

The highs and lows of herring: A meta-analysis of patterns and factors in herring collapse and recovery

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Abstract

Pacific and Atlantic herring populations (genus *Clupea*) commonly experience episodic collapse and recovery. Recovery time durations are of great importance for the sustainability of fisheries and ecosystems. We collated information from 64 herring populations to characterize herring fluctuations and determine the time scales at low biomass and at high and low recruitment, and use generalized linear models and Random Survival Forests to identify the most important bottom-up, top-down and intrinsic factors influencing recovery times. Compared to non-forage fish taxa, herring decline to lower minima, recover to higher maxima and show larger changes in biomass, implying herring are more prone to booms and busts than non-forage fish species. Large year classes are more common in herring, but occur infrequently and are uncorrelated among regionally grouped stocks, implying local drivers of high recruitment. Management differs between Pacific and Atlantic herring fisheries, where at similarly low biomass, Pacific fisheries tend to be closed while Atlantic fisheries remain open. This difference had no apparent effect on herring recovery times, which averaged 11 years, although most stocks with longer recovery periods had not yet recovered at the end of the observation period. Biomass recovery is best explained by median recruitment and variability in sea surface height anomalies and sea surface temperatures—higher variability leads to shorter recovery times. In addition, the duration of recruitment failure is closely linked with low biomass. While recovery times rely on the nature of the relationship between spawning biomass and recruitment, they are still largely governed by complex and uncertain processes.

KEYWORDS

Atlantic herring, Pacific herring, random forest, recovery time, recruitment, spawning biomass

1 | INTRODUCTION

Population collapses of exploited forage fish may lead to serious socio-ecological repercussions and a significant challenge to sustainable fisheries management. Atlantic herring (*Clupea harengus*, Clupeidae) and Pacific herring (*Clupea pallasii*, Clupeidae) are commercially and culturally important small-bodied pelagic fish that play

an integral role in coastal ecosystems in the world's northern oceans (Smith et al., 2011). Fishery closures prompted by low herring abundance deprive the livelihoods of local fishing communities and affect long-standing traditions that define cultural identities focused on herring, especially in the North Pacific (Gauvreau, Lepofsky, Rutherford, & Reid, 2017; Hamada, 2015; Jones, Rigg, & Pinkerton, 2017; Menzies, 2016; Thornton & Kitka, 2015). Prolonged closures

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or poor landings translate to widespread economic effects, including the collapse of markets based on herring (Dickey-Collas et al., 2010). Herring collapse may also lead to significant changes in key predator-prey interactions since herring are an important prey linking primary production to the highest level consumers including marine mammals, seabirds and larger fish (Ainsworth, Pitcher, Heymans, & Vasconcellos, 2008; Smith et al., 2011; Surma, Pakhomov, & Pitcher, 2018; Surma, Pitcher, et al., 2018), although how much predators are truly impacted is debated (Hilborn et al., 2017). The seasonal migration of Pacific herring in particular to spawn in intertidal and upper subtidal water provides an annual pulse of marine nutrients to marine and terrestrial predators (Fox, Paquet, & Reimchen, 2015, 2018; Willson & Womble, 2006).

Most exploited herring populations collapsed in the 20th century, and overfishing was implicated as the most prevalent cause of collapse (Hay et al., 2001). Many herring fisheries recovered after fishing stopped, and while management approaches have improved, they still cannot anticipate and prevent all causes of collapse. Natural variability for herring is similar to that of other forage fish, which display large and irregular fluctuations attributed to a tighter coupling with environmental variability (i.e. through bottom-up forcing) and where collapses occur naturally (Checkley, Alheit, Oozeki, & Roy, 2009; Peck et al., 2014).

Explaining post-collapse population dynamics is important for understanding recovery. Across all fish taxa, intense overfishing that continues through collapse periods delays recovery (Neubauer, Jensen, Hutchings, & Baum, 2013), but for forage fish, intense overfishing does not explain differences in recovery time (Essington et al., 2015). Furthermore, while some argue that forage fish are more likely to recover than other fish taxa (Hutchings & Reynolds, 2004), others suggest they are more vulnerable to collapse because of schooling behaviour effects on catchability (Pitcher, 1995) and show enhanced sensitivity to environmental variability resulting from heavy exploitation (Essington et al., 2015; Pinsky & Byler, 2015; Pinsky, Jensen, Ricard, & Palumbi, 2011).

Several prominent examples of herring collapse (Hay et al., 2001; Pearson, Elston, Bienert, Drum, & Antrim, 1999) highlight the lack of resilience for at least some populations. Notably, the large Norwegian spring-spawning stock of Atlantic herring crashed to record low spawning biomass (<1 million tons) during 1968–1988 compared to averages of 8 million tons before this period and 5 million tons afterwards. Similarly, Hokkaido–Sakhalin herring in the western Pacific experienced a steady decline through the mid-1950s after catches peaked at nearly 1 million metric tons in 1897. Since then, catches have remained below 40,000 metric tons, with no indication that a resumption of large-scale commercial fishing is probable. Finally, Prince William Sound herring (Gulf of Alaska, Northeast Pacific) declined from 130,000 tons of spawning biomass in 1988–1989 to <30,000 tons by 1994 and has not rebounded since.

These herring collapses have shown long recovery times even though fishing was drastically reduced or halted. Their occurrence begs questions regarding the expected recovery times for herring and the intrinsic and extrinsic factors that may control differences

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in these times amongst herring. Intrinsic factors relating to species biology, such as the age at maturity, growth and body size, are related to generation times (Bjørkvoll et al., 2012; Hsieh et al., 2006; Inchausti & Halley, 2003; Pinsky & Byler, 2015). Extrinsic factors include bottom-up influences on recruitment and growth originating from the physical environment (Brunel & Dickey-Collas, 2010; Hay, Rose, Schweigert, & Megrey, 2008; Ito et al., 2015; Williams & Quinn, 2000). Strong top-down influences from predators have also been suggested as important for herring (Moran, Heintz, Straley, & Vollenweider, 2018; Read & Brownstein, 2003; Schweigert, Boldt, Flostrand, & Cleary, 2010; Surma & Pitcher, 2015; Tjelmeland & Lindstrøm, 2005). Finally, just like questions about whether chicken or the egg came first, there has been a long debate about whether

low recruitment is a result of low spawning biomass, or low spawning biomass is a result of periods of low recruitment for herring (Gilbert, 1997; Myers & Barrowman, 1996), with more recent evidence backing recruitment-driven biomass in forage fish (Szuwalski et al., 2019; Szuwalski, Vert-Pre, Punt, Branch, & Hilborn, 2015). The nature and more specifically direction of this relationship will have significant implications for expected recovery times.

Here we investigate four key questions about herring collapse and recovery by adopting a comparative, cross-population perspective on herring dynamics. Across herring populations, we ask: (a) To what extent do herring biomass, recruitment, and catch dynamics fluctuate, and how does this compare to other fish species? (b) How often and for how long should we expect low biomass and recruitment to occur for herring? (c) What factors are most important in explaining the frequencies of low biomass and high recruitment? (d) What factors are most important in explaining the durations of periods of low biomass and recruitment? This study is based on the largest compilation of information on Atlantic and Pacific herring ($n = 64$ populations), which enables us to answer these questions.

2 | METHODS AND MATERIALS

We collected historical records of catches and time series of estimated adult biomass and recruitment for herring populations worldwide and defined collapse and recovery based on trends in biomass. We used generalized linear models to predict the expected number of “collapsed” years from covariates representing stock-specific biology and population dynamics, environmental conditions, predator trends and fishing histories; and Random Survival Forests (Ishwaran, Kogalur, Blackstone, & Lauer, 2008) to explore whether these same covariates may explain differences in time to recovery.

2.1 | Data sources and types

We obtained spawning biomass, recruitment and catch time series from government agencies, public databases and the published literature (Table S1; Trochta & Branch, 2018). The collated data set included 54 spawning biomass, 46 recruitment and 64 catch time series (Figure 1). Data were not available for all fished herring stocks now and in the past (e.g. Barents and White Sea populations; Hay et al., 2001), although the data in this study still have comprehensive global coverage. Furthermore, not all herring stocks have formal stock assessments, and as a result, some biomass time series are raw population survey estimates ($n = 27$) and others are outputs from stock assessments ($n = 27$). Since variability characteristics,

specifically the spectral frequencies and autocorrelation structure, of survey time series differed substantially from those for stock assessment outputs (see Figure S1), we applied a 3-year moving average to survey data so that survey and stock assessment information show more similar frequencies and autocorrelation for analysis (see Figure S2). Eight time series had at least one missing year that we interpolated with the moving average. Nine time series missing more than two consecutive years were not interpolated. Assessment estimates were also derived from different modelling approaches (catch-at-age analyses, state-space models or virtual population analyses), although there were no noticeable differences in variability of estimates amongst approaches. No catch data are available for Squaxin Pass. For all stocks and types of data, we calculated the minimum of each time series and the largest interannual changes across herring stocks.

2.2 | Identifying and characterizing collapse

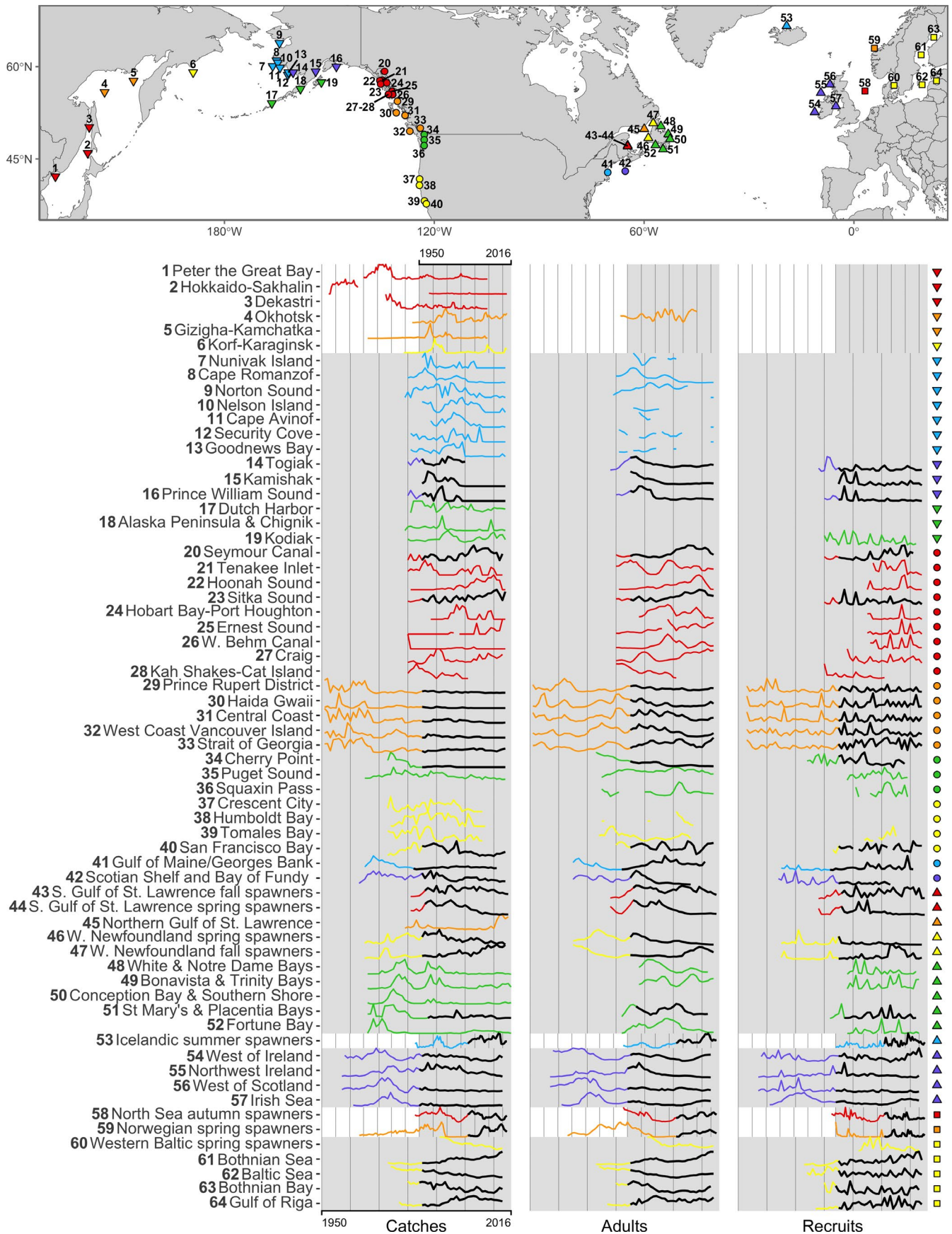
Population collapses are generally recognized as substantial declines in abundance from some baseline. Fish population collapses are often defined in reference to the biomass at maximum sustainable yield (B_{MSY}), which provides a defensible theoretical basis and management relevance (Neubauer et al., 2013; Pinsky et al., 2011). However, estimates of absolute abundance are unreliable (Hilborn, 2002), and when combined with the frequency of large-scale fluctuations and regime shifts in forage fish, make MSY and B_{MSY} difficult to estimate (McClatchie, Hendy, Thompson, & Watson, 2017). Instead, we focus on relative trends from surveys and stock assessments since these can be more accurately estimated and still provide information on the potential extent and duration of low abundance, assuming consistency in survey and assessment methodology within a time series.

