



Forecasting herring biomass using environmental and population parameters



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ARTICLE INFO

Handled by A.E. Punt

Keywords:

Abundance

California Current

Clupeid

Prediction

Management

ABSTRACT

Forecasting abundance and understanding year class strength is key to the ecosystem-based fisheries management of herring and other small pelagic fish. Using the San Francisco Bay herring population, we tested the hypothesis that abundance (spawning stock biomass; SSB) could be predicted prior to the commencement of annual fisheries using estimates of i) previous SSB (SSB_{lag1}), ii) young-of-the-year production (YOY), and iii) environmental conditions. A time series model including SSB_{lag1} , YOY lagged 3 years (YOY_{lag3}), and environmental conditions in the season before spawning explained 67% of the variance in annual biomass, with better predictive error in comparison with simpler models. YOY_{lag3} was by far the strongest predictor. It was robust over the entire study period (1980–2017) and also for a more limited period (1991–2017) when observed variance in SSB increased. We attribute the predictive power of YOY productivity to age structure, as almost 70% of the population is comprised of young fish. We hypothesize that an age truncation effect, probably resulting from a combination of long-term environmental effects and fisheries impacts, supports this model, which effectively predicts year class strength. Assuming the population age structure remains the same in the future, our model provides management with an early warning indicator of upcoming SSB with a 3-year lead, which could be applied in harvest control rules.

1. Introduction

Since the early days of fisheries oceanography, one of the principal goals has been to understand and predict population fluctuations of small pelagic fish relative to production, recruitment, and ocean conditions (Hjort, 1914; Freon et al., 2005; Watanabe, 2007). Though hundreds of studies on fish production and recruitment have been conducted on a wide diversity of species, our ability to forecast small coastal pelagic fish populations is fraught with issues, including weak to non-existent stock-recruitment relationships (e.g., Stocker and Noakes, 1988) and non-stationary relationships (Myers, 1998). Today, with the confounding effects of fisheries removals, which may exacerbate effects of ocean conditions (Essington et al., 2015), and climate change, which may cause fish redistributions (reviewed by Poloczanska et al., 2013), the challenge of prediction has become both more acute and urgent. Understanding how marine climate impacts future abundance is fundamental to stock assessment and designing and implementing appropriate harvest control rules (Lindgren et al., 2010; Hollowed et al., 2013). In particular, a combination of environmental or fisheries-related changes to population age structure may result in unexpected

consequences for production, recruitment, and population dynamics (Anderson et al., 2008).

Owing to their neritic distribution and centennial history of exploitation (e.g., Cushing, 1961), herring have been the focal point of dozens of observational and modeling studies seeking to understand and predict variation in abundance for management purposes. In northern Europe, herring have been exploited since the 10th century, and time series research on landings clearly shows decadal-scale fluctuations in abundance relative to various interrelated meteorological and hydrographic variables (Alheit and Hagen, 1997). Similar relationships in herring abundance, growth, and size-at-age have been established at interannual time scales using observations (e.g., Williams and Quinn, 2000a,b; Beamish et al., 2004; Cardinale et al., 2009) and models (e.g., Hay et al., 2008; Rose et al., 2008; Ito et al., 2015). In the northeastern Pacific, Pacific herring (*Clupea pallasii*) are important for fisheries and food chains (Beamish et al., 2004; Szoboszlai et al., 2015). A recent meta-analysis of herring population trends and variability in the California Current Ecosystem (CCE) showed a secular decline in biomass estimates since 1980 for many stocks along the U.S. west coast, but data were limited to a ~30-year period (Thompson et al., 2017).

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Table 1
Environmental and herring population data used in this study. Period of data, resolution, location/region and source are specified.

Data	Label	Period	Location	Units	Temporal resolution	Source
Herring						
Spawning stock biomass	SSB	1980–2016	SFB	Kmt	Seasonal sum across months Dec–Mar, upscaled from eggs to Kmt	CDFW, Herring Management Program
Trawl CPUE Age-0, Age-1, and Age-2 +	YOY, Age-1, Age-2 +	1980–2015	SFB	Number of fish	Seasonal average over several months, Age-0: Apr–Oct, Age-1: Feb–Apr, Age-2 + : Dec–Mar.	CDFW, San Francisco Bay Study/Interagency Ecological Program for San Francisco Estuary
Herring Condition Index	HCI	1984–2015	SFB	No units	Seasonal average of Fulton's K across winter months	CDFW, ABMP/HMR
Environmental						
Midwater trawls temperature and salinity	Trawl-T Trawl-S	1980–2016	35 stations throughout SFB	°C, PSU	3-month running averages, over 9 months each year	CDFW, San Francisco Bay Study/Interagency Ecological Program for San Francisco Estuary
Sacramento River Delta outflow	Outflow	1996–2016	SFB	Acre-ft.	3-month running average	California Department of Water Resources
Farallon Islands sea surface salinity	Far-SSS	1979–2015	Gulf of the Farallones	PSU	3-month running average	SIO, Shore Station Program
Buoy N26 sea surface temperature	N26-SST	1982–2015	37.8°N, 122.8°W	°C	3-month running average	National Data Buoy Center/National Oceanic and Atmospheric Administration (NOAA)
Bakun Upwelling Index	BUI	1979–2015	39°N	m ³ /s/100m	3-month running average	Pacific Fisheries Environmental Laboratory/NOAA
Multivariate El Niño Southern Oscillation Index	MEI	1979–2015	Tropical Pacific	No units	3-month running average	Earth System Research Laboratory/NOAA
Pacific Decadal Oscillation	PDO	1979–2015	North Pacific	No units	3-month running average	Joint Institute for the Study of the Atmosphere and Ocean, University of Washington
North Pacific Gyre Oscillation	NPGO	1979–2015	North Pacific	No units	3-month running average	E. Di Lorenzo
Multivariate Ocean Climate Indicator	MOCI	1979–2015	Central California (34.5–38°N)	No units	Seasonal value for winter, spring, summer, and fall	Farallon Institute

Notably, in the same study, stocks along the Canadian west coast studied over a longer period (~60 years) demonstrated decadal-scale variability.

