



# Local Watershed Properties Cannot Explain Divergent Dynamics of Pacific Herring in an Urbanizing Estuary

Leah R. Davis<sup>1</sup> · Fabienne Urfer<sup>2</sup> · Timothy E. Essington<sup>2</sup> · Blake E. Feist<sup>3</sup> · Tessa B. Francis<sup>4</sup>

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## Abstract

Pacific herring (*Clupea pallasii*) is a foundational species in Puget Sound (Washington State, U.S.A.) and is subject to many anthropogenic threats. We assessed the overall status of the Puget Sound Pacific herring sub-stock complex and asked whether watersheds with less urban or agricultural land cover, less impervious surface, and lower human density were associated with better stock status. To this end, we developed multiple metrics of sub-stock population status; characterized watershed properties with respect to land use/land cover, percent impervious surfaces, and human density; and used statistical model selection to evaluate the weight of evidence in support of our hypotheses. Overall, the status of sub-stocks was poor; metrics for most sub-stocks indicate a decline from 1996–2021. However, the status metrics of sub-stocks were not related to recent (2016) watershed characteristics or the rate of change in watershed characteristics from the mid-1990s to 2016. While the cumulative effects of local human land use throughout Puget Sound may be contributing to the deterioration of spawning biomass, these results also suggest that other drivers that operate at larger scales (e.g., predation, disease, climate) are likely important.

**Keywords** Impact assessment · Ecosystem-based management · Forage fish · Watersheds

## Introduction

Conservation and restoration efforts are increasingly taking a more holistic, ecosystem-based approach to guide activities to protect or reverse declines in key species or biodiversity. In practice, the application of ecosystem approaches requires a fundamental understanding of the benefits and

consequences of human activities and the ecosystem services that are subsequently impacted (Tallis et al. 2010; Guerry et al. 2012; Halpern et al. 2013). This can be challenging in many ecosystems where linkages among components are complex and poorly understood. Furthermore, it is difficult to unravel the linkages between human activities and ecosystem response when the ecosystem is subject to multiple human disturbances (Ban et al. 2010; Hodgson et al. 2019). Conservation and restoration resources can be wasted on ineffectual investments when the links between human activities and ecosystem responses are poorly understood.

The Salish Sea consists of inland marine waters that span Washington State and British Columbia. The southern portion of the Salish Sea, Puget Sound, has been subject to multiple anthropogenic and natural changes over the past five decades (Essington et al. 2021; Puget Sound Partnership 2010). These include changes in local eelgrass extent (Shelton et al. 2017), armoring of shorelines (Williams et al. 2021), a near-doubling in the regional human population since 1990, increased abundance of pinnipeds (Jeffries et al. 2003), increased hatchery production of Pacific salmon, and an approximately 1 °C increase in annual average surface sea temperature (Essington et al. 2021).

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Leah Davis, Fabienne Urfer, and Timothy E. Essington are joint first authors.

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✉ Timothy E. Essington  
essing@uw.edu

<sup>1</sup> Department of Biological Sciences, Simon Fraser University, Burnaby, B.C. V5A 1S6, Canada

<sup>2</sup> School of Aquatic and Fishery Sciences, University of Washington, Seattle, WA 98195, U.S.A.

<sup>3</sup> Conservation Biology Division, Northwest Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration, Seattle, WA 98112, U.S.A.

<sup>4</sup> Puget Sound Institute, University of Washington, Tacoma, WA 98421, U.S.A.

While much attention has been paid to culturally significant species such as killer whales (*Orcinus orca*) and Chinook salmon (*Oncorhynchus tshawytscha*), less attention has been paid to declines in critical prey species such as Pacific herring (*Clupea pallasii*) over the past several decades (Greene et al. 2015; Siple et al. 2017).

Pacific herring are a forage fish species that play important ecological roles as prey to marine mammals, fishes (including salmonids), and seabirds (Lance and Thompson 2005; Lance and Jeffries 2006; Duffy et al. 2010; Lance et al. 2012). Consequently, local or regional-scale declines can potentially impair the status of valued predator species. This is particularly true for Chinook salmon and endangered Southern Resident killer whales (National Marine Fisheries Service (NMFS) 2005), as the former feed heavily on Pacific herring and the latter preferentially feed on Chinook salmon (Ford and Ellis 2006). For these reasons, herring spawner biomass is currently viewed as a “vital sign indicator” as a part of the ecosystem-based management approach to recover and protect Puget Sound (Puget Sound Partnership 2021). Commercial fisheries for Pacific herring are limited: catches are not permitted to exceed 10% of estimated spawning biomass (Essington et al. 2021), but rarely approach that limit (Sandell et al. 2016). Fishing is largely restricted to the southern and central basins of Puget Sound.

There are many potential drivers underlying the decline in Pacific herring in Puget Sound (The Salish Sea Pacific Herring Assessment and Management Strategy Team 2018). Mortality rates are likely elevated due to disease outbreaks (Hershberger et al. 2002), exposure to organic pollutants (West et al. 2008), and predation by a large and growing pinniped population (Jeffries et al. 2003). At the same time, nearshore spawning and juvenile nursery habitats may be degraded by shoreline armoring (Dethier et al. 2017) and other forms of habitat degradation (e.g., estuarine wetland habitat loss (Simenstad et al. 2011)). Given the rapid rate of human population growth around Puget Sound (Manson et al. 2022), anthropogenic effects in the watershed are likely to continue or increase in the future. Despite this, we currently have a limited understanding of the relative magnitudes of these threats, how they interact, and which are most responsible for the decline in Pacific herring.