To standardize relative biomass trends, we divided each time series by the mean values falling within the upper 90th percentile of data in that time series. This is preferable to a time series maximum or mean since those are sensitive to the value and frequency of outliers of both low and high abundance. The threshold for low abundance, or collapse, is defined to be 30% of the mean of those observations within the upper 90th percentile of each time series (abundances that are not necessarily contiguous):

$$\widehat{\text{biomass}}_i = \frac{\text{biomass}_i}{\text{mean}(\text{biomass}_{90\text{th}})}$$

where biomass_i is the original estimate for year i , and $\widehat{\text{biomass}}_i$ is the normalized estimate for year i . The mean of the highest abundances

FIGURE 1 Herring time series from west (point 1) to east (point 64). Observations of each time series are divided by their respective historical maxima so they are visualized on the same scale. The filtered versions of the spawning biomass (Adults) series are shown for those stocks whose estimates came from surveys. The unique colour–shape combinations indicate the management area or stock complex to which each time series belongs in both the map and time series. The shaded regions represent a reference time frame (1950–2016), since some records start earlier and are “zoomed out” above to show their entirety. The select herring stocks and years used in the analyses of this paper are emboldened in black [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]



is hereinafter referred to as Mean High Biomass. This same normalization calculation is applied to the catch and recruitment time series used for analysis, where the observed catches are divided by Mean High Catch to produce relative catch and the observed recruitment values are divided by Mean High Recruitment to produce relative recruitment. These Mean High values were based on the full time series, even for analyses that focused on standardized values for only the most recent 30 years.

We examined both the frequency and duration of collapse periods. Since time series among herring populations vary widely in coverage, we used only the last 30 years of each time series to determine the frequency or number of years below Mean High Biomass (calculated over entire time series). For most herring fisheries, the 30 most recent years follow peak industrial fishing and the implementation of harvest control rules based on stock assessments (Hay et al., 2001). Biomass collapse duration is defined as the number of consecutive years in which biomass is below 30% of Mean High Biomass. Since these durations can be censored if the period of low biomass includes the starting or ending year of the time series, we use a Kaplan–Meier analysis (Kaplan & Meier, 1958) to produce a time-to-recovery curve (or the time to the end of observations, whichever comes first). In this analysis, recovery is when biomass exceeds the collapse threshold. The calculated recovery probability at each observed time interval is the cumulative proportion of stocks collapsed beyond the preceding intervals on the time-to-recovery curve. Only stocks with two or more years of low biomass or low recruitment are included in the analysis to limit the effect of high-frequency variability (i.e. measurement error). Collapse durations are also identified within the 30 most recent observations from each time series.

Recruitment dynamics may closely couple with population collapse and recovery. Consequently, low biomass provides an incomplete characterization of collapse because recruitment failure can underlie prolonged collapse while strong recruitment promotes recovery; low biomass is thus only a symptom. We use a threshold of 50% of Mean High Recruitment with which to determine the frequency of years above (moderate-to-strong recruitment) and the maximum duration below (recruitment failure) this threshold. A Kaplan–Meier analysis is also applied to low recruitment durations to calculate recruitment times to recovery. This Kaplan–Meier analysis is identical to the one outlined in the preceding paragraph.

2.3 | Statistically modelling collapse predictors

We used negative binomial linear mixed-effects (NBLME) models, either zero-inflated or not depending on the data (see Supporting Information for more details). Predictor variables are listed in the next section. Random intercepts in the NBLMEs that reflect regional groupings based on management definitions (groupings are colour coded in Figure 1) did not change the results, so we only present results from the NBLMEs without random effects models for simplicity. We test the significance of these NBLMEs using a parametric bootstrapping procedure that simulates zero-inflated counts to which an intercept-only model and each predictor model are fit (see

Supporting Information). All models are coded in R 3.3.2 (R Core Team, 2016) using the *glmmTMB* package (Brooks et al., 2017). These models were applied in the following ways:

1. To predict the number of years that biomass was below the collapsed threshold (30% of Mean High Biomass in the base case). The model was zero-inflated model.
2. To predict the number of years of high recruitment (above 50% of Mean High Recruitment). The model was not zero-inflated.

We used Random Survival Forests (Ishwaran et al., 2008) to assess which factors best predict the number of years to recovery from low biomass or low recruitment (see Supporting Information). Random Survival Forests ranked the importance of various effects and are an adaptation of random forest analysis for survival or event time data. Variable importance (VIMP) was assessed by calculating the out-of-bag prediction error, which in this context was measured using Harrell's concordance index (Harrell, Califf, Pryor, Lee, & Rosati, 1982). Partial plots of predictor effects were generated by inputting predictor values into the fitted Random Survival Forest to obtain ensemble estimates (i.e. the average of 20,000 regression trees) of the expected numbers of biomass recoveries or high recruitment events, which is analogous to a cumulative hazard function in survival analysis (Ishwaran et al., 2008). Models were implemented using the *randomSurvivalForest* package in R (Ishwaran & Kogalur, 2016). These models were applied to the 30 most recent years for each population and address the following problems:

1. Predicting the number of years to recovery from low biomass (falling below 30% of Mean High Biomass).
2. Predicting the number of years to recovery from low recruitment (falling below 50% of Mean High Recruitment).

2.4 | Predictor descriptions

We developed and explored a suite of hypotheses for intrinsic and extrinsic factors that might influence the duration of low herring biomass or recruitment as measured by the number of collapsed years and time to recovery. Specifically, we evaluated effects from both bottom-up (oceanographic conditions) and top-down (trends in predator abundance), fishing, and stock-specific traits related to life history and population dynamics. The following factors (bold) were used to represent these effects (in no particular order).

Latitude ($^{\circ}$ N) of each herring stock's spawning location (Table S2) is included because it has previously explained differences in key population dynamics processes such as spawn timing, maturity and growth of eastern Pacific herring (Hay, 1985; Hay et al., 2008). We assume latitude is a proxy for the climatic gradient in the northern hemisphere.

Freshwater inputs characterize the physical processes and habitat quality of estuaries in which herring spawn and their progeny survive and grow to maturity (Fortier & Gagné, 1990; Hay & McCarter,

1997). Mean freshwater flux (km^3/year) come from the Global Runoff Data Centre's (GRDC) global hydrological model *WaterGAP* (Doll, Kaspar, & Lehner, 2003), based on river discharge measurements from the global network of GRDC stations (GRDC, 2014). The provided decadal means from 1961 through 2009 were binned within 5° degree latitudinal zones along coastlines. We identified the coastal zone in which each herring stock's spawning grounds are located and for this predictor used the mean of the decadal means encompassed by each stock's time series.

Sea surface temperature (SST) and sea surface height anomalies (SSHA) are both attributes of physical ocean processes (e.g. basin circulation, eddies, currents, hydrographic discontinuities, ocean heat content, stratification) working over very different spatial and temporal scales, which leads to various hypotheses on how, when and where they impact herring dynamics (Somarakis, Tsoukali, Giannoulaki, Schismenou, & Nikolioudakis, 2018). We constrained the list of environmental hypotheses by extracting SST and SSHA metrics at specific locations and times. For low biomass, this was the approximate timing and location of peak spawning activity; for low and high recruits, this was the period following peak spawning at this same location (i.e. the egg-to-larval stages or the "critical period"). SST and SSHA for these locations and times are mapped in Figures S4 and S5.

Sea surface height anomalies (cm) came from the JPL Physical Oceanography DAAC (Boulder, 2013; Hamlington, Leben, Strassburg, & Kim, 2014) and are based on satellite altimetry measurements and historical tide gauge data. The resulting data products are weekly imagery composites from June 1950 through 2010 with 0.5° degree spatial resolution. SSHA time series were created by first identifying the $0.5^\circ \times 0.5^\circ$ cell nearest each stock's spawning location (Table S2), then taking the median of a $2^\circ \times 2^\circ$ composite centred on the identified cell. The *Mean SSHA (cm)*, *SD of SSHA* (standard deviation) and *Linear trend in SSHA (cm/year)* over the herring time series were used in the analyses to determine the effect of average oceanographic conditions, in addition to variability and long-term trends in sea level (Tables S3 and S4; Figures S4 and S5).

Sea surface temperature ($^\circ\text{C}$) came from NOAA's Extended Reconstructed Sea Surface Temperature (ERSST v3b) dataset. The ERSST is a smoothed and filtered product derived from the International Comprehensive Ocean-Atmosphere Data set with monthly averages at 2° spatial resolution (Smith, Reynolds, Peterson, & Lawrimore, 2008). The SST time series for each stock was extracted from the latitude and longitude coordinates of the $2^\circ \times 2^\circ$ cell nearest the spawning location of each stock (Figures S4 and S5). The *Mean SST ($^\circ\text{C}$)*, *SD of SST* and *Linear trend in SST ($^\circ\text{C}/\text{year}$)* over the range of years matching the 30 most recent years from each stock's time series were used to assess the influence of different averages in the thermal environment, interannual thermal variability and long-term temperature trends, respectively (Tables S3 and S4).

Predator trends are included to determine their potential association with herring biomass collapse or recruitment failure. Predation information (e.g. consumption rates) is sparse although

there are some data for key marine mammal and fish predators of herring. Marine mammal trend data were obtained from Magera, Flemming, Kaschner, Christensen, and Lotze (2013). We focused on pinnipeds, ignoring cetaceans since cetacean numbers are estimated over large swathes of the ocean (e.g. Northeast Pacific humpbacks) with little information on how populations might feed on individual herring populations. Pinniped populations were paired with herring stocks based on their population area descriptions. Fish predator data were obtained from the RAM Legacy Stock Assessment Database (Ricard, Minto, Baum, & Jensen, 2011) for stocks identified to cohabit areas with herring stocks based on area descriptions. Trends in predator populations (slope and 95% confidence intervals) were estimated using robust linear regression ("lmRob" function) in the *robust* library in R (Wang et al., 2017) with code provided by Magera et al. (2013). The three predictors used were:

1. *No. of increasing fish or pinniped populations*, the number of significantly increasing predator populations.
2. *No. of decreasing fish or pinniped populations*, the number of significantly decreasing predator populations.
3. *Mean of standardized population trends: Pinnipeds or Fishes*, the mean of the linear slope coefficients of predator time series identified as potential predator populations for a herring stock.