At the southern-most end of its range in the northeast Pacific, the San Francisco Bay (SFB) herring stock biomass has become more variable through time (Thompson et al., 2017), but nonetheless remains relatively large compared to other stocks in the CCE south of British Columbia (Siple and Francis, 2016). Variability in the SFB spawning stock biomass (SSB) is poorly understood, with occasional biomass levels low enough to trigger fisheries closures (e.g., 2009–2010; CDFW, 2017a). From November–March, adult herring enter SFB and spawn in the shallow subtidal habitats of the shoreline. Upon hatching, larval fish develop in the bay; juveniles typically migrate to the ocean in September–October (Fish et al., 2012). Management of the fishery on this stock includes the following data collections: 1) annual fall-winter surveys of spawning and egg deposition, conducted by California Department of Fish and Wildlife (CDFW), which are subsequently scaled up to estimate standing stock biomass, 2) monthly mid-water trawl surveys of reproductive output by CDFW to estimate production of young-of-the-year (YOY) (Feyrer et al., 2015), and 3) an annual general assessment of ecosystem conditions before each spawning season (CDFW, 2017a). A variety of regional measurements of environmental conditions within SFB and in the adjacent ocean are collected during monthly CDFW surveys, including measurements of temperature and salinity. Other related environmental factors are available for synthesis, including regional to large-scale ocean climate indicators. García-Reyes and Sydeman (2017) synthesized many of these indicators into seasonal Multivariate Ocean Climate Indicators (MOCI). MOCI couple the shared variation in basin-scale drivers, such as the Pacific Decadal Oscillation (PDO) and the North Pacific Gyre Oscillation (NPGO), with regional oceanographic processes such as upwelling (e.g., Bakun upwelling index) and local oceanic responses (e.g., temperature and winds).

We took a broad exploratory approach to understanding potential environmental and biological predictors of the SFB herring population. An exploratory approach was needed because prediction of population fluctuations was a key goal of the study and both basin-scale and regional environmental drivers are known to affect fish, seabirds, and marine mammals of the central-northern California Current (e.g., Thompson et al., 2012; García-Reyes et al., 2013; Sydeman et al., 2014). We therefore surmised that herring would be similarly responsive to drivers at multiple temporal and spatial scales. Moreover, it is well known that environmental conditions within and outside SFB, in the Gulf of the Farallones and even further afield, may strongly covary (Cloern et al., 2010; Feyrer et al., 2015). Consequently, we test a general hypothesis that lagged ocean conditions and herring productivity can be used to predict fluctuations in the SFB herring population. We expected herring biomass to be positively related to herring productivity, lagged 2 or 3 years to the year in question and assuming that higher productivity resulted in higher recruitment and higher biomass. We expected herring biomass to be positively correlated with regional upwelling and associated features (cold temperatures, high ocean salinity, negative PDO/positive NPGO). We did not have *a priori* expectations concerning other features of the environment such as outflow of freshwater into SFB, nor SFB temperature and salinity. To test this hypothesis, we integrated herring population data with information on bay and ocean conditions. This study is designed to contribute to a new fisheries management plan (FMP) for the SFB herring fishery under development by the State of California in partnership with commercial fishers and the conservation community. Forecasting tools are needed for SFB herring abundance assessments, management strategy evaluation, and in application of harvest control rules that may be designed to maintain escapement and productivity as well as the trophic role of herring in the coastal ecosystem (Rice and Duplisea, 2014).

Table 2

Spearman rank correlation (ρ) and Pearson correlation (expressed as R^2) between spawning stock biomass (SSB) and herring population indicators. Lag, in years, is shown in parentheses. Only nominally significant correlations ($p < 0.05$) are shown, and correlations with p -values < 0.005 are shown in bold.

Indicator	1979–2015	1991–2015
SSB	$\rho = 0.65$ (lag 1) $R^2 = 0.41$ (lag 1)	$\rho = 0.51$ (lag 1) $R^2 = 0.34$ (lag 1)
Age-2+	none	$R^2 = 0.24$ (lag 1)
Age-1	$\rho = 0.35$ (lag 3)	$\rho = 0.42$ (lag 3) $R^2 = 0.22$ (lag 3)
YOY	$\rho = 0.55$ (lag 2) $\rho = 0.64$ (lag 3) $R^2 = 0.25$ (lag 2) $R^2 = 0.34$ (lag 3)	$\rho = 0.57$ (lag 2) $\rho = 0.70$ (lag 3) $R^2 = 0.31$ (lag 2) $R^2 = 0.57$ (lag 3)
HCI	none	none

2. Methods

2.1. Herring data

Information on the SFB herring population (SSB, productivity, condition, age structure) has been collected by the CDFW since the early 1970s, with consistent methodology from ~1979 to the present for most variables (Fish et al., 2012; CDFW, 2017b). For our analyses we used: (1) estimates of herring SSB based on egg deposition surveys conducted by CDFW in winter and summed across the SFB (Watters et al., 2004), (2) YOY productivity estimates, proxied by catch-per-unit-effort (CPUE; number caught/tow volume*10,000) of age-0, age-1, and age-2 fishes from CDFW's Bay Study midwater trawl surveys conducted monthly at 35 stations, summed across stations and averaged across months (April–October for CPUE age-0, February–March for CPUE age-1 and December–March for CPUE age-2+), thereby producing a single annual estimate for each age class (Fleming, 1999; Fish et al., 2012), and (3) Fulton's K condition index (Ricker, 1975; Nash et al., 2006) in which $K = 100 * \text{wet mass(g)} / \text{length}^3(\text{cm})$; this index is developed from fisheries-independent surveys conducted since 1984 (Table 1; CDFW, 2016). More details of the data sets and methods used to obtain these data are provided in Supplementary Material (see Table SM1, Figs. SM1–SM3). In relation to herring biomass, we examined four relevant predictors: previous SSB lagged by 1 year, CPUE age-0 (hereafter referenced as YOY) lagged 1, 2, and 3 years, CPUE age-1 lagged 1, 2, and 3 years, and Fulton's K lagged 1, 2, and 3 years, for a total of ten herring covariates. In each of these cases, we expected relationships to be positive, assuming that greater productivity and body condition resulted in larger future biomass.

2.2. Environmental data

We compared herring SSB with anomalies in environmental data taken within SFB as well as in the adjacent Gulf of the Farallones, and Pacific Ocean basin-scale climate indices. Local data (Table 1) included temperature and salinity of the water column (hereafter Trawl-T, Trawl-S) collected at each of the 35 stations in SFB during the midwater trawl surveys conducted by the CDFW, delta outflow into SFB (Outflow, see below), sea surface temperature from the NOAA/NDBC buoy 46026 located in the Gulf of the Farallones (N26-SST), sea surface salinity measured at the Farallon Islands (Far-SSS), and the 39°N Bakun Upwelling Index provided by NOAA with a 3° latitude resolution (BUI). The Net Delta Outflow Index is described: <https://www.water.ca.gov/Programs/Environmental-Services/Compliance-Monitoring-And-Assessment/Dayflow-Data>. We also used the climate indices Multivariate ENSO Index (MEI), PDO, NPGO, and MOCI (Supplementary Tables SM2 and SM3, and Figs. SM4–SM9). Environmental data had a monthly resolution, which we smoothed to seasonal values using

averages across months or running monthly means. To explore the use of these data as predictors of SSB, we took 3-month running means of data one month at a time from May to December, except for MOCI which already had a 3-month resolution. We examined running means in environmental conditions using time lags of 1–3 years to explore leading relationships between YOY abundance and SSB in subsequent years. For this exploratory analysis, we evaluated a total of 297 covariates (11 environmental indices, 9 running means across months [including seasonal averages], and 3 annual lags). While a large number of potential covariates were examined, we used this analysis to select the lags at which covariates appeared best related to SSB, based on correlation coefficients (see below), and then included these in time series models developed using multiple regression.