Pacific herring populations are strongly structured, owing to their tendency to annually spawn in multiple distinct and relatively fixed nearshore locations, and at distinct times of year (Ware et al. 2000; Sandell et al. 2016). The State of Washington has been monitoring and assessing herring spawning biomass for up to 50 years (Stick et al. 2014). The differences in spawning behavior create 21 sub-stocks of Pacific herring in Puget Sound that have unique temporal abundance dynamics (Siple and Francis 2016). The Puget Sound sub-stocks

are genetically distinct from the coastal Pacific herring stocks (Gustafson et al. 2006), and some (but not all) are distinct from each other. This structure is related to differences in spawning timing (Petrou et al. 2021) and location (Sandell et al. 2016).

Pacific herring spawn on submerged vegetation in nearshore subtidal and intertidal zones, and this tight connection to shorelines makes them potentially vulnerable to land-based activities that alter and degrade nearshore habitats. The spatial mosaic of population trends and potential vulnerability to land use provides an opportunity to identify some of the landscape features associated with local trends in spawning. Puget Sound herring spawning regions vary widely with respect to natural and anthropogenic land cover and use. This leads to differing levels of potential anthropogenic local disturbances to each sub-stock’s nearshore environment. Land use near spawning regions (particularly urbanization) can affect herring through the changes in run-off that delivers sediment, nutrients, micro-organisms, and toxic contaminants (Mallin et al. 2001; Freeman et al. 2019) and may affect herring egg survival (Shelton et al. 2014). Moreover, although submerged seagrass (principally *Zostera* sp.) areal extent does not show a relationship with urbanization (Shelton et al. 2017), their spatial dynamics are more variable near landscapes with high human density (Munsch et al. 2023).

Here, we evaluate Pacific herring sub-stock dynamics to determine whether there are associations between their status and local land use characteristics. Specifically, we (1) evaluated the status of herring sub-stocks using multiple methods and metrics to provide a robust characterization of the overall status of Puget Sound herring, (2) evaluated differences in landscape characteristics among watersheds adjacent to herring spawning areas and how those have changed through time, and (3) asked whether stock status metrics are related to watershed characteristics or changes therein. While this work does not attempt to identify the causal pathways that link local land use to sub-stock status, it will reveal whether there is any association between land use (or change in land use) and sub-stock status.

## Methods

Our approach was to summarize the status of each of the 21 sub-stocks within Puget Sound using multiple metrics, evaluate the similarity among them, and then ask whether those metrics were associated with local land cover characteristics. Here, we briefly describe the sampling program for herring spawning biomass, the metrics of stock status and watershed characteristics, and the analyses that evaluated how the two were related.

## Study Site

The Salish Sea is an estuary system located along the Pacific Coast of North America, spanning the U.S.A.—Canada Border. Puget Sound refers to the portion of the Salish Sea that lies within the U.S.A., Washington State (Fig. 1). Puget Sound is a fjord-like estuary, receiving marine water via the Strait of Juan de Fuca. Maximum tidal range varies by location, exceeding 4 m in the southern portions of Puget Sound and approximately 2 m at more northern locations (Mofjeld and Larsen 1984). Water circulation is complex owing to the presence of sills, multiple channels, and embayments (MacCready et al. 2021). Peak tidal currents are high (1–3 m/s) in channels but are generally lower (ca. 0.5 m/s) within larger basins. Water residence time is approximately 150 days (MacCready et al. 2021). A summary of relevant anthropogenic and natural changes in Puget Sound is provided in (Essington et al. 2021).

## Spawning Herring Biomass Time Series

Annual estimates of herring spawning biomass were calculated using spawn deposition surveys, described in detail by Stick et al. (2014). Briefly, spawning grounds were sampled

at least bi-weekly by grappling aquatic vegetation along 200–400 m stretches of spawning habitat, and spawn deposition is evaluated as eggs per square inch of substrate. These estimates are converted to spawning biomass (metric tons) via assumptions on the sex ratio and size-specific fecundity, as described by Stick et al. (2014). Prior to 1996, the spawn deposition surveys were also accompanied by paired acoustic and trawl sampling for some of the larger sub-stocks, and the two methods have produced similar estimates (Sandell et al. 2016). The entire data set spans 1973 to the present, but we used only data from 1996 to 2021 because this period includes continuous coverage for 19 of the sub-stocks.

## Spawning Biomass Status Metrics

Population reference points are not readily calculated for these sub-stocks. For that reason, conventional biological reference points used in fisheries management are not available and would not be appropriate for these sub-stocks that are not subject to notable levels of fishing mortality. Instead, we evaluated several empirical and model-based metrics associated with each time series. These range from simple and empirical status metrics to more complex and model-based metrics. Our intention was to examine multiple measures of the status of herring sub-stocks and confirm that our findings regarding associations between status metrics and local watershed land use/land cover were robust to the choice of status metric.