Peak fishing pressure is summarized from each stock's catch record in three ways to represent the effects of fishing since fishing mortality rates were not available for most herring stocks:

1. *No. years relative catch >0.75* is the number of years in the most recent 30 years that catch remained above 75% of Mean High Catch as a measure of the period of sustained high exploitation.
2. *Mean of highest Catch/Biomass ratio* is the mean of the three largest ratios of relative catch to relative biomass in each year for the most recent 30 years. A larger mean ratio indicates that catch was high when biomass was low, which is indicative of unsustainable fishing.
3. *Years Catch increased while Biomass decreased* is the number of years in the most recent 30 years where catches are maintained or increased from the previous year while biomass decreased from the previous year. A greater number of years again indicates a greater tendency to overfish, which may prolong collapse durations.

Zero catch (no. years) is also included for an effect of fishery closures on collapse times, which could associate with more (i.e. low biomass drives decisions to close fishing) or less (i.e. more closures promotes recovery) years of low biomass or recruitment.

First age at maturity is included to reflect differences in regeneration times that is hypothesized to impact the resilience of populations (Table S2).

Log(max catch) (metric tons) or the log of maximum catch is a measure of total population size, that has been shown to

be strongly correlated with maximum sustainable yield (e.g. Srinivasan, Cheung, Watson, & Sumaila, 2010), since large populations are able to produce large catches. This is used in preference to estimates of absolute biomass since such estimates are highly uncertain and are unavailable for most populations. The expectation is that larger populations may be more resilient than smaller populations (Table S2).

Mean age 5 weight (g) came from various literature sources (Hay et al., 2001, 2008; ICES, 2014; Ito et al., 2015; Naumenko, 2002; Stick, Lindquist, & Lowry, 2014) and is used to evaluate the potential effect of differences in body size on herring vulnerability. Differences reflect somatic growth rate and asymptotic weight. Age 5 is used to standardize mean weights for comparison amongst stocks. This measure may impact population trends through variability in individual body condition, intrinsic population growth rates and size selective predation (Table S2).

CV of biomass over the most recent 30 years is a measure of the variability of relative biomass (biomass divided by Mean High Biomass).

Median relative biomass over the most recent 30 years is included in the NBLME models and Random Survival Forests predicting recruitment years to evaluate the importance of the relationship between biomass and recruitment.

CV of recruitment measures the variability of relative recruitment (recruitment divided by Mean High Recruitment) over the most recent 30 years. The irregular pulses characteristic of recruitment time series is likely a measure of environmental variability.

Median relative recruitment is used to evaluate how well average recruitment associates with low biomass year counts and durations.

CV of R/SSB is the time series of recruits per spawning biomass (R/SSB) and is obtained by taking the ratio of recruits to spawners, standardized by dividing by Mean High R/SSB, and reflects changes in each population's ability to produce new recruits. The CV is obtained after standardization since each stock's units on spawning biomass and recruitment differ from one another. The interpretation of the resulting relative R/SSB metrics is only useful when compared among stocks.

Median R/SSB is defined as the median R/SSB (after standardization as described above) is used to find whether average productivity is well below the peaks or close to the peaks for each population.

3 | RESULTS

3.1 | To what extent do herring biomass, recruitment and catches dynamics fluctuate?

Our database reveals highly varied biomass dynamics with dramatic changes in abundance for most stocks (Figure 1). The average CV of relative biomass for 53 herring stocks with time series longer than 10 years was 0.58 (95% confidence interval, CI, 0.30–0.93), compared to a median CV of 0.44 (95% CI 0.11–1.10) for the 307 non-forage fish species in the RAM Legacy database (Table 1; Figure

S3). The average minimum relative biomass was 0.097 of Mean High Biomass (95% CI 0.001–0.315) compared to a median of 22.2% (95% CI 1.1%–67.6%). Out of the 53 herring populations, 28% (15) fell below 5% of Mean High Biomass, and 96% (51) fell below our collapse threshold of 30% of Mean High Biomass, in at least 1 year. Of the 51 collapsed stocks, 7 were at their lowest level in the final year, and 39 had recovered to above the collapse threshold after their low point. Recovery time among these 39 stocks averaged 13 years but was highly variable (95% CI 4–38 years). Far fewer non-forage fish ($n = 307$) fell below 5% of Mean High Biomass (10% vs. 28%), or below the collapse threshold (66% vs. 96%), but the time to recovery was similar, with a median of 12 years (95% CI 1–48 years).

Extreme interannual fluctuations (i.e. first differences of time series) are larger in herring than non-forage fish species. The magnitudes of the largest declines (median –28%, 95% CI –13 to –60%) are similar to the largest increases (28%, 95% CI 6%–61%) in 48 herring stocks with continuous time series of biomass (excluding Goodnews Bay, Humboldt Bay, Nelson Island, Nunivak Island, and Security Cove). These fluctuations are much greater than those in non-forage fish species, with biggest declines of –14% (95% CI –3 to –58%) and biggest increases of 12% (95% CI 0%–64%) (Table 1). These extreme interannual changes typify the “boom and bust” nature of herring population dynamics in which seldom, short periods of extreme changes are followed by longer periods of much smaller changes. On the whole, interannual changes for herring stocks averaged –0.1% (95% CI –3.2 to 4.1%) which was similar to those for non-forage fish species (–0.7%, 95% CI –3.5% to 3.4%).

More herring stocks display pulses of strong cohorts compared to other fish, although such pulses are uncommon amongst stocks. Assuming log-normally distributed recruitment, herring stocks have much higher recruitment CV (median 0.16, $n = 45$, 95% CI 0.04–0.64) than non-forage fish (median 0.03, $n = 263$, 95% CI 0.005–0.14). For the herring stocks, 39% (17 of 45) had single-year recruitment increases greater than Mean High Recruitment, compared to only 21% of non-forage fish species (55 of 263).

Directed fisheries on herring stocks are also more likely to experience closures (i.e. zero catches ignoring by-catch from other fisheries) than non-forage fish species: 48% (31 of 64) were closed in at least 1 year compared to 14% (67 of 490) non-forage fish stocks. Similar results are obtained when examining stocks with catches <5% of Mean High Catch (73% of herring stocks vs. 45% of non-forage fish stocks). Herring stocks are more than twice as likely to be closed in recent years (after 2005, 28%; 1995–2005, 13%), largely because of recent depressed levels of many Pacific herring stocks—indeed, Pacific herring account for 24 of 25 of all herring stocks with catches <5% of Mean High Catch.

3.2 | How often should we expect low biomass and high recruitment to occur for herring?

For this analysis, we focused on the 30 stocks that have at least 30 years of biomass estimates and used the last 30 years of each time series (summarized in Figure 2). The median biomass of each stock is correlated with median recruitment (Spearman's $\rho = 0.69$, $p < .001$),

TABLE 1 Characteristics of time series of herring stocks collected for this study and non-forage fish stocks from the RAM Legacy database

	Herring	Non-forage fish
Biomass		
No. series available	53	307
CV of relative biomass	0.58 (0.30–0.93)	0.44 (0.11–1.10)
Minimum relative biomass	0.097 (0.001–0.315)	0.222 (0.011–0.676)
No. stocks below 5% Mean High Biomass	15	30
No. stocks below 30% Mean High Biomass	51	202
No. stocks with max. biomass >30% following the historical minimum	39	120
Median years to reach max biomass >30% following the minimum	13 (4–38)	12 (1–48)
Median value of this maximum biomass following the minimum	1.00 (0.11–1.25)	0.500 (0.056–1.22)
Largest 1-year decrease in biomass	0.28 (0.13–0.60)	0.14 (0.03–0.58)
Largest 1-year increase in biomass	0.28 (0.06–0.61)	0.12 (0.004–0.64)
Median interannual change in biomass	–0.001 (–0.032–0.041)	–0.0065 (–0.035–0.034)
Recruitment		
No. series available	45	263
Median CV of log relative recruitment	0.16 (0.04–0.64)	0.03 (0.005–0.14)
No. stocks with at least one exceptionally large cohort (>Mean High Recruitment)	17	55
Proportion of years with exceptionally large cohorts	0.031 (0.017–0.057)	0.009 (0.026–0.05)
Median relative recruitment of stocks with exceptionally large cohorts	0.22 (0.05–0.43)	0.46 (0.08–0.90)
Catch		
No. series available	64	490
No. series where catch = 0 at least once	31	67
No. series where catch <5% of Mean High Catch at least once	47	222
Median time when catch = 0	9 (1–25)	–

Note: For values derived from distributions, the median is shown first followed by the 95% confidence intervals in parentheses. For entries indicating the number of stocks meeting a certain criterion (e.g. "No. stocks..."), this applies across all years available for a stock so that a single instance when a criterion is met qualifies that stock.

but not with median relative productivity (R/SSB) ($\rho = 0.19$). Instead, CV of recruitment is correlated with relative productivity ($\rho = 0.61$, $p < .001$). Median catch is also correlated with median biomass, but less so ($\rho = 0.40$, $p = .02$), and the correlation is almost significant for Atlantic herring ($\rho = 0.45$, $p = .06$), but is significant for Pacific herring ($\rho = 0.65$, $p = .02$).

To address the frequency of collapse in biomass, we focused on the lower tails of this distribution (Figure 2). Collapse frequency is defined as the total number of years that biomass is below 30% of Mean High Biomass for each stock. Comparing among all stocks, biomass is collapsed for 8 years on average. Atlantic herring are collapsed in fewer years (median 6.5 years) than Pacific herring (median 8.5 years), and one-quarter of stocks are collapsed for half the time of the most recent 30 years (Figure 3). The herring stocks with the most collapsed years (more than 15 years) are those in the Irish Sea, Northwest Ireland, West of Scotland, Western Newfoundland fall and spring spawners, Haida Gwaii, Kamishak and Prince William Sound.

For recruitment, the analysis focused on the frequency of moderate-to-strong recruitment events: those above 50% of Mean High Recruitment (Figure 3). Recruitment was above this threshold for a median of 8 years out of the most recent 30 years and differed little between Atlantic and Pacific herring. Stocks with few strong cohorts (3 or fewer years out of 30) are from West of Scotland, St. Mary's & Placentia Bays, West Newfoundland spring spawners, the Scotian Shelf and Bay of Fundy, Southern Gulf of St. Lawrence, Togiak, Kamishak and Prince William Sound. Counter-intuitively, only four stocks with few strong cohorts also had many years of low biomass, namely West of Scotland, Kamishak and Prince William Sound. In these stocks, strong year classes occurred for a relatively short period before entering a protracted period of low recruitment with low variability.

3.3 | For how long should we expect low biomass and recruitment to persist among herring?

Biomass collapse duration, or the number of years to recovery, is the consecutive number of years (minimum 2 years) below 30% of Mean High Biomass. Such collapses occurred in 23 of the 30 stocks (Figure 3). The median collapse duration is 11 years and does not differ between Pacific and Atlantic herring. Only six stocks were collapsed for more than 15 years.

Prolonged recruitment failures are defined as the consecutive number of years below 50% of Mean High Recruitment ($n = 30$ stocks). The median duration is 10 years, with shorter periods for Pacific herring (7.5 years) than Atlantic herring (11.5 years). For 14 of the stocks, long periods of recruitment failure (some up to 30 years) had not ended by the most recent year of data. This highlights large uncertainty in the outlook of herring recruitment dynamics because the absence of strong cohorts can span time scales of decades.