2.3. Forecasting herring biomass

To date, estimates of the current year SSB have been used for projection of subsequent SSB for SFB herring management. To enhance this approach, we considered how annual indices of SSB were related to herring productivity and temporal environmental variability as well as previous SSB (expressed as $SSB_{\text{lag}1}$). For SSB, the index reflected summed estimates of biomass from December through March ("year" is designated as that of the January considered, i.e., December 1980–March 1981 is assigned as biomass 1981). For production, we averaged monthly CPUE of age-0 fish from trawl surveys designated as April through October (YOY); CPUE age-1 was February through April (Age-1), and CPUE age-2+ (Age-2+) was December–March. During the first year of data collection (1979) only January–March were used since data from the preceding December were not available. SSB and productivity time series had no significant trends through time (see also Thompson et al., 2017). We did not transform SSB used in the model as the original data were only roughly non-normal, and the forecasting model performance was better (higher R^2 and lower Akaike Information Criteria, AIC) using untransformed SSB.

To evaluate potential terms for use in forecasting models, we first explored correlations between SSB and indicators of herring productivity and condition (Table 2) and environmental variability (Table 3). We used Spearman rank correlations and assumed significance when $p < 0.05$. We correlated SSB for each year with productivity and environmental data for lags of up to three years. Subsequently, based on promising correlations, we developed multivariate models of biomass using forward and backward stepwise regression that included select herring indicators (e.g., $SSB_{\text{lag}1}$, $YOY_{\text{lag}2}$, $YOY_{\text{lag}3}$; see Results) and one environmental variable at a time. We included not only the environmental indices with best correlations (higher correlations, lowest p -values and consistent correlations in more than two contiguous 3-month averages), but also indices that have been shown to influence herring in other locations and seasons (i.e., salinity).

To select the best model we considered the AIC and adjusted R^2 values for all years from 1991 through 2016 (see below for justification of this period). We tested the uncertainty in model selection using a jackknifing technique where we removed one year at a time and re-computed AIC and adjusted R^2 statistics. Jackknifing is a standard technique to estimate biases in model selection and parameter estimation in regression; the reader is referred to Wu (1986) for more in-depth descriptions of this procedure. We also evaluated the skill of the best model by predicting values for all years and subsequently removed one year of data at a time, recalculated the model using the remaining years, and then used this model to predict the removed year value (i.e., a cross-validation procedure, see Kleinbaum et al., 1988). We then quantified the skill of prediction (i.e., predictive error, Table 4) by averaging the error of the predicted values over all years versus observed over all years (expressed in percentage). All analyses were done in Matlab v.2017.

Table 3

Spearman rank correlations (ρ) and R^2 between SSB and environmental indicators for the periods 1979–2016 and 1991–2016. Only nominally significant correlations ($p < 0.05$) are shown. Months (3-month averages) with significant correlations and lags are indicated in parentheses. An asterisk (*) indicates significant correlations for lags of 2 and 3 years.

Indicator	1979–2016	1991–2016
Trawl-T	–	–
Trawl-S	–	$\rho = 0.48$ $R^2 = 0.08$
Outflow	–	(Aug–Oct, lag 3) $\rho = -0.59$ $R^2 = 0.13$
Far-SSS	–	(Jul–Sep, lag 3) –
N26-SST	–	$\rho = -0.41$ $R^2 = 0.1$ (May–Jul, lag 3)
BUI	$\rho = -0.41$ $R^2 = 0.18$ (Oct–Dec, lag 3)	–
MEI	–	–
PDO	–	$\rho = -0.46$ $R^2 = 0.11$ (Apr–Jun, lag 3)
NPGO	–	$\rho = 0.45$ $R^2 = 0.15$ (Jul–Sep, lag 3)*
MOCI	–	$\rho = -0.46$ $R^2 = 0.14$ (Jul–Sep, lag 3)

Table 4

Regression model results and statistics used to predict SFB herring SSB, 1991–2016. F-statistics, p-values, adjusted R^2 , and AIC values are given for forward stepwise regression (backward selection procedures resulted in the same models). Predictive error is the averaged prediction errors from the cross-validation. Lag in years for each term is indicated with subscript. Fall MOCI correspond to the months October to December, and N26-SST are values from the 3-month average from September to November.

Term	Coefficient	t-stat	p-value
SSB ~ SSB_{lag1}			
F _{1,22} = 11.3, p-value < 0.01, Adjusted R ² = 0.31, AIC = 204, Predictive Error = 119%			
SSB _{lag1}	0.57	3.36	< 0.005
SSB ~ YOY_{lag3}			
F _{1,23} = 31.1, p-value < 0.0001, Adjusted R ² = 0.56, AIC = 201, Predictive Error = 77%			
YOY _{lag3}	0.025	6.42	< 0.0001
SSB ~ SSB_{lag1} + YOY_{lag3}			
F _{2,21} = 16.6, p-value < 0.0001, Adjusted R ² = 0.58, AIC = 193, Predictive Error = 81%			
SSB _{lag1}	0.25	1.58	0.13
YOY _{lag3}	0.02	3.85	< 0.001
SSB ~ SSB_{lag1} + YOY_{lag3} + (Fall MOCI_{lag1})²			
F _{3,20} = 16.3, p-value < 0.0001, Adjusted R ² = 0.67, AIC = 188, Predictive Error = 64%			
SSB _{lag1}	0.31	2.15	< 0.05
YOY _{lag3}	0.02	3.13	< 0.01
(Fall MOCI _{lag1}) ²	-1.1	-2.59	< 0.05
SSB ~ SSB_{lag1} + YOY_{lag3} + N26-SST_{lag1}			
F _{3,20} = 14.6, p-value < 0.0001, Adjusted R ² = 0.64, AIC = 190, Predictive Error = 63%			
SSB _{lag1}	0.28	1.90	0.07
YOY _{lag3}	0.018	3.57	< 0.005
N26-SST _{lag1}	-6.28	-2.17	< 0.05

3. Results

SSB showed less variability prior to 1990, particularly during the mid to late 1980s (Fig. 1). After 1990, variability increased (see also Thompson et al., 2017). The interannual coefficient of variation of the early period (1980–1989) was 30% vs. 97% after 1990. Even when 2006 was removed (a data point one order of magnitude above any other and therefore considered an outlier), the coefficient of variation was 78% for the period 1991–2016. Average biomass for the second period dropped to 28.9 thousand metric tons (Kmt) versus 45.1 Kmt (24.9 Kmt without 2006) in the previous period. There was no significant linear trend ($p > 0.05$) in the entire time series due to the second period of strong variability. While we focused on the period 1991–2016 for forecasting, we tested the correlation between biomass and indicators in two periods: the entire data period (1979–2016) and the period with higher variability (1991–2016). This result corresponds to a well-known shift in biological systems during the late 1980s to early 1990s (Hare and Mantua, 2000; Sydeman et al., 2001; Thompson et al., 2017).