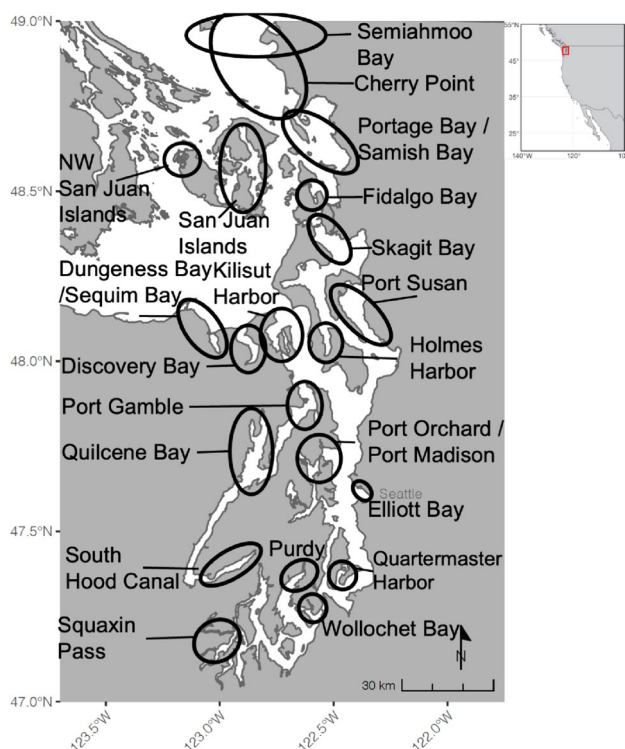
These metrics were as follows:

- Did the lowest observed biomass occur after 2010 (“lowest biomass”)?** This categorical metric was applied to sub-stocks with a population estimate time series that extended prior to 2000. This included all sub-stocks except Purdy, Wollochet Bay, and Elliot Bay.
- Log-ratio of last to first spawning biomass estimate.** Here, we calculated the log (base  $e$ ) ratio of the last estimated biomass estimate available ( $t_{\text{last}}$ ) to the first year of biomass estimate available from 1996 onward ( $t_{\text{first}}$ ):
- Log-ratio of long-term maximum to contemporary mean.** Here, we calculated the log (base  $e$ ) ratio of the maximum observed biomass from 1996 onward to the mean biomass since 2010:

$$\log(B_{t_{\text{last}}} + 1) - \log(B_{t_{\text{first}}} + 1). \quad (1)$$

$$\log(\max_t(B_t) + 1) - \log(\bar{B}_t + 1) \quad t \geq 2010 \quad (2)$$

We note that this is similar to the stock status metric described by Sandell et al. (2016), but they used a longer period to calculate mean biomass and focused on the most recent ca. 25 years of data.



**Fig. 1** Puget Sound Pacific herring spawning locations. Each encircled area shows the extent of spawning locations for each sub-stock. Not all shorelines within each encircled area are used for spawning (Sandell et al. 2016). Inset shows location of study area

- (d) **The fraction of years since 1996 that no spawning biomass was present.** This was the sum of the number of years with estimated biomass equal to 0, divided by the number of annual biomass estimates since 1995 ( $n_t$ ):

$$\frac{1}{n_t} \sum_{t=1996}^{t_{\text{last}}} \begin{cases} 1 & \text{if } B_t = 0 \\ 0 & \text{otherwise} \end{cases} \quad (3)$$

- (e) **Linear regression of biomass vs. time.** For each sub-stock, we fit an ordinary least squares regression of biomass as a function of year and then used the resulting t-statistic of the estimated slope as our metric of the direction of change. We used the t-statistic because this metric accounts for the effect size magnitude, its uncertainty, and the direction of the effect.
- (f) **Sub-stock growth rate from the state-space model.** We estimated a simple density-independent population growth rate parameter from the data (years 1995–2020) using a state-space model to account for both observation and process error.

This model admits that there is variability in two places—in the underlying population dynamics and in the observations in each year. It does this by estimating the “true” state of the sub-stock in each year and relating that to the observed density.

Under this model, the true sub-stock population biomass in each year  $t$  ( $B_t$ ) is

$$B_t = \begin{cases} B_1 & \text{if } t = 1 \\ B_{t-1} e^{\beta + \epsilon_t} & \text{if } t > 1 \end{cases} \quad (4)$$

$$\epsilon_t \sim \text{Normal}(0, \sigma^2)$$

where  $\beta$  is the average population growth rate,  $B_1$  is the population biomass in the first year (1996), and  $\epsilon_t$  are normally distributed random variables with mean 0 and standard deviation equal to  $\sigma$ . The observed biomass in each year ( $B_{t,\text{obs}}$ ) is presumed to be a Tweedie-distributed random variable:

$$B_{t,\text{obs}} \sim \text{Tweedie}(B_t, \phi, p) \quad (5)$$

where  $\phi$  and  $p$  are estimated parameters. When  $p$  is constrained to lie between 1 and 2, the Tweedie family becomes a Poisson-Gamma distribution, which allows for zeros and is otherwise constrained to positive continuous values. This makes the Tweedie distribution more useful than similar likelihood functions (log-normal, Gamma) which are not defined for  $y_i = 0$ .

Parameter estimation was conducted using Template Model Builder (Kristensen et al. 2016) to integrate over the random effects  $\epsilon_t$  and to estimate the fixed effects ( $B_1$ ,  $\beta$ ,  $\sigma$ ,  $\phi$ , and  $p$ ).