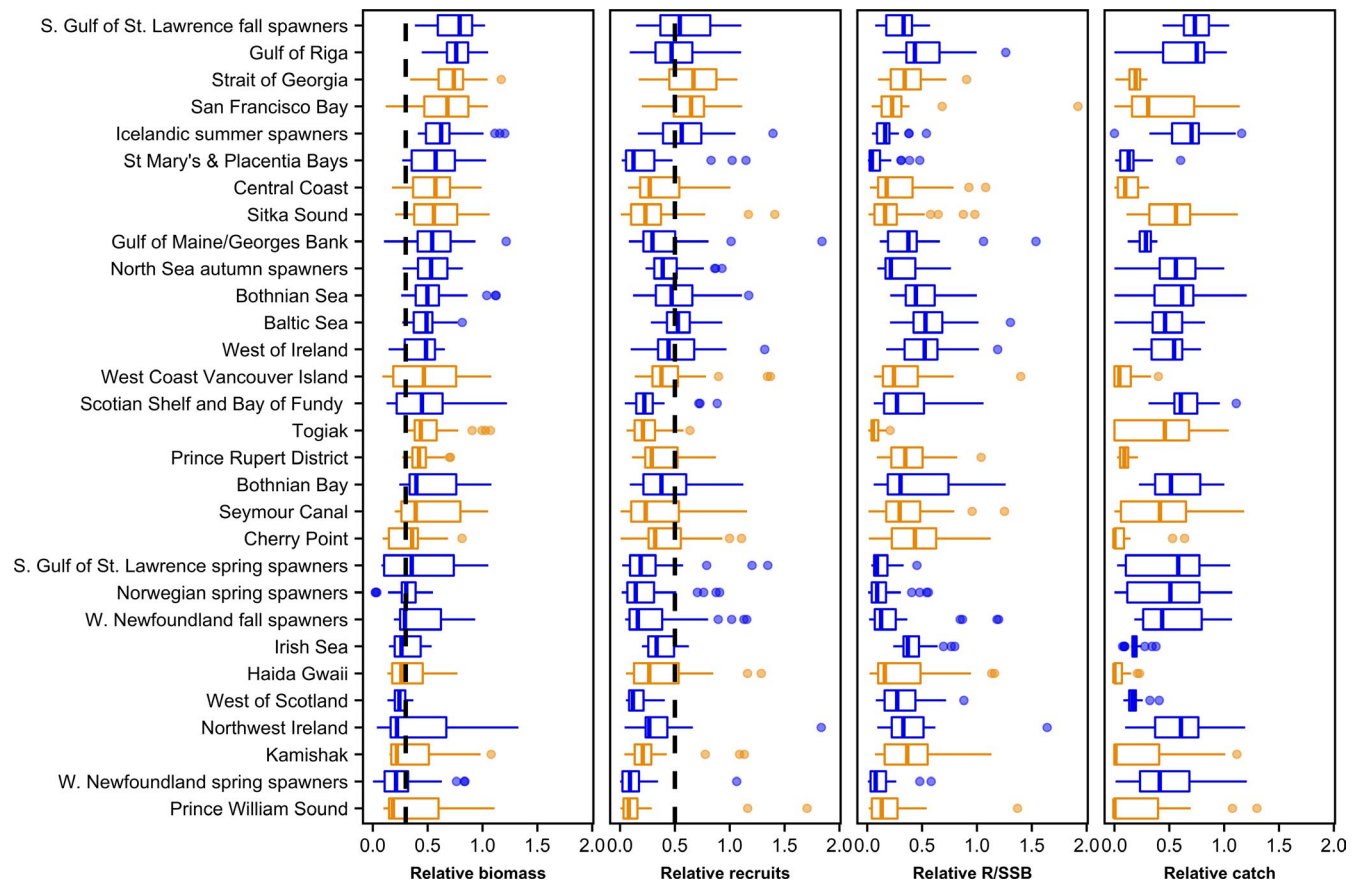


FIGURE 2 Box plots of time-series distributions for stocks used in our analysis (at least 30 years of observations). Each time series is divided by its respective mean high value (i.e. mean of the values in the 90th percentile). Stocks are ordered by their median relative biomass from the largest median at the top to lowest median at the bottom and colour coded by species (Atlantic herring are blue and Pacific herring are orange). The 30% of Mean High Biomass and 50% of Mean High Recruit thresholds used to identify collapse levels are also shown by dashed lines in the relative biomass and relative recruits plots [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/faf.12452)]

3.4 | What factors are most important in explaining the frequencies of low biomass and high recruitment?

The variability seen in biomass collapse frequencies is the result of a complex suite of environmental, fishing and biological factors (Figures 4 and 5). Since many factors are tested which increases the risk of Type I error, we applied the Holm–Bonferroni method (Holm, 1979) to adjust the significance associated with our bootstrapped p -values. Greater frequencies of low biomass were most associated (based on NBLMEs) with lower median recruitment (Holm–Bonferroni $p < .01$), and secondarily with lower SST standard deviation (Holm–Bonferroni $p < .1$). We found no other significant associations between low biomass and all other factors (Table 2). Stock groupings (as colour coded in Figure 1) as a random effect did not impact estimates.

The frequency of high recruitment years was also analysed using NBLMEs (Table 3), which found that across stocks, the number of years with high recruitment is positively associated with median biomass (Holm–Bonferroni $p < .01$) and negatively associated with biomass CV (Holm–Bonferroni $p < .01$), and the

mean of the highest catch-to-biomass ratio (Holm–Bonferroni $p < .05$).

These results were further checked with a suite of sensitivity tests to determine if any outlier values had a significant impact on the results (Supporting Information), which marginally changed significance of some of the minor predictors, but had no major influence on the key predictors.

3.5 | What factors are most important in explaining the durations of low biomass and recruitment?

For 23 stocks with low biomass (the other 7 of 30 stocks did not have low biomass persisting longer than 2 years), the most important predictors of the duration of low biomass were identified using VIMP in Random Survival Forests analysis (all predictors are shown in Figure 6). These predictors were, from most to least important, SD of SSHA, trend in SSHA, CV of recruitment, median relative recruitment and trend in SST (Figure 7). Other variables were unimportant (within or near the shaded region in

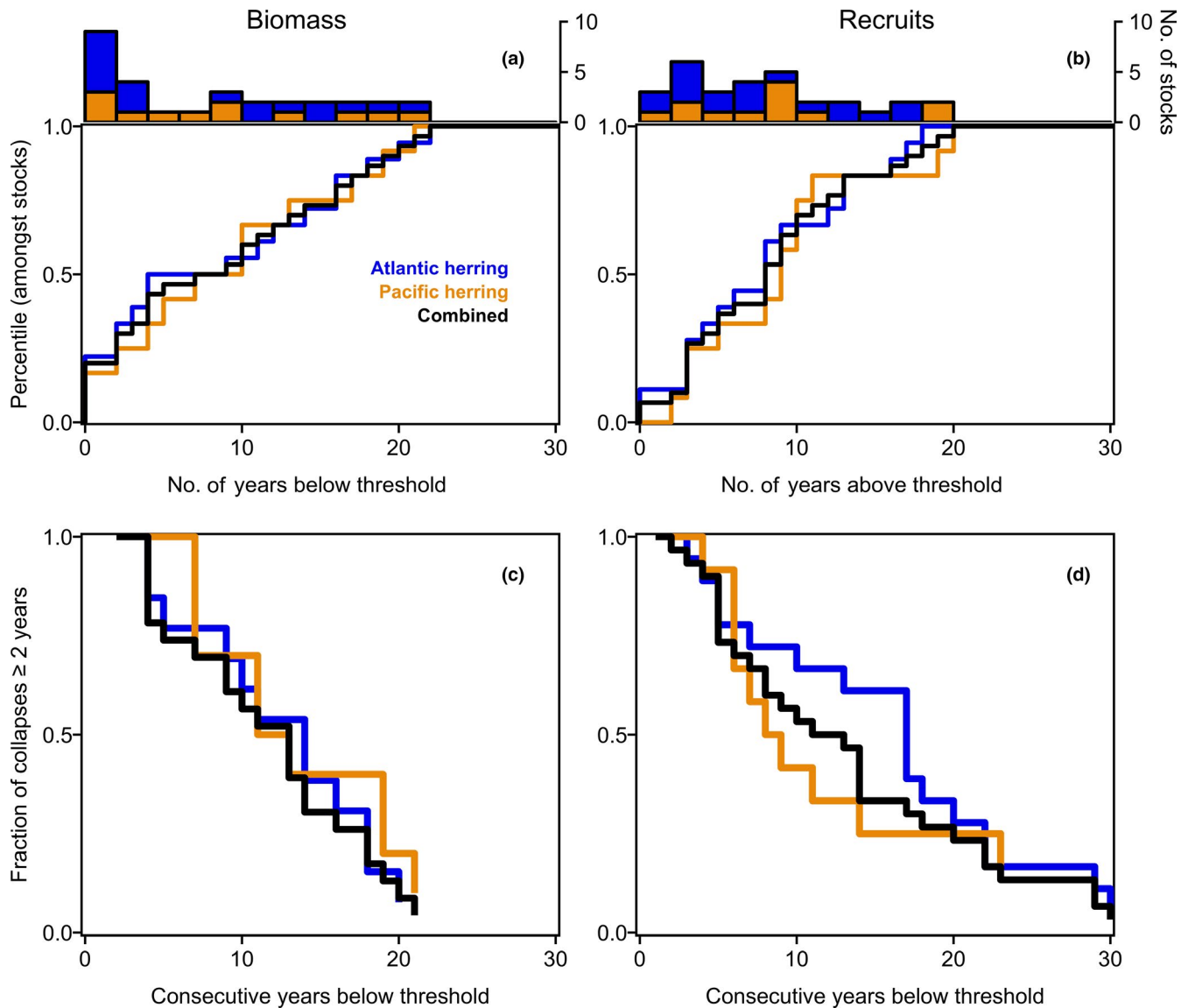


FIGURE 3 Distributions of the number of years below or above a threshold amongst herring stocks ($N = 30$). Both the histogram (top) and empirical cumulative distribution (bottom) are shown for (a) the total number of years in which biomass falls below 30% of Mean High Biomass and (b) the total number of years recruits exceed 50% of Mean High Recruitment. Also shown are the frequencies of events with more than X consecutive years of (c) biomass below 30% of Mean High Biomass ($N = 23$) and (d) recruits below 50% of Mean High Recruitment ($N = 30$). The minimum period considered was more than 2 years. Since stocks may show multiple periods longer than 2 years below the stated thresholds, each stock's maximum period is considered. For all stocks, only the 30 most recent years of each stock's time series are used to determine the number of years on all plots [Colour figure can be viewed at wileyonlinelibrary.com]

Figure 7). The out-of-bag error rate using Harrell's concordance index (Figure S6) was 0.32, where values < 0.5 indicate better predictive accuracy.

The generated Random Survival Forests were then used to determine the partial dependencies, that is how each predictor affected the probability that biomass collapse would last a given number of years. In Figure S8, the probabilities that a stock would be collapsed for 5 or 10 years are shown as a function of each predictor, depicting that collapse probability declines with increasing SD of SSHA, increases with CV of recruitment, decreases with median relative recruitment and has non-linear dependencies with the other two predictors.

For 30 durations of low recruitment (i.e. times between high recruitment events; Figure 8), the most important predictors from the Random Survival Forests were median relative biomass, SD of SSHA, the highest relative catch-to-relative biomass ratio and mean predatory fish trend (Figure 9). The error rate was 0.23. The results were little changed when two outliers were removed.