Correlations with SSB_{lag1} were stronger for the entire period than for the period after 1990, which is consistent with the lower variability of SSB before 1990 (Table 2). This pattern indicates that SSB_{lag1} became less reliable as a forecasting indicator after ca. 1990. Correlations of SSB with YOY were similar for both periods at lag 2 years, but higher for the second period for lag 3 years (Fig. 2), indicating that this relationship became stronger through time. No correlations with the condition index (HCI) and CPUE age-2+ were found.

Correlations between SSB and environmental indicators from 3-month averages at different lags showed that for the entire period (1979–2016) only the upwelling index (BUI) had a nominally significant correlation at lag 3 years (Table 3). In contrast, for the period 1991–2016 there were significant correlations with many of the environmental indices from San Francisco Bay, the Gulf of the Farallones, and large-scale climate indices (Table 3), however, notably, not with BUI. Trawl-T, Far-SSS and MEI did not show significant correlations with SSB for either period. All indicators that correlated significantly in the second period did so at lag 3 years, except NPGO, which was also correlated at lag 2 years.

We tested multiple regression models in the following order: 1) two univariate models, one with SSB_{lag1} as a predictor and another with YOY_{lag3} as a predictor (Table 4, Fig. 3), 2) a model with both of these predictors, and 3) multivariate models that include these two predictors plus one environmental indicator. We used the period 1991–2016 in the regression models, as it is the period with best environmental correlations and is more relevant for present-day forecasting. Statistics for the first two univariate models, the bivariate model and the best of the multivariate models, are shown in Table 4. YOY_{lag3} was the best single predictor of SSB ($R^2 = 0.56$), but the model fit improved by adding SSB_{lag1} ($R^2 = 0.58$) and an environmental variable (Fall, i.e., October–December, MOCI): adjusted R^2 increased to 0.67. Note that the model included MOCI squared, which may reflect a non-linear effect of the environmental terms. Fig. 3 shows the modeled SSB versus observations. Including other environmental variables in regressions did not improve model fit or the explanatory power.

A jackknife analysis of model selection based on AIC and adjusted R^2 criteria was also performed. In this analysis, we removed one year at a time, and recalculated the AIC and adjusted R^2 values for the five model structures shown in Table 4; in all, a total of 130 models were estimated. Jackknifing indicated that in 24 of 26 instances (92.3%), the model including YOY_{lag3}, SSB_{lag1}, and Fall MOCI was selected. Jackknifing also gave an estimation of the accuracy of the model predictions, which we report as the average predicted error (Table 4). The model using only SSB_{lag1} had an average predicted error of 119%, while using only YOY_{lag3} reduced that error to 77%. The lowest predictive error, 64%, was found for the model including SSB_{lag1}, YOY_{lag3}, and MOCI. Skill was relatively similar for a model including buoy (N26) SST

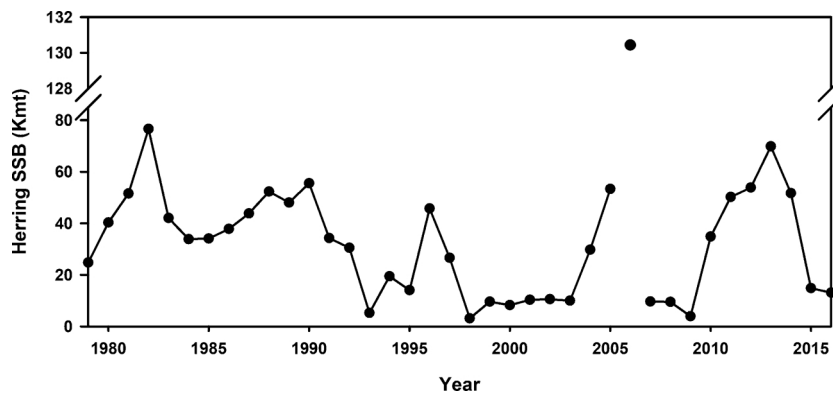


Fig. 1. Herring spawning stock biomass (SSB, Kmt) for the San Francisco Bay estimated from egg deposition surveys, summed from December to March each year. Note the anomalously high SSB in 2006.

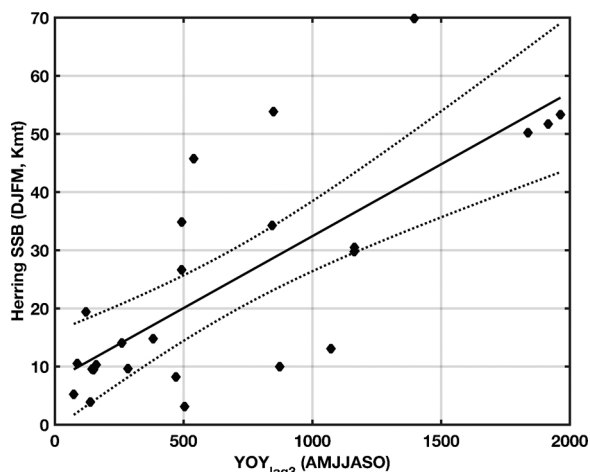


Fig. 2. Linear model predicting herring SSB using YOY_{lag3} as the independent variable, for the period 1991–2015. The black line shows the predicted values and the dashed lines indicate the 95% confidence intervals. YOY_{lag3} explains 56% of herring stock biomass in the current year.

instead of MOCI.

4. Discussion

We hypothesized that lagged herring productivity and ocean conditions could be used to forecast herring fluctuations in the San Francisco Bay population, indexed by SSB. The best model we

developed indicated that SSB depends on the abundance of the spawning population from the previous year, productivity as indicated by YOY from three years prior, and environmental conditions in the fall season immediately prior to spawning, which are best proxied by the Multivariate Ocean Climate Index (MOCI). The fall MOCI indicates that environmental conditions from October–December, prior to the herring spawning season, contributes to predicting SSB; this relationship may reflect the effects of the environment on spawners and their body condition, though we did not find a relationship between measures of body condition and SSB. Overall, this model explained 67% of the variance in SFB herring SSB from 1991 through 2016. A similar model, including SST from NOAA buoy N26 (September through November) instead of the MOCI, explained 64% of the variance, but was not selected based on AIC criteria or predictive skill. These models utilize environmental data coincident with the spawning season, whereas data preceding the spawning season may be of more benefit to management, despite having slightly lower explanatory power and skill.