A summary of sub-stock population metrics is provided in Table 1. Additionally, we calculated the Pearson correlation between each pair of numerical metrics to evaluate the extent to which each metric provided novel information on sub-stock status (Table 2). The sub-stock growth rate estimates from the state-space model were highly correlated with the other metrics (generally ca. 0.5 or greater magnitude). For that reason, we used growth rate as our primary continuous population status metric in subsequent analyses. Because the lowest biomass was a categorical predictor and could thus not be included in correlation analysis, it was also considered in subsequent analyses.

## Characterizing Watershed Properties

We sought to characterize watershed properties in uplands immediately adjacent to herring spawning sites to capture the most localized effect of watersheds on herring sub-stocks. These localized watershed properties could potentially alter egg/larval survival through effects on water quality or habitat for spawning (e.g., submerged aquatic vegetation). To this end, we first associated each spawning area with the corresponding riverine subbasins (USGS 6th field hydrologic units or HUC12) that were immediately adjacent and characterized the landscape conditions within those subbasins. Landscape conditions were calculated for each subbasin by overlaying them on three different geospatial data layers, representing land use/land cover (LULC), imperviousness, and human population density. We characterized landscape conditions from two periods bookending a two-decade time range: 1996 and 2016. We used Esri ArcGIS (v. 10.1) to intersect the HUC12 subbasins with the three geospatial data layers and to calculate proportions and weighted mean values for the three landscape condition data layers. For the LULC (Office of Coastal Management 2014, 2019) categorical data layer overlay, for each sub-watershed, we calculated the proportion of area that each LULC category represented in each subbasin. We combined several LULC categories into either forest, agriculture, developed, estuarine, and palustrine LULC (Table S1), which reduced the number of LULC categories from 24 to 11. We removed the snow/ice category for analysis because it was always small and did not change from 1996 to 2016. In contrast to the categorical LULC data layer, the human population (available for 1998 and 2016; (Bright and Coleman 2000; Bright et al. 2017)) and surface imperviousness (available for 1996 and 2016; (Wickham et al. 2021)) data layers consisted of continuous, gridded (30 m resolution) geospatial data, so we calculated weighted mean human population density and imperviousness for each subbasin.

We used two separate ordination methods and data sets to characterize land cover in a summary metric. The first used



**Table 1** Summary of assessment metrics for each sub-stock

Sub-stock	$t^a$	$B^b$	Frequency of Zeros	$\log(\text{maximum}:\text{mean})^c$	$\log(\text{final}:\text{initial year})^c$	Lowest biomass?
Cherry Point	−5.67	−0.12	0.00	−2.25	−4.46	Yes
Discovery Bay	−1.46	−0.05	0.15	−1.41	−6.45	Yes
Dungeness Bay	−2.75	−0.07	0.07	−3.51	−0.13	No
Elliot Bay	−0.34	−0.03	0.10	−3.77	−2.40	NA
Fidalgo Bay	−9.50	−0.23	0.15	−1.01	−5.53	Yes
Holmes Harbor	0.22	0.01	0.00	−1.86	1.84	Yes
San Juan Islands	−2.53	−0.07	0.18	−1.32	0.00	Yes
Kilist Harbor	−4.78	−0.39	0.48	−0.55	−5.54	Yes
NW San Juan Islands	−4.01	−0.43	0.59	−2.12	−4.97	Yes
Port Gamble	−7.45	−0.10	0.00	−6.25	−1.63	Yes
Port Orchard/Port Madison	0.90	0.05	0.07	−3.55	1.12	Yes
Port Susan	−4.00	−0.10	0.00	−1.57	−3.91	Yes
Purdy	−0.36	−0.04	0.07	−3.41	−0.63	NA
Quartermaster Harbor	−8.96	−0.21	0.15	−1.49	−7.12	Yes
Quilcene Bay	6.10	0.07	0.00	−2.21	2.56	No
Samish/Portage Bay	0.64	0.01	0.04	−3.21	−4.60	Yes
Semiahmoo Bay	2.17	0.02	0.00	−0.66	0.88	No
Skagit Bay	−2.56	−0.04	0.00	−1.08	−0.68	Yes
South Hood Canal	−2.68	−0.06	0.04	−3.19	−6.10	Yes
Squaxin Pass	−1.42	−0.03	0.00	−5.17	4.33	No
Wollochet Bay	−2.87	−0.32	0.27	−2.71	−4.87	NA

The column “Lowest biomass?” indicates whether the lowest estimated biomass occurred since 2010

NA means that the biomass time series did not extend past the year 2000

<sup>a</sup> $t$  is the  $t$ -statistic for the slope of a linear regression of population size vs. year

<sup>b</sup> $\beta$  is the estimated population growth rate, as estimated via a state-space model

<sup>c</sup> $\log(\text{maximum}:\text{mean})$  and  $\log(\text{final}:\text{initial})$  refer to (natural) logarithms of the ratio of observed biomass (or biomass-derived quantities) for each sub-stock. Maximum means the largest observed over the time series, final means the last year observed, and first means the first year observed

the 2016 watershed data as a proxy for the overall state of the landscape over the entire period. To reduce the dimensionality of land use/land cover, we used principal coordinates analysis (PCoA) to collapse these metrics into two axes. Proportional land use/land cover data were first arcsine square root transformed to approximate assumptions of normality (Zar 2010). We then calculated a Bray-Curtis dissimilarity matrix of the resulting transformed land use data and reduced the dimensionality using the first two dimensions of the PCoA analysis (Legendre and Gallagher 2001). We used the scoring on each dimension as candidate predictor variables to explain spatial differences in herring sub-stock status.