Partial dependency plots revealed that higher proportions of stocks with low recruitment are associated with lower median relative biomass, lower SD of SSHA, higher catch-to-biomass ratio and lower rates of decline in predatory fish abundance (Figure S9). However, low recruitment only strongly depends on these predictors

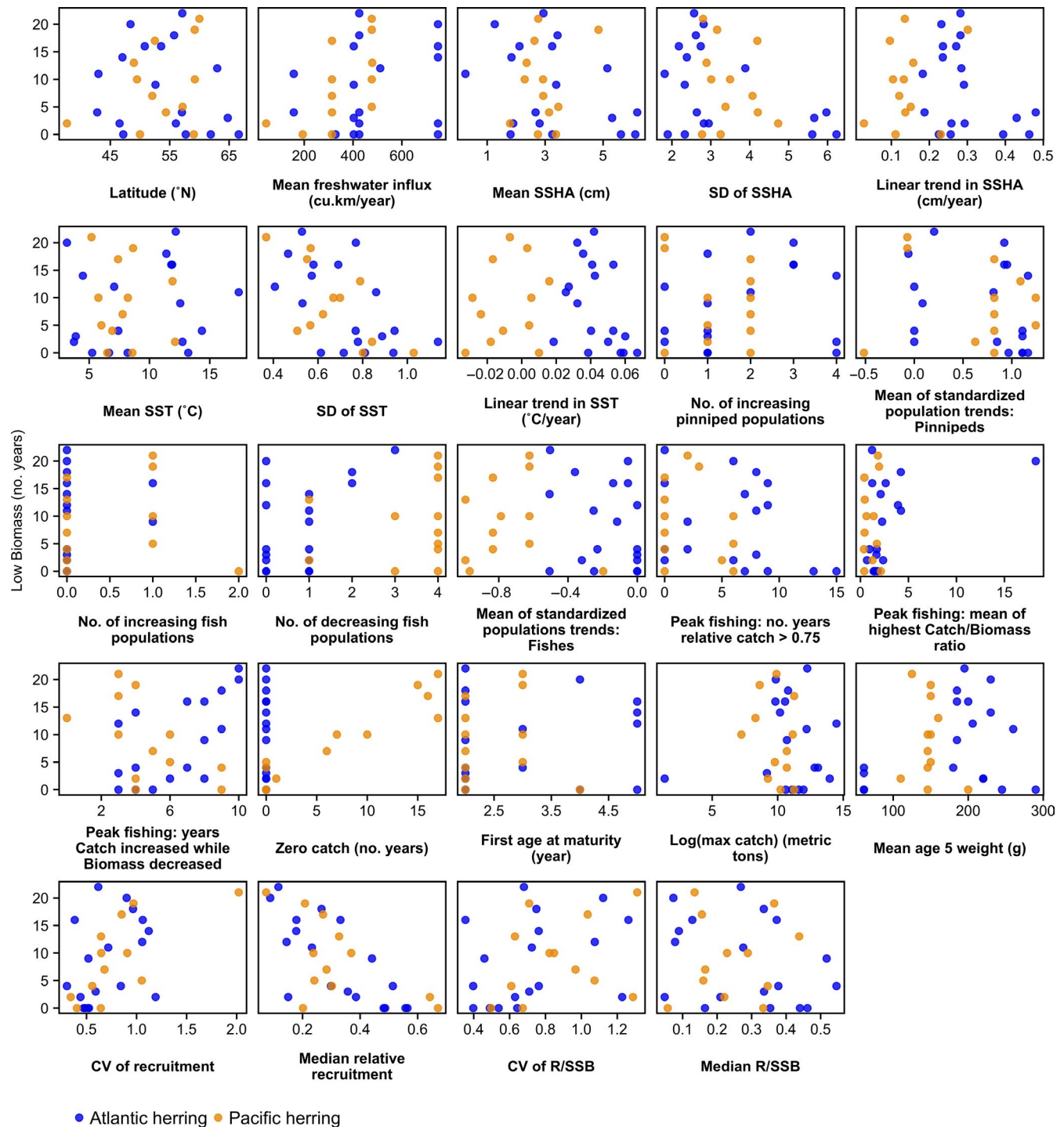


FIGURE 4 Observed low biomass year counts <30% of Mean High Biomass with their respective covariate values for each of the variables explored with the zero-inflated generalized linear mixed-effects models. Observations are coloured by species (Atlantic herring = blue, Pacific herring = orange) [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/faf.12452)]

at the lower end of predictor ranges, suggesting that predictor importance relies on a small subset of observations (Fig. S9).

Sensitivities in the Random Survival Forest analysis were also checked, including removing collinear predictors and re-running on times derived from different collapse thresholds (Supporting Information). While predictive accuracy of the analyses changed, ranking of the key predictors did not which largely upholds the key findings presented here.

4 | DISCUSSION

Our study characterizes population collapse and subsequent recovery of herring stocks, finding that herring have more extreme interannual swings in biomass and recruitment than non-forage fish species. For herring stocks, the average duration at low biomass is 11 years, moderate-to-high recruitment occurs

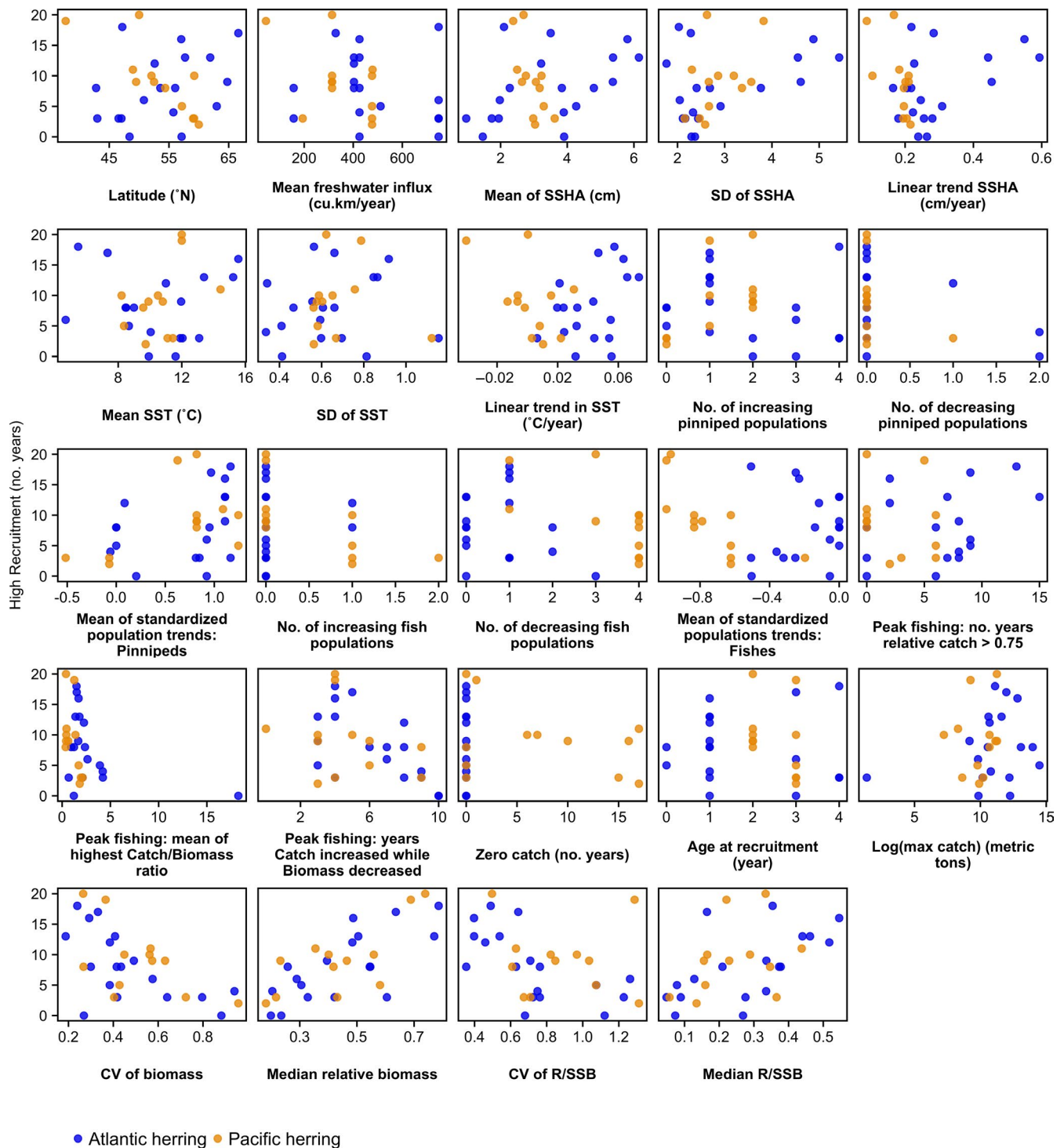


FIGURE 5 Observed high recruit year counts >50% of Mean High Recruitment with their respective covariate values for each of the variables explored with the zero-inflated generalized linear mixed-effects models. Observations are coloured by species (Atlantic herring = blue, Pacific herring = orange) [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/faf.12452)]

approximately one-fourth of the time (8 of 30 years) on average, and consistently low recruitment spans a decade on average. Our investigation of explanatory factors highlights how spawning biomass and recruitment relate to physical environmental conditions, fishing, region and predators (both for Atlantic herring and Pacific herring).

4.1 | Herring experience more population variability than non-forage taxa

Compared to non-forage fish species in the RAM Legacy database, herring biomass drops to lower minima, recovers to higher maxima and exhibits larger maximum interannual increases and decreases.

TABLE 2 Estimated parameters for single-variable zero-inflated negative binomial GLMMs predicting the number of low biomass years among herring populations ($n = 30$)

Explanatory factor	n	Conditional model			Zero-inflated model			No. sims	p
		Eff.	L 95% CI	U 95% CI	Eff.	L 95% CI	U 95% CI		
Median relative recruitment	30	-0.57	-0.87	-0.26	1.56	0.23	2.88	991	.000***
SD of SST	30	-0.45	-0.71	-0.18	0.83	-0.21	1.87	991	.004*
CV of recruitment	30	0.25	-0.01	0.51	-1.92	-3.98	0.14	997	.012
CV of R/SSB	30	0.06	-0.22	0.34	-1.95	-3.83	-0.06	993	.021
SD of SSHA	30	-0.48	-0.84	-0.12	0.13	-1.07	1.33	988	.039
Peak fishing: no. years relative catch >0.75	30	0.04	-0.33	0.41	1.73	-1.23	4.69	986	.046
Zero catch (no. years)	30	0.19	-0.04	0.42	NA	NA	NA	895	.051
Latitude (°N)	30	0.17	-0.16	0.49	0.80	-0.41	2.01	990	.265
Mean freshwater influx (cu.km/year)	30	0.24	-0.05	0.54	-0.16	-1.13	0.81	994	.287
First age at maturity (year)	30	0.20	-0.09	0.49	0.44	-0.45	1.33	1,000	.299
Mean age 5 weight (g)	30	0.32	-0.10	0.74	0.12	-1.10	1.35	992	.362
Peak fishing: mean of highest Catch/Biomass ratio	30	0.15	-0.09	0.40	-0.91	-3.87	2.05	998	.374
Mean SSHA (cm)	30	-0.11	-0.43	0.21	0.60	-0.35	1.55	989	.392
Log(max catch) (metric tons)	30	0.07	-0.26	0.40	0.66	-0.57	1.89	991	.480
No. of decreasing fish populations	30	0.16	-0.12	0.44	-0.24	-1.24	0.76	999	.514
Mean of standardized population trends: Pinnipeds	30	-0.16	-0.45	0.14	0.28	-0.79	1.36	995	.524
Linear trend in SSHA (cm/year)	30	-0.03	-0.39	0.33	0.56	-0.40	1.53	988	.531
Linear trend in SST (°C/year)	30	0.03	-0.32	0.39	0.68	-0.88	2.23	999	.573
Median R/SSB	30	-0.11	-0.41	0.19	0.33	-0.65	1.32	997	.618
No. of increasing fish populations	30	0.15	-0.17	0.48	0.19	-0.69	1.07	999	.640
Peak fishing: years Catch increased while Biomass decreased	30	0.05	-0.19	0.30	-0.41	-1.42	0.61	992	.671
Mean of standardized population trends: Fishes	30	-0.03	-0.34	0.28	0.37	-0.69	1.42	986	.784
No. of increasing pinniped populations	30	0.09	-0.20	0.37	-0.06	-1.04	0.92	1,000	.860
Mean SST (°C)	30	0.00	-0.27	0.28	-0.26	-1.27	0.74	996	.894

Note: The estimated intercepts (Int.), effect coefficients (Eff.), and the lower (L 95% CI) and upper 95% confidence interval bounds (U 95% CI) on the effect are provided for each model. All variables are scaled by their mean and standard deviation. The p -values are empirically derived, based on the proportion of parametrically bootstrapped likelihood ratios between the full and null models (only the means in the conditional and zero-inflated models with a random-intercept on herring locale) that are as extreme as the observed likelihood ratio. These bootstrapped likelihood ratios derive from converged model fits from the null model (no. sims). Given the large number of predictors, we also apply the Holm–Bonferroni method on the empirical p -values to correct for Type I errors (***, .01; **, .05; *, .1).