Models including only SSB or YOY had lower explanatory power (31% and 56%, respectively), but were significant, regardless of inclusion of environmental parameters. Therefore, we conclude that herring population parameters are more important than environmental parameters to prediction, and could be used in annual stock assessments. Current fishing quotas are based on the prior season’s estimate of SSB, with harvest percentages set to 5% since 2010–11 (CDFW, 2016). Thus, our approach could enhance the current stock assessment and harvest control process, which involves making an annual estimate of abundance from the winter egg deposition surveys (Watters et al., 2004). Overall, the variance explained by our model was similar to other models developed for herring populations worldwide (e.g.,

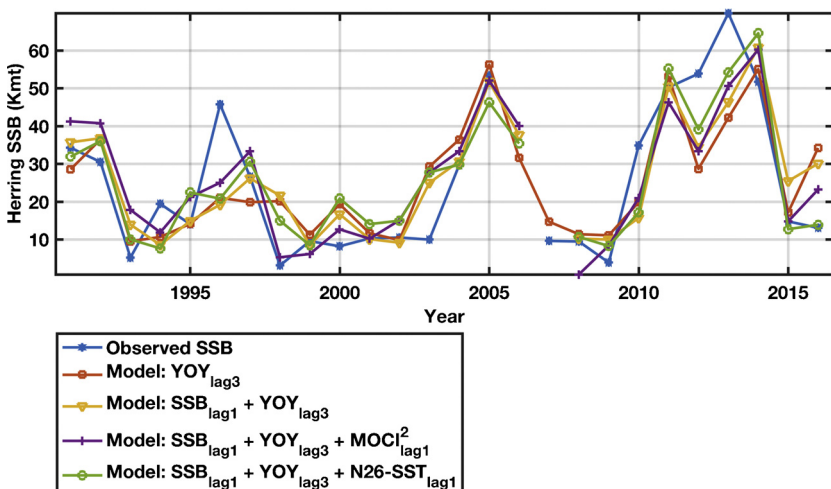


Fig. 3. Observed and modeled SFB SSB time series for 1991–2016. Note there is no observation for 2006, but predicted values indicate ~37 K metric tons (Kmt). Observed SSB is shown in blue and other colors indicate the different models for SSB that include the terms YOY_{lag3} , SSB_{lag1} , Fall $MOCI_{lag1}$, and NDBC Buoy 46026 September–November SST_{lag1} . (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Axenrot and Hansson, 2003; Cardinale et al., 2009; Schweigert et al., 2010). For example, using a similar 3-variable approach with lagged SSB, YOY productivity, and the environment, Axenrot and Hansson (2003) explained a total of 93% of the variation in the incoming year-class. YOY were most strongly correlated with adjusted $R^2 = 0.42$, compared to our adjusted $R^2 = 0.57$ for the period 1991–2017; SSB was the weakest predictor. They used the North Atlantic Oscillation (NAO), a large-scale climate index to proxy environmental conditions important to herring recruitment, finding a strong relationship with adjusted $R^2 = 0.35$, compared to adjusted $R^2 = 0.09$ for the best environmental variable in our study. Mechanistically, Axenrot and Hansson argued that food availability and mild spring conditions, factors conducive to fecundity and larval growth and survival, were behind the correlation with the NAO, but they also considered that mild winters could affect the phenology (timing) of spawning, a possibility we consider for SFB spawners as well.

4.1. Stationarity in predictor variables

SSB_{lag1} and current SSB were better related over the entire time series (1979–2016), which included years of relative stability, rather than during the latter period of greater population variability (1991–2016). The correlations between SSB_{lag1} and current SSB explained 40% of the variance from 1979 to 2016, in comparison to 34% of the variance from 1991 to 2016, indicating no substantial change in the predictive power of this relationship over time. This modest change could be reflective of greater serial correlation in SSB in the early period, which is apparent upon examination of the data.

In contrast, productivity (YOY) was a better predictor of SSB from 1991 through 2016 (57% of the variance explained), compared to the overall time series, 1979–2016 (34% explained). Unlike SSB_{lag1} , YOY explained only 2% of the variance in SSB in the early period. While SSB_{lag1} and productivity showed relationships with SSB throughout the history of SFB herring population monitoring, only SSB_{lag1} showed reasonable stationarity, a key characteristic for predictive models to be used in a management context. Mechanistically, the 3-year lagged correlation of YOY with SSB is consistent with maturity at age 2–3 years for the SFB population (O'Farrell and Larson, 2005).

4.2. Environmental covariates

The environmental variables MOCI and SST are indicators of ocean conditions prior to spawning, leading SSB measurements, but only on the scale of months. Both MOCI and SST are proxies for coastal upwelling and current transport processes, including water mass incursions from the south and north (Checkley and Barth, 2009). Oceanic water temperatures and regional climate influences co-vary with conditions within SFB, and indicate that warmer temperatures lead to lower SFB herring SSB. The variance explained in correlations between SSB and environmental indicators increased after 1990, suggesting that herring became more sensitive to environmental variability after the regime shift of the late 1980s/early 1990s (Hare and Mantua, 2000). Sydeman et al. (2013) showed that ocean-climate variability associated with the NPGO shifted after 1990, so the change in herring responsive to the environment may be related to strengthening of the NPGO at that time. Cloern et al. (2010) also indicated a general increase in the abundance of a suite of species in SFB around 1990, also possibly mediated by changes in the NPGO. The environmental term in our model improved estimates over a model using only herring population indicators, but its contribution was quite small (~10%). In short, warm ocean temperatures appear to impact herring biomass negatively; this conclusion is consistent with previous results indicating that herring populations in the NE Pacific generally prefer colder conditions (e.g., Schweigert et al., 2010).

Conditions in SFB itself were not included in our forecasting model. This result may mean that ocean conditions are more important than

bay conditions in setting year class strength and explaining variation in SSB, but it is likely that environmental factors in both estuarine and marine habitats are important (O'Farrell and Larson, 2005; Reum et al., 2011). Some conditions, such as temperature, co-vary between the ocean and bay, making it difficult to resolve which habitat is more important. Kimmerer (2002) found higher SFB herring egg production and egg survival during periods of high outflow from the delta (more fresh water). However, we found no correlations with SFB delta inflow around the timing of spawning at 0 or 1-year lags. Salinity showed significant, although weak correlations with SSB at a 3-year lag, which suggests a possible influence on survival, perhaps for the YOY age class. Laboratory studies indicate higher survival of larvae at lower levels of salinity (Griffin et al., 2004). Significant correlations between salinity and YOY were also found for a lag of one year ($\rho = 0.55$, $p < 0.01$, previous year April–June). However, this correlation was with salinity in the Gulf of the Farallones, not in SFB; although salinity in these two locations co-varies (see Fig. SM5), salinity in the gulf is related to oceanographic processes, not only SFB discharge processes.