**Table 2** Pearson’s correlation between sub-stock status metrics

	$\beta$	Frequency of zeros	$\log(\text{maximum}:\text{mean})$	$\log(\text{final}:\text{initial year})$
$t$	0.63	−0.28	−0.68	0.61
$\beta$	—	−0.87	−0.49	0.62
Frequency of zeros	—	—	0.33	−0.46
$\log(\text{maximum}:\text{mean})$	—	—	—	0.51

See Table 1 for descriptions of status metrics

We also calculated the change in land use/land cover from 1996 to 2016 to evaluate whether spawning sub-stock status was associated with land use/land cover change. To this end, we first transformed proportional land use/land cover using arcsine square root transformation and then calculated the difference between 2016 and 1996 transformed proportions. Because these differences could be positive or negative, we could not use principal coordinates on land cover change to reduce the dimensionality. Instead, we used principal components analysis applied to the correlation matrix of transformed land cover differences. The change in land use/land cover was not easily reduced to a few dimensions; the first two axes accounted for only 40% of the variability in land cover change. Consequently, we included loadings on the first three axes as predictor variables in subsequent analyses, which accounted for nearly 57% of the variability in land cover change.

As additional predictor watershed metrics, we used the proportion of adjoining landscape watersheds consisting of impervious surfaces and the change in imperviousness between 1996 and 2016. We also used two measures of human population in each sub-watershed as a predictor

of herring population status: human population density in 2016 and the change in human population density between 1998 and 2016, expressed as an annual growth rate:  $\log(N_{2016}/N_{1998})/18$ .

### Relating Population Status to Watershed Characteristics

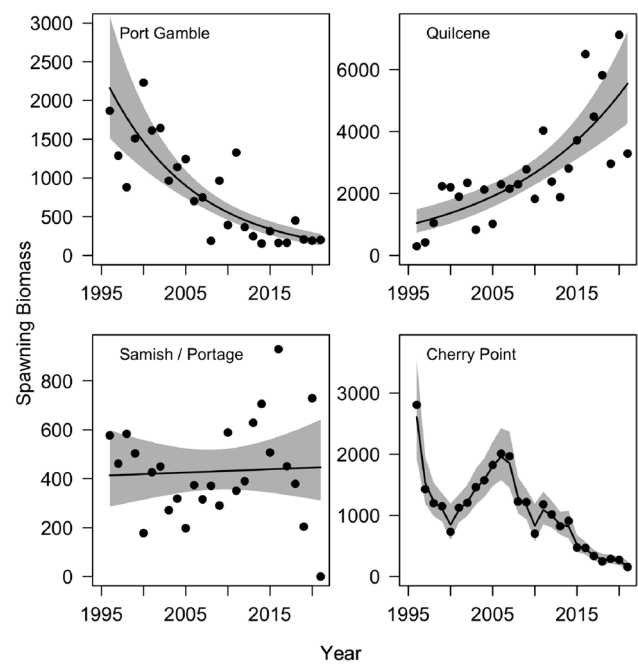
We fit generalized linear models to relate the herring status metrics to different combinations of predictor variables. Because of the correlation of herring status metrics, we focused on two response variables: the binomial response variable, the lowest biomass, and the estimated sub-stock growth rate,  $\beta$ . For both response variables, we fit seven alternative models that represented a priori hypothesis for how herring sub-stock status was related to land use and other predictor variables: (1) intercept only, (2) 2016 land cover, (3) %2016 imperviousness, (4) 2016 human density, (5) change in land cover from 1996 to 2016, (6) change in imperviousness from 1996 to 2016, and (7) change in human population density from 1998 to 2016. We assumed Gaussian errors for models fit to the estimated  $\beta$  and weighted each estimate by the inverse of its standard error. We used a small sample size-corrected AIC (AICc) to judge the weight of support for each model.

All analyses were conducted using R version 4.1.2 (R Core Development Team 2021).

## Results

Dynamic state-space model estimates converged for all sub-stocks and revealed a range of dynamic behaviors among the sub-stocks. For six sub-stocks (three shown in Fig. 2: Port Gamble, Quilcene, Samish/Portage), the model attributed most of the inter-annual variation to observation error combined with time-invariant sub-stock growth rate. For instance, Port Gamble exhibited a consistent and negative sub-stock growth rate, Quilcene exhibited a consistent and positive growth rate, and Samish/Portage exhibited a consistent growth rate near 0 (Fig. 2). For the remaining sub-stocks, the models attributed inter-annual variation to a combination of persistent trends combined with higher inter-annual variation in growth rates. For instance, Cherry Point (Fig. 2) dynamics are estimated to result from a sharply negative average growth rate, but with substantial fluctuations in growth rate over the years.

