recruitment variability.

3.7. Forecasting comparison with 10-year rolling median

The generalized Ricker model with S and YOY pollock abundance estimated recruitment more accurately than the 10-year rolling median recruitment used for forecasting (Fig. 3). For this comparison, the coefficients and intercept values were taken from the fitted linearized Ricker model with herring stock size and YOY pollock abundance from model set A.

For the 1990–2009 brood years, the 10-year rolling median recruitment was unrelated to recruitment ($R^2 < 0.01\%$, $p = 0.984$), and deviated from observed recruitment by an average of 131%. In contrast, recruitment modeled using S and YOY pollock abundance was significantly correlated with observed recruitment ($R^2 = 35.9\%$, $p = 0.005$), and deviated by an average of 63%.

3.8. Bayesian assessment estimates

The association between herring recruitment and GOA YOY pollock abundance was present whether based on stock and recruitment estimates from the current ASA model or Bayesian estimates. Bayesian assessment estimates (Muradian, 2017) for 1980–2009 were similar to current ASA model values for stock biomass (Bayes $S = 1.15*S + 445$; $R^2 = 0.975$; mean absolute percent difference = 19.3%) and recruitment (Bayes $R = 1.10*R - 21.5$; $R^2 = 0.981$; mean absolute percent difference = 30.0%). For model set A, the only significant terms in the full regression model were S ($p = 0.003$) and YOY pollock ($p < 0.001$), and these terms were included in the 10 best models ($\Delta AICc < 3.50$). The lowest-scoring model contained only S and YOY pollock, accounted for 53% of the variability in herring ln(R/S), and was highly significant ($p < 0.001$). These findings closely matched the results using the ASA model estimates, as reported above for model set A. Using either approach, S and YOY pollock were the only significant terms in the full

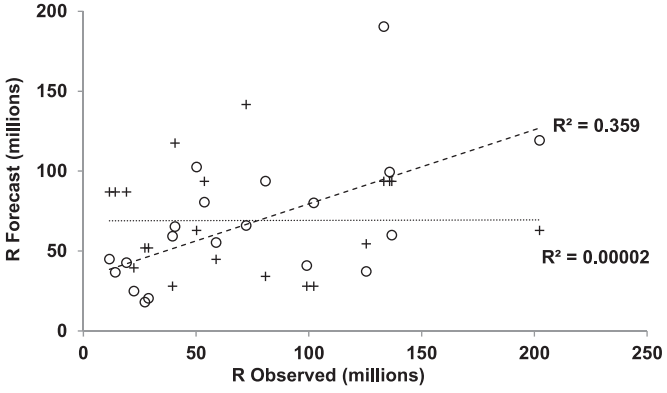

Fig. 3. PWS Pacific Herring age-3 recruits (millions), predicted by Ricker model with GOA YOY Walleye Pollock (○), and rolling 10-year median recruitment (+), plotted versus observed recruits (millions).

model, were present in the best-scoring models, and explained over half of the variability in herring ln(R/S).

3.9. Juvenile pollock survival versus abundance

Using juvenile pollock survival instead of abundance to predict herring recruitment yielded similar results. Juvenile pollock survival to age 1, defined as the number of age-1 "recruits" relative to female spawner biomass (data from Dorn et al., 2014), or ln(R/S), was more strongly correlated with herring ln(R/S) (R^2 = 0.409, $p < 0.001$) than was YOY pollock abundance (R^2 = 0.282, p = 0.002). The model including pollock ln(R/S) and herring S was a weaker predictor of herring ln(R/S) (R^2 = 55%, $p < 0.001$) than the model using YOY pollock abundance (R^2 = 61%, $p < 0.001$). For model set A, juvenile pollock survival and herring S were the only significant terms in the full regression model, yielded the second-lowest AICc score (ΔAICc = 0.88), and were present in the 10 best models (ΔAICc < 3.02). The agreement between model results based on either pollock survival or abundance follows from the strong positive correlation between YOY pollock abundance and juvenile pollock survival (R^2 = 0.668, $p < 0.001$).