Mechanistically, the shift in herring SSB variance after ~1990, the relationships established for herring and other species (Cloern et al., 2010) both within and outside SFB, and the general importance and role of upwelling in the region (e.g., García-Reyes et al., 2013) suggest that productivity, food supply, and trophic relationships are possible mechanisms of response between the environment and SFB herring (see also Ito et al., 2015; Thompson et al., 2017). However, as noted above, the environmental component to predicting SSB was small and (perhaps more importantly) short-term, with fall MOCI immediately preceding the winter spawning season negatively influencing biomass. This timing suggests that a short-term behavior mechanism may be at work. Indeed, in this case it is hard to imagine how a longer-term trophic mechanism could lead to lower or higher biomasses on the scale of a few months. Instead positive (i.e., warmer) MOCI values in fall may affect the timing of migration into SFB, leading to changes in SSB. Warmer conditions may lead to a delayed or deferred migration into SFB and spawning effort. If sufficiently delayed, overall annual SSB could be reduced. High resolution information on timing of herring spawning would be required to determine how environmental conditions affect migration patterns, but given the short-term nature of the response and the fact that other diadromous fish are known to trigger migration to spawning ground in relation to environmental conditions (e.g., Mundy and Evenson, 2011), we consider this mechanism plausible for SFB herring.

4.3. Age structure and forecasting

Our model of herring SSB functions partly because the vast majority of the SFB population is comprised of younger age classes (ages 2 and 3), representing newly-recruited fish (Fig. 4). Therefore, we interpret our model as effectively predicting recruitment/year class strength. Other models focusing on year class strength have also been reasonably successful (e.g., Axenrot and Hansson, 2003). This interpretation is supported by the fact that the YOY_{lag3} relationship was selected in the final best model. By age 3, most of the fish would have matured, while the proportion of the population that is mature at age 2 may be more variable between years, depending upon environmental conditions. We do not know, however, if maturity-at-age has changed over time.

As can also be seen in Fig. 4, there has been a modest long-term decrease in the proportion of fish aged 6+ years over the study period, which suggests truncation of the age structure in this population. Other herring populations are typically comprised of a larger percentage of fish in older age classes (e.g., Hay et al., 2008). Corresponding with the decrease of older fish, the proportion of 2- and 3-year-old fish appears to have increased through time, but more research is needed to determine if this apparent pattern is robust. A complexity in understanding evident changes in age structure is that the proportion of 4- and 5-year-old fish appears to increase periodically after major El Niño Southern Oscillation (ENSO) events have affected the central California

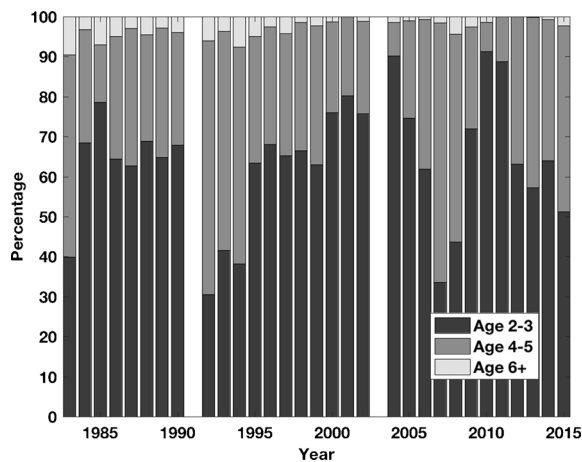


Fig. 4. Herring population age structure expressed as a percentage of total population observed: ages 2–3 years (black), 4–5 years (dark grey), and 6–9 years (light grey).

Current Ecosystem (e.g., 1992–1994, 1998–2000; Jacox et al., 2016). This pattern suggests that ENSO negatively impacts recruitment/year class strength, with a resulting short-term increase in the relative proportion of age-4 and age-5 fish in the population. It is also possible ENSO is affecting maturation as reduced body condition is observed with the ocean warming that occurs during ENSO (CDFW, 2017b).

4.4. Implications for management

Future research on age structure, potential age truncation effects, and the effects of fishing mortality in general is warranted, both with respect to forecasting population abundance as well as assessing potential fisheries impacts. In particular, we think that investigating the nexus of environmental influences and fisheries effects could be fruitful for management. While it is a reasonably clear hypothesis that environmental events affect age structure, some of these changes may be aliased by fisheries effects. For example, the fishery has progressively reduced mesh size in order to maintain catch, but as a consequence, smaller (and younger) fish have been targeted (CDFW, 2017a,b). Therefore, models of age structure for this population could provide interesting advice for management regarding mesh size. Relative to our forecasting model, understanding how the effects of age structure may be influencing the relationship between YOY_{lag3} and SSB would provide insight into the potential long-term value of this model for management.

This study is significant as herring population fluctuations are difficult to predict. Moreover, for our study population, a new Fisheries Management Plan is under development by the State of California, and early forecasts of abundance are needed for application of harvest control rules. While our model development was successful overall, model predictions were not always accurate. In particular, low SSB values (e.g., 2003 and 2016) were not always well predicted. Given these kinds of constraints, as well as the apparent non-stationarity in predictive relationships, we recommend that this model be retested annually. Our model has several notable advantages with respect to retesting: it is very simple, based on readily available information, and has relatively high predictive power. CDFW collects information on herring YOY production annually and plans to continue this effort for the foreseeable future. The environmental data used in the model are also regularly updated and readily available. The model itself can be easily run in simple spreadsheet programs. Most importantly, however, the model provides a 3-year lead to managers on potential herring year class strength. Assuming that age structure remains consistent into the future, model forecasts of SSB could be reasonably applied in harvest control rules to better manage the fishery for both the stock and local

ecosystem.

Funding sources

This project was funded by the Gordon and Betty Moore Foundation and National Fish and Wildlife Foundation, administered by SeaChange Analytics, Inc.

Acknowledgements

We thank S. Valencia for facilitating this project and CDFW for contributing data for analysis. We acknowledge members of the SFB Herring FMP Steering Committee for supporting this effort.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.fishres.2018.04.020>.