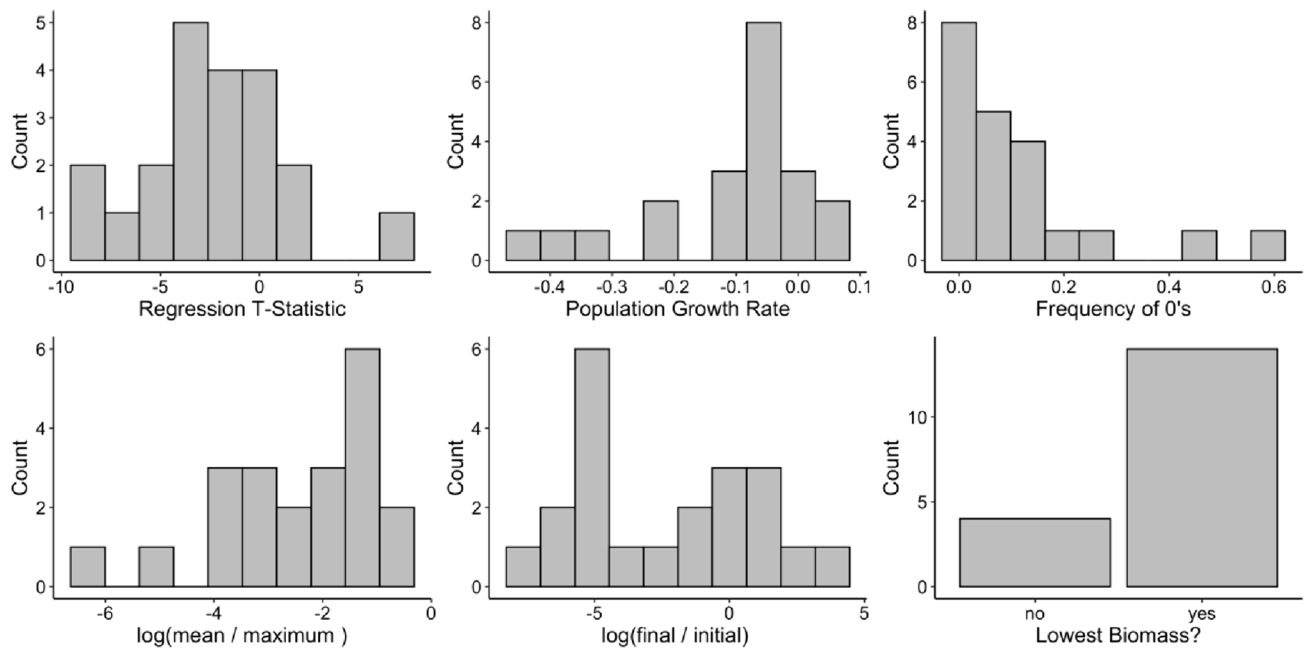
The distribution of the response metrics overall points to a widespread decline in Puget Sound herring sub-stock status from 1996 to 2021 (Fig. 3). The median responses for the  $t$ -statistic of the slope, growth rate, and log-ratio of first to last year biomass were all negative, and all but 4 of the 18 sub-stocks meeting the inclusion criteria (see the “Methods”



**Fig. 2** Time trends in spawning biomass (mt) and fitted models for four representative Puget Sound herring sub-stocks. Each point is an observation, the solid lines denote the maximum likelihood estimate for the true sub-stock spawning biomass in each year, and the shaded areas are the approximate 95% confidence intervals of the predicted value

section) experienced their lowest biomass between 2010 and 2021. For three sub-stocks, 25% of the post-1995 annual spawning biomass estimates equaled 0 (Table 1). The log-ratio of mean to maximum observed biomass will be negative for any stochastic process, but 9 of the 21 sub-stocks had mean contemporary biomass levels that were < 10% of the maximum observed biomass (Table 1).

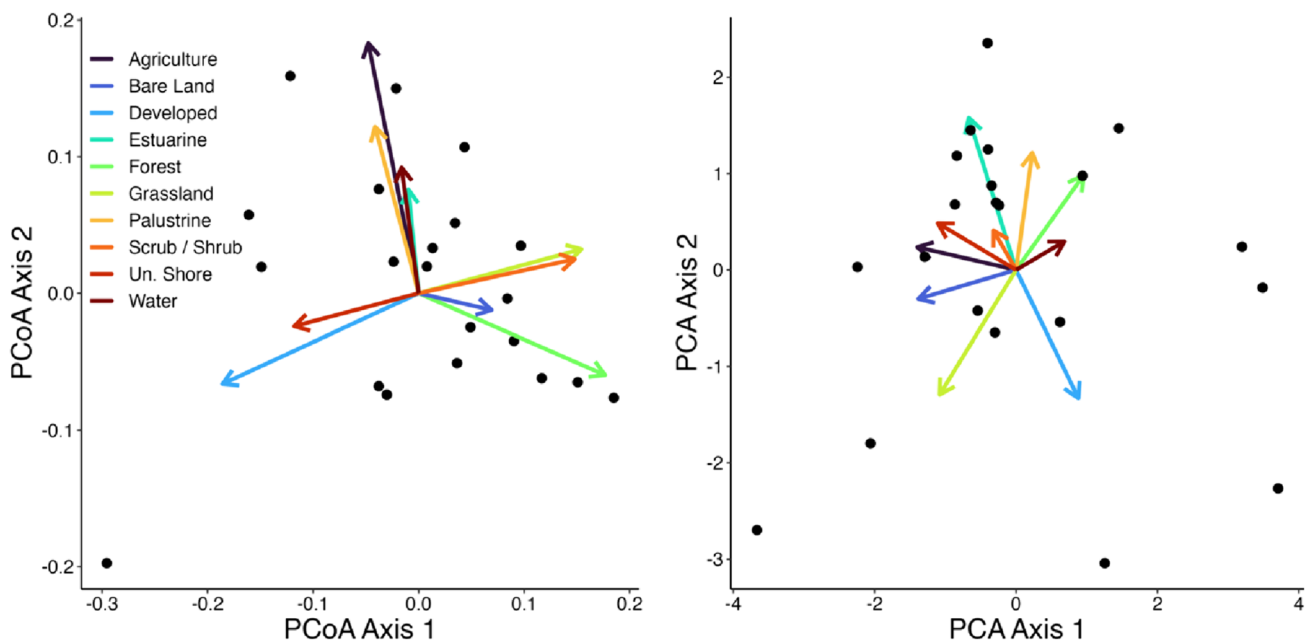
Spatial differences in contemporary (2016) sub-watershed land use/land cover adjacent to herring spawning sites were well described by two principal coordinate axes, which accounted for 80% of the dissimilarity in land use/land cover among sites. Generally, the first principal coordinate axis was correlated with greater forest, grassland, and scrub/shrub land cover/land use and less development (Fig. 4). The second axis was correlated with greater agriculture and palustrine land use/land cover. The changes in land use/land cover from 1996 to 2016 were not as well characterized by the first two principal component analysis axes and, generally, multiple land cover types loaded on the first two axes. Generally, the first axis was associated with a decline in agriculture and bare land cover, while the second axis was associated with an increase in estuarine, forest, and grassland cover and a decline in developed and grassland land cover (Fig. 4). The third axis (not shown) was largely associated with increased forest land cover and a decline in scrub/shrub land cover.