4. Discussion

4.1. Pollock-herring association

The positive relationship found between PWS herring recruitment and concurrent GOA YOY pollock abundance may reflect their common responses to variation in abundance or quality of zooplankton prey. Young-of-the-year pollock and herring co-occurring in nearshore habitats of PWS have a high degree of dietary overlap and show similar seasonal changes in diet composition (Sturdevant et al., 1999). In contrast, diets of YOY pollock and Pacific Cod differ in PWS (Sturdevant et al., 1999) and the southeastern Bering Sea (Strasburger et al., 2014), as reflected in diverging gill raker morphology as they grow (Lee, 1985). These observations, and the lack of relationship between YOY Pacific Cod and herring, could support the hypothesis that the pollock-herring relationship is driven by diet effects. Zooplankton abundance has been shown to influence recruitment for some stocks, e.g., Atlantic Cod in the North Sea (*Gadus morhua*; Beaugrand et al., 2003) and Baltic Sea herring (*Clupea harengus*; Cardinale et al., 2009), and reduced zooplankton abundance may have contributed to the herring population decline in the early 1990s (Cooney et al., 2001; Pearson et al., 2012). Zooplankton may also influence predation pressure on herring if, for example, greater euphausiid abundance promotes prey switching by predators such as adult pollock and whales. Though zooplankton abundance and quality may help explain herring survival to recruitment age, zooplankton data for PWS have not been consistently available since the late 1990s. Continuous plankton recorder data has been collected since 2000 in the GOA (Batten et al., 2016), but limited years overlap with this study and the opportunistic sampling can miss peak zooplankton abundances in some years. Zooplankton sampling may not reflect diets due to selective feeding by herring (Purcell and Sturdevant, 2001), so diet monitoring would also be needed to describe prey-based links to recruitment.

Diet influence on YOY herring and pollock does not rule out predator influence. While herring are generally minor prey items for Pacific Cod or pollock captured in GOA shelf surveys (A'mar and Palsson, 2014; Dorn et al., 2014), predation may be higher in the nearshore PWS habitats that juvenile herring occupy. Pollock and herring in PWS tend to occupy different depths in the water column (Stokesbury et al., 2000; Thomas and Thorne, 2001), which should limit predation opportunities. However, observations of significant herring consumption by Pacific Cod and pollock in PWS indicate predation by both gadids may be important (Willette et al., 1999: Bishop and Powers, 2013). High YOY pollock abundance may promote prey switching from juvenile herring to pollock and satiation of predatory adult pollock and Pacific Cod (Bishop and Powers, 2013). Cannibalism on juvenile pollock is well documented and a significant factor in pollock population dynamics in the Bering Sea (e.g., Bailey and Dunn, 1979; Mueter et al., 2011), though less so in the GOA (Dorn et al., 2014). In the GOA, predator consumption of juvenile pollock tends to level off rather than increase linearly when the juveniles are highly abundant, suggesting predator swamping may occur (Dorn et al., 2014). Predators may be overwhelmed when oceanographic conditions promote high abundances of juvenile pollock, resulting in higher survival rates for both juvenile pollock and herring. Evidence for reduced predation mortality in response to high juvenile fish abundance is limited (Liermann and Hilborn, 2001), but has been shown for some species (e.g., Yellow Perch, *Perca flavescens*, Forney, 1971; Sockeye Salmon, *Oncorhynchus nerka*, Ruggerone and Rogers, 1984). Bottom-up and top-down mechanisms are thus both potentially contributing to the association between pollock and herring. Evaluating the role of gadid predators in controlling herring recruitment requires abundance and diet data specific to PWS.

4.2. Oceanographic influences

The lack of influence of SST on PWS herring recruitment was unexpected, given previous findings positively linking SST to pre-recruit survival of north Pacific Herring (Zebdi and Collie, 1995; Williams and Quinn, 2000). SST in winter before spawning affected recruitment for 12 GOA and British Columbia herring stocks by potentially influencing timing of larval hatching with respect to favorable spring conditions (Williams and Quinn, 2000). Temperature is often cited as a factor influencing herring recruitment, with high temperatures generally promoting stronger recruitment at higher latitudes (Myers, 1998; Williams and Quinn, 2000), but the effects may be indirect and depend on local conditions. High temperature needs to be accompanied by high food consumption to promote herring growth and survival, but high temperature may not aid growth if it exceeds the optimal range for PWS herring (Batten et al., 2016). High temperatures can also be associated with lower zooplankton abundance in autumn and winter, which could negatively affect herring condition (Foy and Norcross, 2001). Such interactions among variables at a local and seasonal scale likely confound any clear relationship of temperature to recruitment. This is not to say that ocean temperature or climate have no effect on herring recruitment, especially given previous work showing mean herring recruitment in some populations responds to multi-year temperature shifts (Hollowed et al., 1995), but it is difficult to ascertain the relationship on a year-to-year basis.

Chlorophyll-*a* may have shown no effect on recruitment because it is too indirect as an indicator of juvenile herring diet quantity and quality. Using chlorophyll as a proxy for herring food assumes that higher chlorophyll concentration reflects higher phytoplankton biomass, which then promotes higher abundance of zooplankton prey. These relationships may not hold if the ratio of chlorophyll to phytoplankton biomass changes or grazing by abundant zooplankton suppresses phytoplankton biomass. High overall phytoplankton biomass also may not benefit herring survival if food quality is low. For example, larval fish growth can be sensitive to dietary changes in relative levels of essential fatty acids (Copeman and Laurel, 2010), which differ among phytoplankton taxa and may be transferred up the food chain (Dalsgaard et al., 2003). Food quality for first-feeding herring larvae may drive the positive relationship observed between GOA diatom abundance and PWS juvenile herring first year growth, which should promote herring survival (Batten et al., 2016). Still, it is unclear how well diatom abundance or first year growth reflect herring survival to recruitment age.