Abbreviations: SSHA, sea surface height anomalies; SST, sea surface temperature.

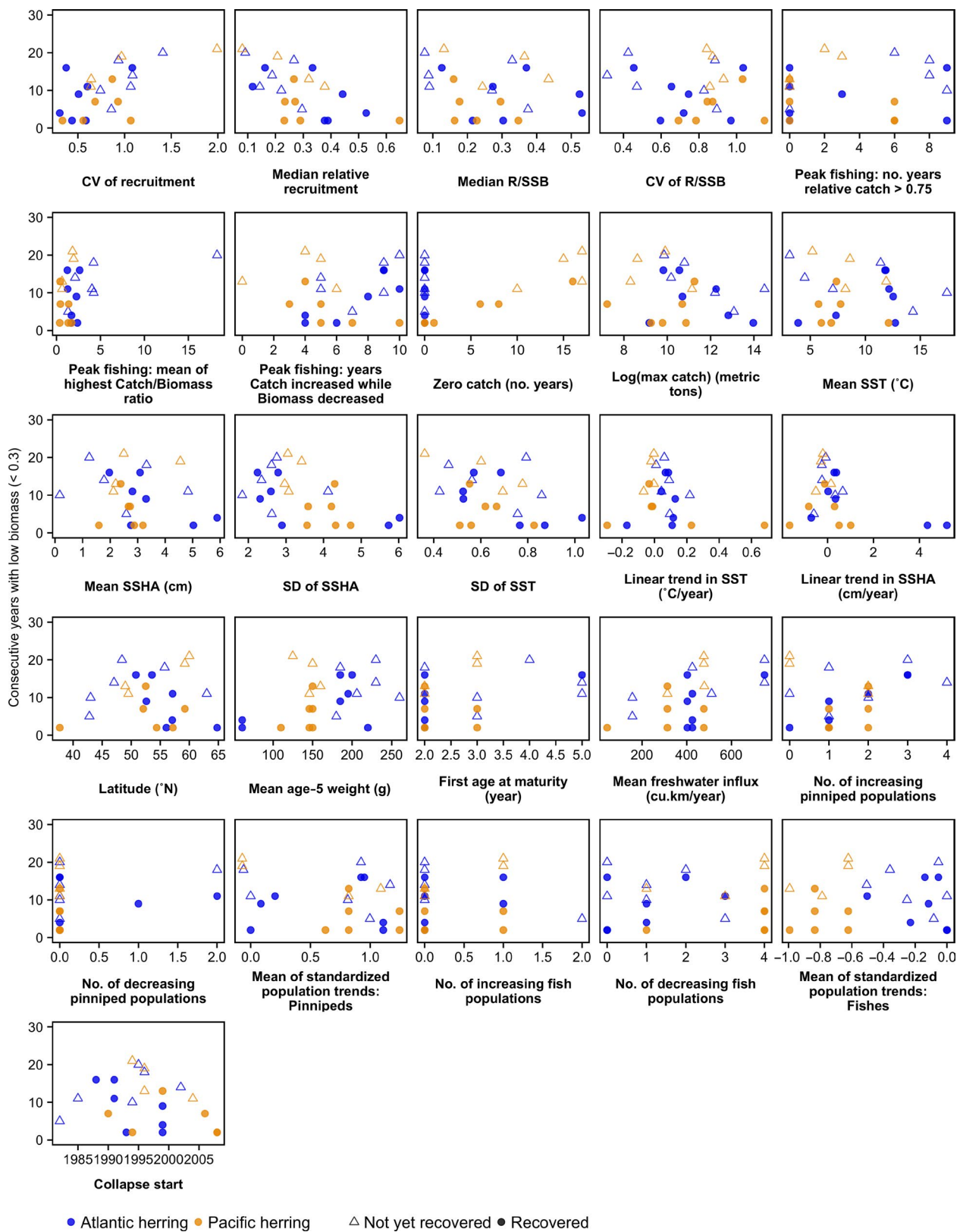


FIGURE 6 Observed low biomass durations <30% of Mean High Biomass ($N = 23$) with their respective covariate values for each of the variables explored with the Random Survival Forest. Observations are identified by species (Pacific herring = orange, Atlantic herring = blue) and also by whether the end of the collapse time was observed within the time series (Recovered = solid circle) or not (Not recovered = empty triangle) [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/faf.12452)]

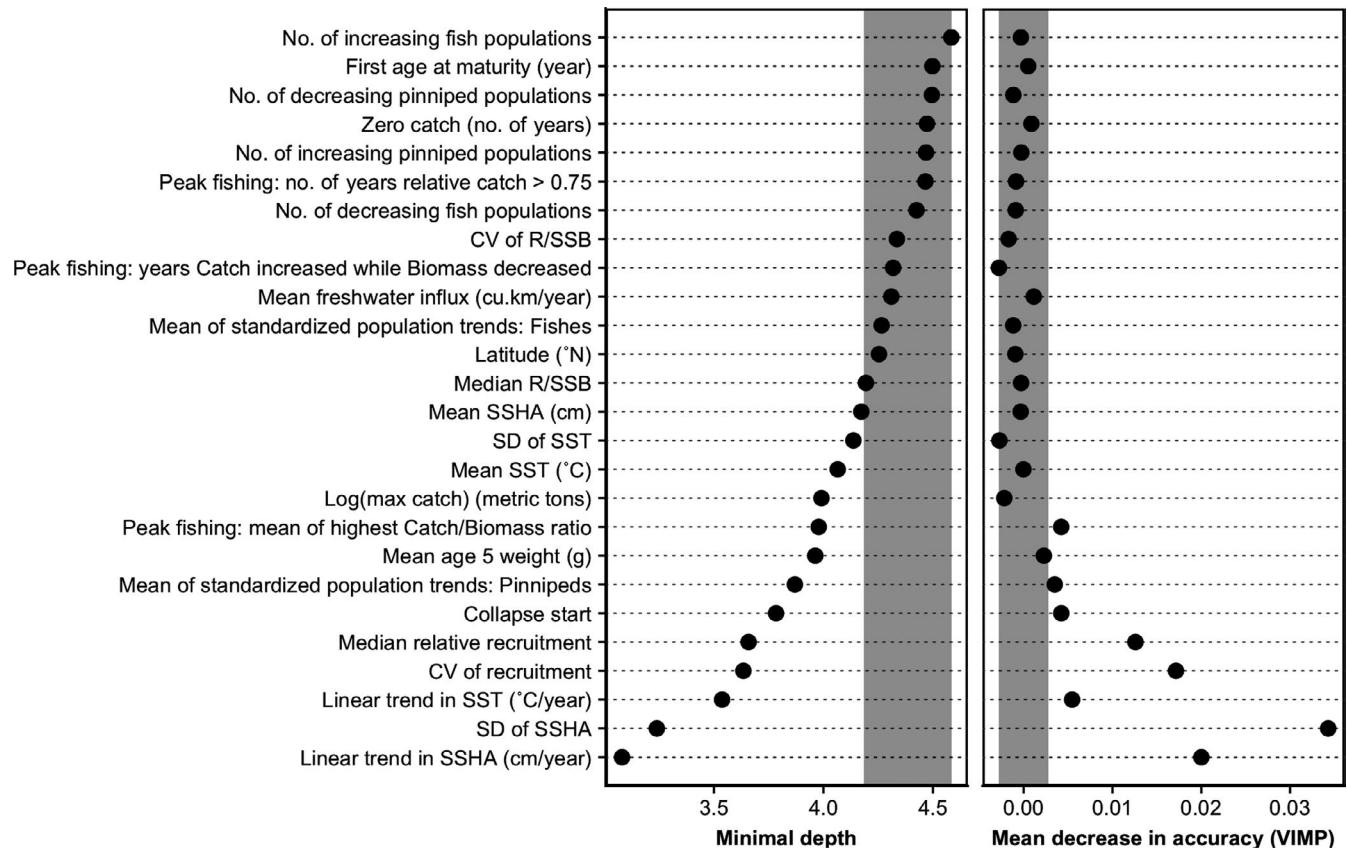


FIGURE 7 Metrics for selecting the most important variables from the Random Survival Forest regression on 23 collapse durations (collapse as biomass <30% Mean High Biomass). Variables are ordered by their importance in terms of minimal depth (top variables at the bottom), or the average node on which the variable is selected to split across all trees in the Random Survival. The lower the node, the more frequently the variable best splits all the data. Variable importance or VIMP is the difference in OOB Harrell's concordance index before and after random permutation, with larger values indicating an increase in error when randomly permuted. The larger the error, the larger the decrease in predictive accuracy and greater chance there is a true difference. Variables near and within the shaded regions are considered unimportant, which is above the median of all minimal depth values, and below the absolute value of the minimum VIMP score

These observations are consistent with previous meta-analyses examining how clupeids decline and subsequently increase, which attributed their resilience to their short-lived, fast-growing life histories (Hutchings, 2001; Hutchings & Reynolds, 2004). However, these life-history traits were also shown to increase clupeid vulnerability to collapse (Pinsky et al., 2011) and to exacerbate their vulnerability to collapse when overfishing occurs (Essington et al., 2015; Pinsky & Byler, 2015).

Herring are more likely to have very large recruitment events than non-forage fish and overall to display greater variability in recruitment. Strong cohorts (>1 unit of relative recruitment) occur in 3.1% of years within Pacific and Atlantic herring, and in survey and stock assessment-derived estimates. Of the 17 herring stocks with the largest cohorts, three pairs within the same region share cohorts in the same years (Prince William Sound and Sitka in 1987 and 1991, Central Coast and Haida Gwaii in 1979, and West Newfoundland fall and spring spawners in both 1982 and 1983). The 1987 and 1991 year classes in Prince William Sound and Sitka also match somewhat smaller recruitment pulses in other central Gulf of Alaska stocks (Kamishak and Kodiak, Figure 1), but it is possible these pairs may just be coincidences since correlations

reported between these stocks in the 1980s ceased to exist thereafter (Rice & Carls, 2007). More commonly, nearby stocks had unmatched large year classes, implying that stock-specific local conditions are important in determining the magnitude of cohorts.

4.2 | Fisheries closed for Pacific herring, but not Atlantic herring

Nearly half of herring stocks experienced very low to no catches during the time frame of analysis, which is a greater proportion than observed in non-forage fish stocks; and half of these herring fisheries remained closed for more than 10 years. Many herring fisheries were closed recently (from the mid-2000s on), and closures were all in the Pacific. Since both Pacific and Atlantic herring stocks showed similar patterns of declines in catches and biomass, that more fishery closures occur among Pacific herring likely reflect a number of differences in fishing dynamics and their management. For example, nearly all Pacific herring stocks in our analyses were fished by a single country (Canada or U.S.), while all Atlantic herring stocks in

TABLE 3 Estimated parameters for single-variable negative binomial GLMMs predicting the number of high recruitment years ($n = 30$)

Explanatory factor	n	Conditional model			No. sims	p
		Eff.	L 95% CI	U 95% CI		
Median relative biomass	30	0.48	0.29	0.67	1,000	.000***
CV of biomass	30	-0.49	-0.73	-0.26	1,000	.000***
Peak fishing: mean of highest Catch/Biomass ratio	30	-0.91	-1.56	-0.25	1,000	.002**
Peak fishing: years Catch increased while Biomass decreased	30	-0.40	-0.66	-0.15	1,000	.005
Median R/SSB	30	0.35	0.11	0.58	1,000	.017
Mean of standardized population trends: Pinnipeds	30	0.31	0.05	0.57	1,000	.050
No. of decreasing pinniped populations	30	-0.32	-0.62	-0.03	1,000	.091
CV of R/SSB	30	-0.24	-0.48	-0.01	1,000	.109
SD of SSHA	30	0.21	-0.02	0.45	1,000	.186
Mean freshwater influx (cu.km/year)	30	-0.20	-0.45	0.06	1,000	.340
No. of increasing fish populations	30	-0.21	-0.48	0.06	1,000	.358
Mean of SSHA (cm)	30	0.15	-0.10	0.41	1,000	.456
Mean of standardized populations trends: Fishes	30	-0.13	-0.36	0.11	1,000	.492
No. of decreasing fish populations	30	-0.13	-0.40	0.14	1,000	.518
Log(max catch) (metric tons)	30	0.14	-0.15	0.43	1,000	.521
Zero catch (no. years)	30	-0.08	-0.35	0.19	1,000	.558
Linear trend SSHA (cm/year)	30	0.07	-0.16	0.30	1,000	.565
Peak fishing: no. years relative catch >0.75	30	0.06	-0.18	0.30	1,000	.579
SD of SST	30	0.05	-0.25	0.34	1,000	.586
Latitude (°N)	30	-0.04	-0.28	0.20	1,000	.590
Age at recruitment (year)	30	-0.03	-0.30	0.24	1,000	.594
Mean SST (°C)	30	0.04	-0.19	0.27	1,000	.595
Linear trend in SST (°C/year)	30	-0.02	-0.24	0.21	1,000	.604
No. of increasing pinniped populations	30	-0.01	-0.30	0.27	1,000	.605

Note: The estimated intercepts (Int.), effect coefficients (Eff.), and the lower (L 95% CI) and upper 95% confidence interval bounds (U 95% CI) on the effect are provided for each model. All variables are scaled by their mean and standard deviation. Adjusted significance of the p -values using the Holm-Bonferroni method are also indicated (***, .01; **, .05; *, .1).