**Fig. 3** Frequency histograms of response metrics over the 21 sub-stocks examined

Neither of the two sub-stock status metrics—the probability that the lowest observed biomass occurred after the year 2010 or the sub-stock growth rate—were related to land cover/land use near spawning areas (Table 3). The model

best supported by the data for both herring response variables included only the rate of human density change, yet in both cases, the effect size was counter to expectations. That is, the probability that the lowest biomass occurred recently



**Fig. 4** Principal coordinate analysis on 2016 land use/land cover (PCoA; left panel) and principal component analysis on change in land use/land cover (PCA; right panel) from 1996 to 2016. Each point denotes landscape adjacent to a sub-stock spawning area, and arrows depict the relative magnitude of correlation or loadings of land use/

land cover categories on the PCoA or PCA axes. Note that “Estuarine” and “Palustrine” land cover refer to several wetland categories, as described by Cowardin et al. (1979). Land use/land cover labeled “Un. Shore” is an abbreviation of “Unconsolidated Shore”

**Table 3** Model selection and estimated coefficients for the seven candidate predictors

Model	Lowest biomass?			Sub-stock growth rate		
	$\Delta$ AIC	Estimated effect size(s)		$\Delta$ AIC	Estimated effect size(s)	
Intercept only	3.07			2.45		
2016 land use/land cover	8.30	0.26	0.20	7.17	0.14	0.08
2016% impervious surface	5.32	−0.42		4.47	0.00	
2016 human density	3.73	−1.82		4.89	0.00	
$\Delta$ Land use/land cover	7.2	−0.33	−1.96	7.71	−0.01	0.03
$\Delta$ Impervious surface	5.53	−0.09		3.18	−0.07	
$\Delta$ Human density	0.00	−1.57		0	1.86	

Multiple effect sizes are listed when multiple covariates (e.g., PCoA or PCA axis loadings) were included in the model, in order of ordination axis importance

$\Delta$  indicates that the covariate used was the change in the metric between 1996 or 1998 and 2016

Effect sizes were scaled by the standard deviation of each predictor variable

was lower, and the estimated herring sub-stock growth rate was greater when human population density change was highest (Table 3). These results arose because several of the landscapes that experienced the greatest rate of human population growth (Semiahmoo Bay, Elliott Bay, Samish/Portage Bay) contained herring sub-stocks that had relatively high growth rates and therefore did not experience their lowest biomass during the recent time period. Notably, none of the models based on land use/land cover or imperviousness were well supported by the data, as the intercept-only model had more support than any of these models (Table 3).

Similar findings were obtained by fitting the same linear models to the other stock status metrics (Table S2). Either the null (intercept only) or the change in human density had the most support but with an effect size opposite our expectations.

## Discussion

Here, we assessed whether local watershed status can explain differences in Puget Sound Pacific herring sub-stock dynamics by first developing and applying multiple status metrics and then evaluating whether these metrics were related to watershed characteristics. Our multi-metric approach confirms earlier analyses that point to variation in sub-stock status and trends and an overall pattern of deteriorating status throughout Puget Sound (Siple and Francis 2016; Sandell et al. 2016). Despite the wide variation in sub-stock status and land use, we did not detect any plausible relationship between the two. While correlative, this analysis suggests that the recent pattern in Pacific herring sub-stock status is likely more strongly governed by drivers that operate at scales larger than the local scale and that conservation and restoration actions focused at those scales are likely to be more effective than local watershed-scale restoration.