4.3. Other biological influences

PWS Pink Salmon fry and adult abundances were expected to affect

herring survival through predation or competition with juvenile herring (Deriso et al., 2008; Pearson et al., 2012), but neither was significantly related to recruitment in this study. The Deriso et al. (2008) study modeled herring spawning stock size, via effects of covariates on recruitment and other parameters in the stock model, whereas this work modeled recruitment. Chinook (*O. tshawytscha*), Coho (*O. kisutch*), and to a lesser degree, Pink Salmon are known consumers of herring (Sturdevant et al., 2012), but predation rates on juvenile herring in PWS are unknown. Though Chinook and Coho Salmon biomasses in PWS are relatively low, high Pink Salmon abundance, including hatchery releases of several hundred million juveniles annually, may constrain herring abundance and recruitment (Deriso et al., 2008). Adult Pink Salmon returning to spawning areas may be important predators of YOY herring (e.g., Stokesbury et al., 2002), but supporting evidence is scant. Stomach contents of PWS Pink Salmon in the summers of 2009 – 2011 indicated they consumed juvenile herring only in 2010 (Sturdevant et al., 2013). The estimated 6.41 million juvenile herring consumed sound-wide that year (Sturdevant et al., 2013) represented 5% of the age-3 cohort that recruited two years later (based on 2009 brood year cohort size of 125.5 million), but this figure assumes all were from the same cohort. Predation by juvenile Pink Salmon on larval or early juvenile herring in summer seems plausible, due to spatial overlap with juvenile herring (Willette et al., 1997) and piscivorous diet (Sturdevant et al., 1999), but has not been documented. Competition for food between juvenile Pink Salmon and herring may be important, as feeding in both species is reduced in shoals with both present (Sturdevant et al., 1999). But the extent of their co-occurrence and zooplankton prey limitation is unclear, and the present study found fry abundance was unrelated to herring recruitment.

The lack of a relationship between murres and herring recruitment is based on only 10 years of available murre abundance data. Murres are the dominant seabird consumer of adult and juvenile herring, and their widely fluctuating abundances could contribute to variable juvenile herring survival (Bishop and Kuletz, 2013; Bishop et al., 2015). The age composition of juvenile PWS herring in murre diets is not well known, but if murres feed across all juvenile age classes (ages 0–2), the effects of a year of high murre abundance may be spread across several herring recruiting classes and thus difficult to detect. The strong biological plausibility of murre predation influencing juvenile herring abundance suggests that further monitoring of murre populations and age composition of herring consumed is needed to better evaluate the effects on herring recruitment.

The finding of no relationship between PWS humpback whale abundance and herring recruitment may be primarily due to whales targeting adult herring aggregations rather than juveniles (Brown, 2003; Rice et al., 2011), which have lower energy content (Paul et al., 1998). The lack of a relationship between summer whale abundance and herring recruitment could also be in part due to seasonality in whale migration and feeding patterns. Recent estimates of whale abundance in PWS indicate that late autumn and winter abundances may exceed those in summer (Rice et al., 2011; Teerlink et al., 2015; J. Moran, Auke Bay Laboratories, USA, unpubl. data). Whales may consume more herring in winter, when euphausiid prey abundance declines in PWS (Foy and Norcross, 2001) and whale energetic needs increase prior to migration and breeding (Rice et al., 2011). If whales are limiting the size of recruiting year classes, annual estimates of the proportion of juvenile herring removed by whales would be required to inform recruitment predictions.

Other predators not included in this analysis may affect juvenile herring and pollock survival. For example, Arrowtooth Flounder (ATF; *Atheresthes stomias*) was identified as the main groundfish predator of herring in triennial GOA surveys in the early to mid-1990s (Yang and Nelson, 2000). The size range of herring consumed (standard length 127–263 mm) indicates that these were mainly age-1 and age-2 juveniles. ATF is also the dominant predator on juvenile pollock in the GOA (Dorn et al., 2014). However, further GOA surveys in 1999 and 2001 found negligible levels of herring predation by ATF (Yang et al., 2006). Recent winter research surveys also indicate ATF represent less than 1% of the demersal fish assemblage in PWS (Bishop and Powers, 2013). ATF in PWS thus seem unlikely to significantly influence herring recruitment.