Abbreviations: SSHA, sea surface height anomalies; SST, sea surface temperature.

the Northeast Atlantic are targeted by multiple countries. A previous study has shown that when more countries jointly fish a stock, this increases the risk of over-exploiting the stock (McWhinnie, 2009). However, Northwest Atlantic herring too have shown no fishery closures (along with high frequencies and durations of low biomass) even though they are not shared between countries (fished and managed by either Canada or U.S.).

Differences also exist in the types of fishers targeting Pacific and Atlantic herring stocks. For example, Northeast Atlantic stocks are dominated by commercial fisheries, while many Pacific herring stocks (mostly in the Northeast) are managed by dividing a total catch among a variety of fishers including large industrial fleets, commercial fishers, recreational fishers, subsistence fishers and indigenous fishers such as the coastal First Nations of British Columbia. Conflicting goals among user groups resulted in stark disagreement between industry and First Nations on the Department of Fisheries and Oceans (DFO) management policy for Haida Gwaii

fishing (Lam et al., 2019), following a court injunction to reverse DFO's decision to open commercial fishing on Haida Gwaii and West Vancouver Island herring (Jones et al., 2017). In other words, cultural considerations (whether pre-emptive or by intervention) may promote more fishery closures amongst Pacific herring stocks, perhaps in addition to other differences in fishing and/or management (e.g. different gear types, management definitions and units of a stock, management areas, seasons).

4.3 | Half of herring stocks collapsed for a decade or more

Biomass in all herring stocks declined below 30% of Mean High Biomass at some point, with an average collapse duration of 11 years. These time scales are similar to those discussed in other studies on the recovery of fished populations after collapse

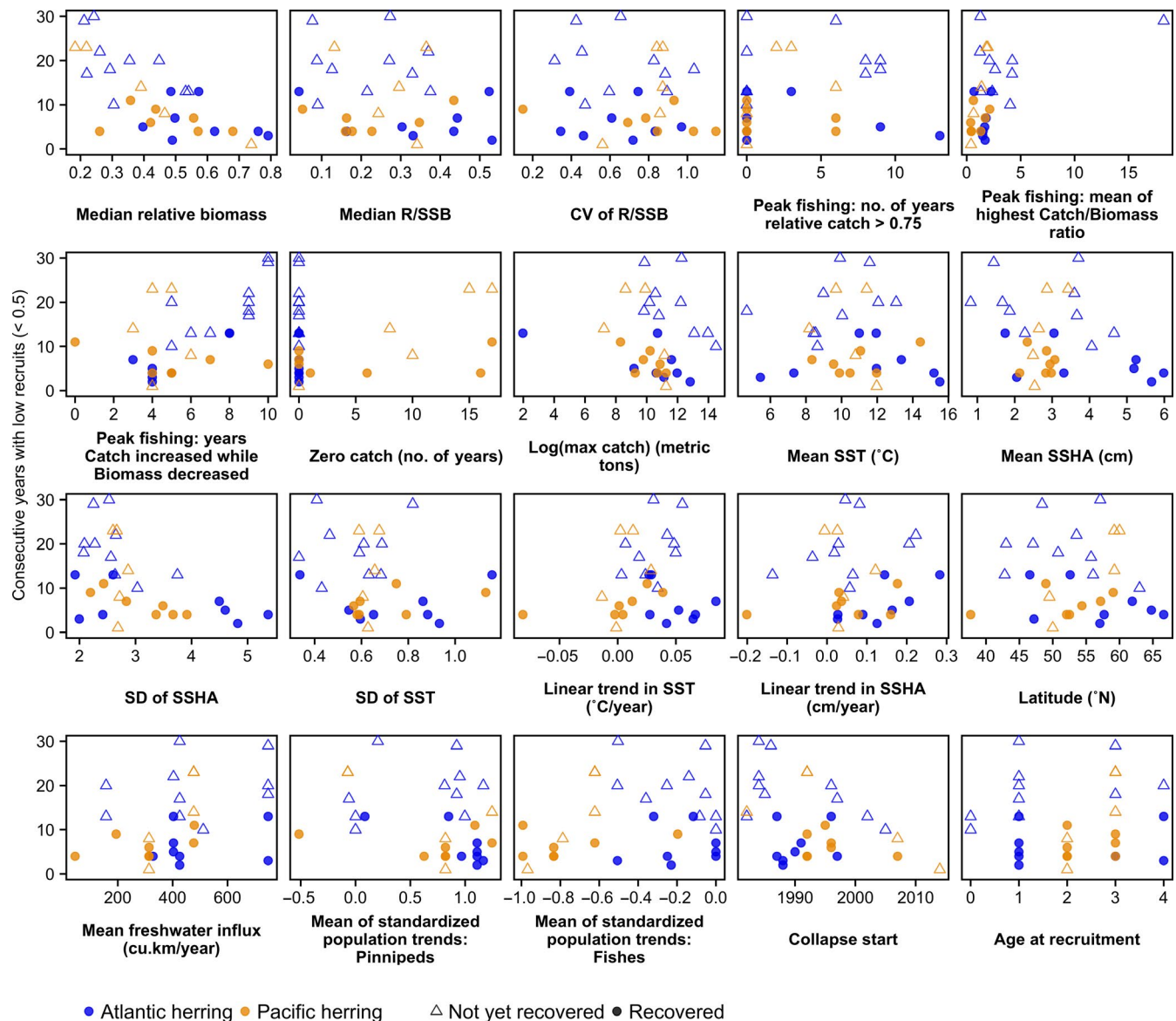


FIGURE 8 Observed low recruitment durations <50% of Mean High Recruitment ($N = 30$) with their respective covariate values for each of the variables explored with the Random Survival Forest. Observations are identified by species (Pacific herring = orange, Atlantic herring = blue) and also by whether the end of the collapse time was observed within the time series (Recovered = solid circle) or not (Not recovered = empty triangle) [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/terms-and-conditions)]

(Neubauer et al., 2013; Petitgas, Secor, McQuinn, Huse, & Lo, 2010). Paleo records of anchovy and sardine abundance of the California coast indicate an average time of 1–2 decades to return to “fishable biomass” (33% of mean peak biomass) (McClatchie et al. (2017). Recovery is not inevitable: only 4 of 12 stocks that had remained collapsed for 11 or more years had recovered above the 30% threshold by the end of the time series. Thus, recovery may involve far longer durations than could be recorded in our data set. This uncertainty is worrisome given that prolonged collapse times also may include severely contracted geographical ranges and the loss of spawning components (Hay et al., 2001; Melvin & Stephenson, 2006). These biological effects can have severe long-term consequences for fishing fleets (Dickey-Collas et al., 2010),

and cultures whose long-standing traditions rely on herring such as roe-on-kelp harvests (Gauvreau et al., 2017; Jones et al., 2017; Menzies, 2016; Thornton et al., 2010).

Herring stocks with long periods of recruitment failure and few strong year classes are notable for a “flatline” in their recruitment time series. We found that protracted periods of herring recruitment failure correlate with higher overall autocorrelation ($\rho = 0.60$, $p < .001$). High autocorrelation in recruitment may be driven by spawner abundance (Somarakis et al., 2018), low-frequency ecological drivers (Pepin, 2015; Pyper & Peterman, 1998; Ricard, Zimmermann, & Heino, 2016) or the combined effects of both (Punt, Szuwalski, & Stockhausen, 2014; Szuwalski et al., 2015; Vert-pre, Amoroso, Jensen, & Hilborn, 2013).

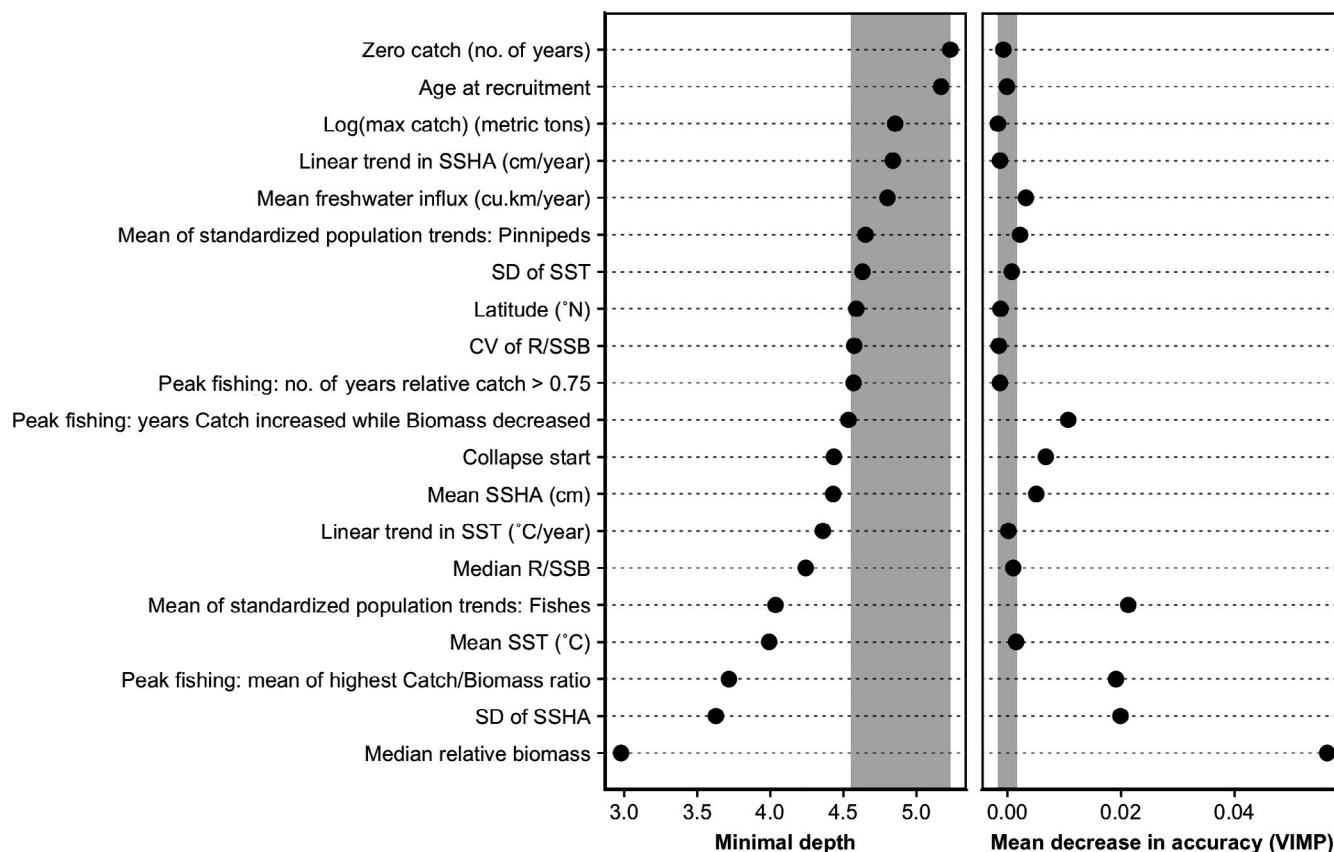


FIGURE 9 Metrics for selecting the most important variables from the Random Survival Forest regression on 30 low recruitment periods (low as recruits <50% of Mean High Recruitment). Variables are ordered by their importance in terms of minimal depth (top variables at the bottom) and displayed alongside their respective variable importance (VIMP). Variables near and within the shaded regions are considered unimportant, which is above the median of all minimal depth values and below the absolute value of the minimum VIMP score

4.4 | Recovery hinges on the link between biomass and recruitment

Distributions of spawning biomass, recruitment, catch and productivity (defined as the relative recruits/spawning biomass, or R/SSB) across stocks reveal no relationship between median spawning biomass and median productivity. Furthermore, the number of low biomass years is best predicted by lower median recruitment and higher recruitment variability, and the duration of low recruitment by low median biomass, while the frequency of high recruitment is best predicted by high median biomass and high biomass CV.