References

- Alheit, J., Hagen, E., 1997. Long-term climate forcing of European herring and sardine populations. *Fish. Oceanogr.* 6, 130–139.
- Anderson, C.N.K., Hsieh, C.H., Sandin, S.A., Hewitt, R., Hollowed, A., Beddington, J., May, R.M., Sugihara, G., 2008. Why fishing magnifies fluctuations in fish abundance. *Nature* 452, 835–839.
- Axenrot, T., Hansson, S., 2003. Predicting herring recruitment from young-of-the-year densities, spawning stock biomass, and climate. *Limnol. Oceanogr.* 48, 1716–1720.
- Beamish, R.J., Benson, A.J., Sweeting, R.M., Neville, C.M., 2004. Regimes and the history of the major fisheries off Canada's west coast. *Prog. Oceanogr.* 60, 355–385.
- CDFW, 2016. Summary of the 2015–16 Pacific Herring Spawning Population and Commercial Fisheries in San Francisco Bay. August 2016 Final Report. California Department of Fish and Wildlife, Aquaculture and Bay Management Project, Herring Management and Research Marine Region 17 pp. Available as PDF. <https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=135492&inline> downloaded from <https://www.wildlife.ca.gov/Fishing/Commercial/Herring/Season-Summaries>.
- CDFW, 2017a. San Francisco Bay Pacific Herring Spawning Stock and Commercial Fishery Management Overview. March 2017 Final Report. California Department of Fish and Wildlife, Aquaculture and Bay Management Project, Herring Management and Research Marine Region 11 pp. Unpublished report.
- CDFW, 2017b. 2016–17 Summary of the Pacific Herring Spawning Population and Commercial Fisheries in San Francisco Bay. July 2017 Final Report. California Department of Fish and Wildlife, Aquaculture and Bay Management Project, Herring Management and Research Marine Region 15 pp. Available as PDF. <https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=148241&inline> downloaded from <https://www.wildlife.ca.gov/Fishing/Commercial/Herring/Season-Summaries>.
- Cardinale, M., Mollmann, C., Bartolino, V., Casini, M., Kornilovs, G., Raid, T., Margonski, P., Grzyb, A., Raitaniemi, J., Grohler, T., Flinkman, J., 2009. Effect of environmental variability and spawner characteristics on the recruitment of Baltic herring *Clupea harengus* populations. *Mar. Ecol. Prog. Ser.* 388, 221–234.
- Checkley, D.M., Barth, J.A., 2009. Patterns and processes in the California current system. *Prog. Oceanogr.* 83, 49–64.
- Cloern, J.E., Hieb, K.A., Jacobson, T., Sanso, B., Di Lorenzo, E., Stacey, M.T., Largier, J.L., Meiring, W., Peterson, W.T., Powell, T.M., Winder, M., Jassby, A.D., 2010. Biological communities in San Francisco Bay track large-scale climate forcing over the North Pacific. *Geophys. Res. Lett.* 37, L21602.
- Cushing, D.H., 1961. On the failure of the Plymouth herring fishery. *J. Mar. Biol. Assoc. U.K.* 41, 799–816.
- Essington, T.E., Moriarty, P.E., Froehlich, H.E., Hodgson, E.E., Koehn, L.E., Oken, K.L., Siple, M.C., Stawitz, C.C., 2015. Fishing amplifies forage fish population collapses. *Proc. Natl. Acad. Sci.* 112, 6648–6652.
- Feyrer, F., Cloern, J.E., Brown, L.R., Fish, M.A., Hieb, K.A., Baxter, R.D., 2015. Estuarine fish communities respond to climate variability over both river and ocean basins. *Glob. Change Biol.* 21, 3608–3619.
- Fish, M., Messineo, J., Hieb, K., 2012. 2010 Bay Study Fishes Annual Status and Trends Report. Interagency Ecological Program Newsletter, Interagency Ecological Program. Available as PDF <https://nrm.dfg.ca.gov/FileHandler.ashx?DocumentID=44774> downloaded from <http://www.dfg.ca.gov/delta/data/baystudy/bibliography.asp>.
- Fleming, K., 1999. Chapter 7: clupeidae. In: Orsi, J. (Ed.), Report on the 1980–1995 Fish, Shrimp, and Crab Sampling in the San Francisco Estuary, California. California Department of Fish and Game, pp. 151–166. Technical Report 63, Available as PDF. http://www.water.ca.gov/LegacyFiles/iep/docs/tech_rpts/Clupeidae.pdf.
- Freon, P., Cury, P., Shannon, L., Roy, C., 2005. Sustainable exploitation of small pelagic fish stocks challenged by environmental and ecosystem changes: a review. *Bull. Mar. Sci.* 76, 385–462.
- García-Reyes, M., Sydeman, W.J., 2017. California multivariate ocean climate indicators (MOCI) and marine ecosystem dynamics. *Ecol. Indiv.* 72, 521–529.
- García-Reyes, M., Sydeman, W.J., Thompson, S.A., Black, B.A., Rykaczewski, R.R., Thayer, J.A., Bograd, S.J., 2013. Integrated assessment of wind effects on Central