Additional factors affecting herring mortality at early life stages were not included in this analysis, mainly due to lack of sufficient time series data on appropriate variables. For example, jellyfish competition and predation can reduce larval Atlantic Herring (*Clupea harengus*) abundance (Moller, 1984; Lynam et al., 2005). In PWS, dietary overlap between jellyfish and juvenile herring occurs (Purcell and Sturdevant, 2001), and jellyfish abundance may vary widely (Purcell et al., 2000). However, jellyfish abundance time series data are lacking, and the effect of jellyfish on herring recruitment remains unclear.

High mortality may also occur through egg predation by seabirds, which consumed nearly one-third of herring spawn in PWS in spring 1994, mainly by gulls (Bishop and Green, 2001). Gull abundance in PWS is limited to 10 years of intermittent survey data (McKnight et al., 2008), similar to the dataset for murres. Total March gull abundance showed non-significant positive trends with herring recruits (R^2 = 0.087, p = 0.409) or recruits-*per*-spawner (R^2 = 0.362, p = 0.066); given the limited data, it is difficult to draw any conclusions regarding the effect of gull abundances on herring recruitment.

There is debate regarding the role of disease mortality due to viral hemorrhagic septicemia virus (VHSV) and *Ichthyophonus hoferi* in regulating PWS herring stock size and recruitment strength (Marty et al., 2003; Pearson et al., 2012). Previous work showed PWS herring stock biomass estimates were improved by adjusting adult mortality rates to account for disease prevalence, and a disease index was negatively correlated with recruitment in the following year (Marty et al., 2003). Adult herring mortality rates have been subsequently modified in the PWS herring ASA model according to indices of VHSV and *I. hoferi* incidence in spawners. Other analyses do not support a significant effect of either disease on herring recruitment (Deriso et al., 2008; Elston and Meyers, 2009; Pearson et al., 2012). VHSV can infect and kill high proportions of YOY herring in lab studies (Kocan et al., 1997), and clearly has the potential to influence the survival of pre-recruit herring, but effectively monitoring disease incidence and inferring mortality is problematic (Hershberger et al., 2007, 2010). Lack of appropriate time series data on disease in larval or juvenile herring in PWS precluded analysis of disease in this study.

4.4. Future directions

The pollock-herring association reported here may be of practical use for PWS herring management by aiding stock size forecasts, because the GOA pollock stock assessment model provides age-1 pollock abundance estimates two years before age-3 herring recruit to the spawning stock. Adopting the proposed Bayesian method for PWS herring stock assessments should not substantially affect the utility of YOY pollock abundance in forecasting herring recruitment.

The positive association between GOA YOY pollock abundance and PWS herring recruitment should prompt further investigation into the mechanism responsible. The link between herring in PWS and pollock in the GOA suggests large-scale processes are key drivers of herring recruitment. A gulf-wide mechanism is supported by this study and by concordance in high abundances of Shelikof Strait age-1 pollock and high proportions of age-3 herring in PWS spawning biomass (Pegau, 2014).

The pollock-herring association, while relevant to herring recruitment, does not directly address the herring population decline in the early 1990s. The herring stock crash appeared to involve high mortality across age classes, rather than simply a weak recruitment event (Deriso et al., 2008). Herring recruits-per-spawner fluctuated in tandem with pollock before and after the crash, instead of dropping independently as expected if recruitment failure caused the crash. While the specific

cause of the crash is debated (Thorne and Thomas, 2008; Pearson et al., 2012), it is clear that factors unrelated to recruitment may exert a large influence on herring stock size.

PWS herring recruitment predictions may be improved by incorporating time series data on YOY herring size and energy stores in autumn. Large body size and high energy stores would reduce predation risk associated with winter foraging and starvation risk associated with low food availability (reviewed in Sogard, 1997; Hurst, 2007). Herring size and energy data could indicate survival likelihood more directly than environmental data, because they reflect the integrated environmental conditions herring experienced and the relative risks of predation and starvation mortality. This approach has been demonstrated with survival of age-0 Bering Sea pollock in autumn: total energy, the product of body mass and energy density, is a strong predictor of survival to age 1 the following summer (Heintz et al., 2013).

4.5. Conclusions

The GOA pollock-PWS herring association reported here demonstrates how monitoring ecosystem components, including co-occurring stocks, can help understand and model recruitment. Large-scale factors such as food availability or predator abundances may drive similar trends among species with similar habitats and foraging patterns during their early life history (e.g., herring and pollock), but not others (e.g., herring and Pacific Cod). While it is difficult to ascertain the relative strength of bottom-up versus top-down mechanisms causing the pollock-herring relationship, they appear to operate over a large, gulf-wide spatial scale. Research into recruitment drivers for either stock is likely to pay dividends for understanding both.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.dsr2.2017.07.004.

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