Both high and low stock-recruitment associations have been previously shown for herring (Myers & Barrowman, 1996), and there is recent evidence for statistically significant stock-recruitment relationships in forage fish (Somarakis et al., 2018). Still, other recent studies have shown that cross-correlations are strongest when recruitment leads spawning biomass across stocks (Szuwalski et al., 2015, 2019) with arguments positing the overwhelming effects of environment and/or life history compared to spawner abundance (*sensu* Pepin, 2015). Our results do not robustly test one claim over the other; instead, our results suggest a strong association between recruitment and biomass at high and low levels as the primary

determinant of collapse times and eventual recovery across herring stocks.

4.5 | Catch patterns and recovery

While catches generally track spawning biomass, catches alone are less useful than time series of fishing mortality. However, fishing mortality values are not available for many stocks. Therefore, we developed three proxies for the duration and magnitude of unsustainable exploitation (the number of years in which relative catch exceeded 0.75; years in which catch increased while biomass decreased; and mean of the highest catch/biomass). The linear mixed models and Random Survival Forest both found little relationship between times at low biomass and our exploitation proxies.

In contrast, results of the linear mixed models and Random Survival Forests found that stocks with larger maximum catch-to-biomass ratios in their record were likely to have fewer years of strong recruitment and longer recruitment failure. This connection could reflect that (a) recruitment failure precludes biomass recovery, which is exacerbated by increased exploitation, or that (b) this is the result of recruitment overfishing, as has been previously noted for

herring stocks (e.g. Cushing, 1971; Dickey-Collas et al., 2010; Hay et al., 2001). Fishing also mainly continues on Atlantic herring, but usually ceases on Pacific herring at the low relative levels we defined. These continuing catches of Atlantic herring imply a risk of increasing fishing mortality and overfishing especially given the density-dependent catchability that is characteristic of forage fish (Pitcher, 1995). Fishery closures that are more common among Pacific herring may negate this risk; however, closing does not seem to guarantee a speedy recovery since long durations of low biomass still exist for several stocks despite being closed to fishing.

4.6 | The importance of oceanographic variability

Variability both in SST and sea surface height anomaly (SSHA) were key predictors of low herring biomass. Greater environmental variability in SSHA and SST were associated with fewer years of low biomass. This makes sense given that higher spawning biomass is driven by occasional large recruitment events, which is in turn driven by recruitment variability. Variability in SSHA is correlated with periods of failed recruitment, and likely also adult mortality and individual growth, given the strong negative correlation between weight-at-age 5 and SSHA variability. While the link between environmental and recruitment variability is implicit in hypotheses postulated by other authors (e.g. the "optimal stability window" hypothesis from Gargett, 1997), the correlation between body condition and variability has not been made before in the literature and warrants further investigation into the mechanisms controlling somatic growth and asymptotic size.

Unlike SSHA variability, we found no relationship between SST variability and recruitment. Interannual temperature variability may indirectly force greater variability in growth and survival through changes in prey availability and distribution (e.g. Corten, 2001; Cushing, 1990; Southward, Hawkins, & Burrows, 1995), or directly force frequent or larger changes in growth and survival (Boltaña et al., 2017) via cumulative changes in individual metabolism and physiology (Pörtner & Knust, 2007; Pörtner & Peck, 2010). In other words, more variable SST may amplify variability in spawning biomass separately from the effect of recruitment variability. However, Pinsky and Byler (2015) found evidence that fast-growing forage fish in more variable thermal environments are more vulnerable to collapse as a result of overfishing. Higher variability in SSHA was associated generally with shortened periods of failed recruitment in our analysis. Recent work has implied strong links between recruitment success of various fish stocks and ocean currents and gyre-related circulation patterns, which directly influence SSHA, in the Northeast Atlantic (Zimmermann, Claireaux, & Enberg, 2019). Other studies have more specifically linked SSHA to recruitment of other species in the Gulf of Alaska and California Current (Stachura et al., 2014), the northern Benguela (Hardman-Mountford, Richardson, Boyer, Kreiner, & Boyer, 2003) and in the Leeuwin Current (Caputi, Fletcher, Pearce, & Chubb, 1996; Pearce & Phillips, 1988). Coastal upwelling, which also influences SSHA variability, is also strongly

correlated with herring recruitment variability (Reum, Essington, Greene, Rice, & Fresh, 2011).

4.7 | Other factors

We found no significant effects of predator trends on the number of years of low biomass or high recruitment, but larger declines in Pacific fish predators were associated with shorter periods of low recruitment. Inference on this potential relationship is complicated by the spatial context: juvenile herring are generally found within coastally enclosed areas (e.g. sounds, bays, and straits), while our data on fish predators span larger regions of open ocean over the eastern Pacific shelf. This spatial (and likely temporal) mismatch motivated our exclusion of other predators such as cetaceans and seabirds from analysis, since these groups migrate over even vaster distances. Seasonal and local estimates of their numbers may be available (e.g. Bishop, Watson, Kuletz, & Morgan, 2015; Surma & Pitcher, 2015; Teerlink et al., 2015), but estimates that are relevant to analysis were not generally available. Nevertheless, predator-prey relationships of cetaceans and seabirds on herring have been implicated as top-down controls on herring (Moran et al., 2018; Read & Brownstein, 2003; Straley et al., 2017) and as recipients of bottom-up effects from herring (Pikitch et al., 2012, 2014; Smith et al., 2011). Herring have also been identified as a key prey item for pinniped populations throughout the Pacific and Atlantic, including Southeast Alaska (Gende & Sigler, 2006; Sigler, Gende, & Csepp, 2017; Womble & Sigler, 2006), British Columbia (Olesiuk, 1999, 2008), Puget Sound (Lance, Chang, Jeffries, Pearson, & Acevedo-Gutiérrez, 2012), the Southern Gulf of St. Lawrence (Hammill, Stenson, Proust, Carter, & McKinnon, 2007), the Gulf of Maine (Overholtz & Link, 2006; Read & Brownstein, 2003) and the North Sea (Sveegaard et al., 2012). A more detailed and thorough investigation of these relationships involving various herring predators is needed, as has been done by Surma, Pitcher, et al. (2018).

Factors that were not found to have any effects were latitude, freshwater influx, first age at maturity, age-5 weight and maximum catch. Given the importance of fishing and oceanographic predictors from our analyses, extrinsic factors may determine herring recovery times to a greater degree than the intrinsic stock-specific characteristics considered here.

4.8 | Challenges of approach

A variety of assumptions in our approach were explored in more detail in sensitivity analyses (Supporting Information). Chief among these was the choice of a threshold to define low or high levels in biomass or recruitment. Naturally, levels below 30% of the Mean High Biomass may or may not equate to true population collapse in some stocks. Other fisheries meta-analyses have taken a similar approach of defining collapse with a reference point determined from the time series themselves to standardize comparisons (e.g.

Essington et al., 2015; McClatchie et al., 2017; Mullan, Fréon, & Cury, 2005; Pinsky et al., 2011; Worm et al., 2009). Applying alternative thresholds did not substantially change our conclusions except for the Random Survival Forest model of low biomass durations. Due to the loss of predictive accuracy, thresholds that were lower (20%) or higher (40%) modified the duration data in a way that made them less informative for our specific objective. For example, changing the threshold to 20% reduced the sample size from 23 to 16 since many stocks did not experience prolonged times below this threshold. Different thresholds in recruitment also did not alter our conclusions.

Testing of the various factors that may explain recovery times is also caveated by the scale with which we conducted this analysis. As with herring predators, ecosystem factors are particularly nuanced because of the time and spatial scales with which herring biological processes and oceanographic variables interact. For example, more localized oceanographic processes may influence herring biomass and/or recruitment than captured in our broad-scale factors so that even if such factors do impact some herring stocks, the cross-stock effect is absent or undetectable. This may explain why we do not find more significant predictors (for more discussion, see Supporting Information). However, small stocks for which only survey estimates are available comprise over half of the biomass data, and they lack stock-specific ecological information needed to develop more appropriate time series for analysis. As a result, our use of broader ecological factors is the best possible given available data, with the caveat that we can only detect effects from the variables for which data are available.

5 | CONCLUSIONS

The data presented bring together a wealth of herring knowledge in the most comprehensive compilation of herring population dynamic data sets to date, extending far beyond the data contained in the RAM Legacy database (Ricard et al., 2011). Stock assessment models do not exist for many herring populations in the Pacific, and Pacific herring have much greater representation in our data set. Few other fish taxa have as many records across stocks and years, and thus, this analysis provides the largest available meta-analysis on a single marine fish group. This “treasure trove” of herring data was first glimpsed in Hay et al. (2001), which served as one of the foundations for this paper and its questions.

We found a wide variety in the extent and duration of collapse and time to recovery in herring, implying that any management strategies must be robust to this broad range of possibilities to avoid the risk of losing substocks and eroding the long-term resilience of stock complexes. Timely reductions in fishing effort may counteract initial rapid and drastic declines, allowing some leverage through robust fisheries management (Bakun & Broad, 2003; Essington et al., 2015). Achieving this timeliness remains an obstacle and requires an ongoing investigation of biology and ecosystem interactions for each stock, since these factors likely change over time. One approach is to

more specifically identify smaller scale environmental indicators of impending productivity changes that would allow prompt reductions in harvest rates (Lindegren, Checkley, Rouyer, MacCall, & Stenseth, 2013). However, the success of this approach relies on the accuracy of these indicators in predicting changes (Punt et al., 2013). Novel methods have demonstrated the promise of accurate predictions from environmental indicators (Deyle et al., 2013), and applying such methods to data sets such as ours along with more context-specific environmental variables would be useful.

Our analyses are correlative, highlighting links between factors and recovery times without offering further evidence for specific mechanisms (Pepin, 2015; Williams & Quinn, 2000). Distinguishing recovery probability based on biologically plausible factors is a useful assessment of the stocks most at risk for prolonged recovery when collapsed. Knowing which factors are important for distinguishing recoveries (e.g. “risk factors”) amongst stocks can inform comparisons of management procedures amongst management areas. Identifying these risk factors also directs research to diagnose their causal pathways to longer or shorter collapses and recruitment failures amongst stocks. Our analyses demonstrate the potential of these data and similar data sets to address important questions on fish population dynamics. The outcome of such analyses has the potential to inform fisheries management on the types of policies that are best suited to promote faster potential recovery times after population collapse.

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DATA AVAILABILITY STATEMENT

Most of the data underlying this study are available at <https://doi.org/10.24431/rw1k32g>. Restrictions apply to the availability of the remaining data, which were used under privacy agreements for this study, and those data may be requested from the data providers identified in Table S1 of the Supporting Information.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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