- California's pelagic ecosystem. *Ecosystems* 16, 722–735.
- Griffin, F.J., Brenner, M.R., Brown, H.M., Smith, E.H., Vines, C.A., Cherr, G.N., 2004. Survival of Pacific herring larvae is a function of external salinity. In: Feyrer, F., Brown, L.R., Brown, R.L., Orsi, J.J. (Eds.), *Early Life History of Fishes in the San Francisco Estuary and Watershed*. American Fisheries Society, Symposium 39. Bethesda, Maryland. pp. 37–46.
- Hare, S.R., Mantua, N.J., 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Prog. Oceanogr.* 47, 103–145.
- Hay, D.E., Rose, K.A., Schweigert, J., Megrey, B.A., 2008. Geographic variation in North Pacific herring populations: pan-Pacific comparisons and implications for climate change impacts. *Prog. Oceanogr.* 77, 233–240.
- Hjort, J., 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. In: *Conseil International pour l'Exploration de la Mer. Rapports et Proces-verbaux des Reunions* 20. pp. 1–228.
- Hollowed, A.B., Barange, M., Beamish, R.J., Brander, K., Cochrane, K., Drinkwater, K., Foreman, M.G.G., Hare, J.A., Holt, J., Ito, S., Kim, S., King, J.R., Loeng, H., MacKenzie, B.R., Mueter, F.J., Okey, T.A., Peck, M.A., Radchenko, V.L., Rice, J.C., Schirripa, M.J., Yatsu, A., Yamanaka, Y., 2013. Projected impacts of climate change on marine fish and fisheries. *ICES J. Mar. Sci.* 70, 1023–1037.
- Ito, S.-I., Rose, K.A., Megrey, B.A., Schweigert, J., Hay, D., Werner, F.E., Aita, M.N., 2015. Geographic variation in Pacific herring growth in response to regime shifts in the North Pacific Ocean. *Prog. Oceanogr.* 138, 331–347.
- Jacox, M.G., Hazen, E.L., Zaba, K.D., Rudnick, D.L., Edwards, C.A., Moore, A.M., Bograd, S.J., 2016. Impacts of the 2015–2016 El Niño on the California Current System: early assessment and comparison to past events. *Geophys. Res. Lett.* 43, 7072–7080.
- Kimmerer, W.J., 2002. Effects of freshwater flow on abundance of estuarine organisms: physical effects or trophic linkages? *Mar. Ecol. Prog. Ser.* 243, 39–55.
- Kleinbaum, D.G., Kupper, L.L., Muller, K.E., 1988. *Applied Regression Analysis and Other Multivariate Methods*, 2nd edition. PWS-KENT Publishing Company, Boston, Massachusetts.
- Lindgren, M., Mollmann, C., Nielsen, A., Brander, K., MacKenzie, B.R., Stenseth, N.C., 2010. Ecological forecasting under climate change: the case of Baltic cod. *Proc. R. Soc. B* 277, 2121–2130.
- Mundy, P.R., Evenson, D.F., 2011. Environmental controls of phenology of high-latitude Chinook salmon populations of the Yukon River, North America, with application to fishery management. *ICES J. Mar. Sci.* 68, 1155–1164.
- Myers, R.A., 1998. When do environment-recruitment correlations work? *Rev. Fish Biol. Fish.* 8, 285–305.
- Nash, R.D.M., Valencia, A.H., Geffen, A.J., 2006. The origin of Fulton's condition factor – setting the record straight. *Fisheries* 31, 236–238.
- O'Farrell, M.R., Larson, R.J., 2005. Year-class formation in Pacific herring (*Clupea pallasii*) estimated from spawning-date distributions of juveniles in San Francisco Bay, California. *Fish. Bull.* 103, 130–141.
- Poloczanska, E.S., Brown, C.J., Sydeman, W.J., Kiessling, W., Schoeman, D.S., Moore, P.J., Brander, K., Bruno, J.F., Buckley, L.B., Burrows, M.T., Duarte, C.M., Halpern, B.S., Holding, J., Kappel, C.V., O'Connor, M.I., Pandolfi, J.M., Parmesan, C., Schwing, F., Thompson, S.A., Richardson, A.J., 2013. Global imprint of climate change on marine life. *Nat. Clim. Change* 3, 919–925.
- Reum, J.C.P., Essington, T.E., Greene, C.M., Rice, C.A., Fresh, K.L., 2011. Multiscale influence of climate on estuarine populations of forage fish: the role of coastal upwelling, freshwater flow and temperature. *Mar. Ecol. Prog. Ser.* 425, 203–215.
- Rice, J., Duplisea, D., 2014. Management of fisheries on forage species: the test-bed for ecosystem approaches to fisheries. *ICES J. Mar. Sci.* 71, 143–152.
- Ricker, W.E., 1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Board Calif.* 191, 1–382.
- Rose, K.A., Megrey, B.A., Hay, D., Werner, F., Schweigert, J., 2008. Climate regime effects of Pacific herring growth using coupled nutrient-phytoplankton-zooplankton and bioenergetics models. *Trans. Am. Fish. Soc.* 137, 278–297.
- Schweigert, J.F., Boldt, J.L., Flostrand, L., Cleary, J.S., 2010. A review of factors limiting recovery of Pacific herring stocks in Canada. *ICES J. Mar. Sci.* 67, 1903–1913.
- Siple, M.C., Francis, T.B., 2016. Population diversity in Pacific herring of the Puget Sound, USA. *Oecologia* 180, 111–125.
- Stocker, M., Noakes, D.J., 1988. Evaluating forecasting procedures for predicting Pacific herring (*Clupea harengus pallasii*) recruitment in British Columbia. *Can. J. Fish. Aquat. Sci.* 45, 928–935.
- Sydeman, W.J., Hester, M., Thayer, J.A., Gress, F., Martin, P., Buffa, J., 2001. Climate change, reproductive performance and diet composition of marine birds in the southern California Current System, 1967–1997. *Prog. Oceanogr.* 49, 309–329.
- Sydeman, W.J., Santora, J.A., Thompson, S.A., Marinovic, B., Di Lorenzo, E., 2013. Increasing variability in North Pacific climate relates to unprecedented ecosystem variability off California. *Glob. Change Biol.* 19, 1662–1675.
- Sydeman, W.J., Thompson, S.A., García-Reyes, M., Kahru, M., Peterson, W.T., Largier, J.L., 2014. Multivariate ocean-climate indicators (MOCI) for the central California Current: environmental change, 1990–2010. *Prog. Oceanogr.* 120, 352–369.
- Szoboszlai, A.I., Thayer, J.A., Wood, S.A., Sydeman, W.J., Koehn, L.E., 2015. Forage species in predator diets: synthesis of data from the California Current. *Ecol. Inform.* 29, 45–56.
- Thompson, S.A., Sydeman, W.J., Santora, J.A., Black, B.A., Calambokidis, J., Peterson, W.T., Bograd, S.J., 2012. Linking predators to seasonality of upwelling: using food web indicators and path analysis to infer trophic connections. *Prog. Oceanogr.* 101, 106–120.
- Thompson, S.A., Sydeman, W.J., Thayer, J.A., Weinstein, A., Krieger, K.L., 2017. Trends in the Pacific herring (*Clupea pallasii*) metapopulation in the California Current Ecosystem. *Calif. Cooperative Ocean. Fish. Invest. Rep.* 58, 77–94.
- Watanabe, Y., 2007. Latitudinal variation in the recruitment dynamics of small pelagic fishes in the western North Pacific. *J. Sea Res.* 58, 46–58.
- Watters, D.L., Brown, H.M., Griffin, F.J., Larson, E.J., Cherr, G.N., 2004. Pacific herring spawning grounds in San Francisco Bay: 1973–2000. *Am. Fish. Soc. Symp.* 39, 3–14.
- Williams, E.H., Quinn, T.J., 2000a. Pacific herring, *Clupea pallasii*, recruitment in the Bering Sea and north-east Pacific Ocean, I: relationships among different populations. *Fish. Oceanogr.* 9, 285–299.
- Williams, E.H., Quinn, T.J., 2000b. Pacific herring, *Clupea pallasii*, recruitment in the Bering Sea and north-east Pacific Ocean, II: relationships to environmental variables and implications for forecasting. *Fish. Oceanogr.* 9, 300–315.
- Wu, C.F.J., 1986. Jackknife, bootstrap, and other resampling methods in regression analysis. *Ann. Stat.* 14, 1261–1295.