We had expected that sub-stocks in regions with more impervious surfaces, higher human density, and more urbanized or developed land cover would have poorer stock status compared to sub-stocks where surrounding watersheds had lower human density and more “natural” land cover types (e.g., palustrine, estuarine, forest). This expectation was based on the connection between watershed land cover and the delivery of toxic contaminants and excess nutrients to nearby coastal areas, all of which could impair egg survivorship. Consequently, the absence of any discernable relationship in our analysis may imply that the effects of these stressors on egg survivorship have a smaller demographic effect than other environmental conditions that govern survivorship at other critical life stages (Cushing 1990; Leggett and Deblois 1994). Alternatively, the linkage between our measures of watershed land cover, human density, and egg and/or juvenile survivorship may have been weak. For instance, other factors influencing egg survivorship such as predation may have more influence. Likewise, post-hatch herring may respond more strongly to more proximate human activity along the land/water interface, e.g., shoreline armoring (Francis et al. 2022); installation of docks and piers that alter prey availability (Cordell et al. 2017), fish behavior (Toft et al. 2007; Ono and Simenstad 2014), and light pollution (Longcore and Rich 2004; Nightingale et al. 2006); and/or offshore influences during later life stages.

Importantly, our analyses were limited to a single spatial scale by evaluating whether local watershed characteristics were associated with herring sub-stock status, and therefore, we could not speak to larger-scale consequences of land use/land cover change (Perry and Ommer 2003). These larger-scale consequences could emerge from the cumulative effect of land cover conversion in Puget Sound, as is true for estuaries around the world (Freeman et al. 2019). Detecting these effects is complicated by the myriad ways watersheds



potentially alter land-sea connections, combined with the challenges of measuring the cumulative impacts of multiple interacting stressors (Hodgson et al. 2019). Moreover, our analysis was correlative and based on a single, recent time period and therefore cannot speak to the effect of long-term historical change to the Puget Sound watershed on Pacific herring and how that may have altered sub-stock resilience. Further analysis that looks to identify associations between watershed characteristics and sub-stock status at a range of scales (e.g., at the basin scale) may prove informative.

Given the widespread nature of sub-stock declines, it is likely that broader regional processes are responsible for much of these declines. Siple et al. (2017) documented declines in adult survival and recruitment of individuals to spawning age in Puget Sound herring. Hershberger et al. (2002) suggests that a recent shift in age structure toward younger fish might be attributable to the high prevalence of a protozoan parasite in older (>5+) Pacific herring. However, no data exist to determine whether the decline in Puget Sound herring coincided with an increase in disease prevalence. Recent increases in pinnipeds (principally harbor seals and California sea lions) (Washington State Academy of Sciences 2022), since the passage of the U.S. Marine Mammal Protection Act (Essington et al. 2021), might also be responsible for increased mortality rates and survival to maturity. Pacific herring comprise a large fraction of the feeding of both of these species (Thomas et al. 2017; Scordino et al. 2022). Finally, annual water temperature has increased by roughly 1 °C since 1950, with most of this change occurring since the late 1970s (Moore et al. 2008; Essington et al. 2021). Changing thermal regimes are expected to alter survivorship through critical life history stages via shifts in ecosystem phenology, leading to mismatches between larval food needs and supply (Asch 2015; Asch et al. 2019). Although local land cover was not associated with stock status, our work cannot rule out whether land cover at broader spatial scales (e.g., basins) affects herring productivity.

An important uncertainty in the analysis of spatially structured populations like Pacific herring is the connectivity among spawning sites and the degree to which spawning site selection depends on natal location and socially governed migratory behavior (Corten 2002; Secor et al. 2009; MacCall et al. 2019). Considerable evidence suggests a strong social and behavioral component to spawning migrations (Corten 2002), which may alternatively mask or amplify signals between local environmental conditions and herring populations. If social cues diminish philopatry, e.g., via stochastic social cues among spawning fish, the linkage between local site spawning productivity and spawning biomass in subsequent years could be diminished. Alternatively, MacCall et al. (2019) illustrated that socially learned spawning behavior leads to the abandonment of less

productive spawning sites when the adult mortality rate is higher. Given the documented increase in adult mortality, we expect this mechanism to lead to a stronger coupling between local land use that affects spawning productivity and spawning biomass trends.

We assessed sub-stock population status using multiple metrics, and we suggest that this approach is likely useful in other contexts where standard status metrics are unavailable or when management targets or limits do not fully capture information about the status. By evaluating hypotheses against multiple metrics, the robustness of our conclusions regarding direct linkages between local watershed characteristics and sub-stock dynamics is strengthened. In our case, the average growth rate appeared to capture much of the information captured in (i.e., was highly correlated with) other metrics. This finding supports previous arguments that simple state-space models could have value in conservation and management practices as indicators of population status, despite the fact that they rely on assumptions that do not reflect all of the population structure and mechanisms that govern vital rates (Holmes et al. 2012; Kindsvater et al. 2018; Auger-Méthé et al. 2021). However, we caution against using our model estimates in forecasting (e.g., via population viability analysis) because vital rates of small pelagic fish such as Pacific herring tend to fluctuate over long time scales (Siple et al. 2019).

We note that land use itself is not expected to be the direct causal driver of herring vital rates. Rather, land cover is a proxy for a suite of local environmental disturbances that might govern larval retention and egg survivorship (Mallin et al. 2001; Shelton et al. 2014; Cordell et al. 2017; Freeman et al. 2019). Some of these direct drivers are related to water quality, e.g., turbidity, toxic contaminants, and micro-organisms. The absence of an association between land use and herring population status could mean that land use does not have a strong localized effect on these direct drivers at time scales relevant for egg survivorship, possibly owing to high rates of tidal water exchange at many locations (Mofjeld and Larsen 1984; MacCready et al. 2021).

Given the vast number of threats marine life faces in the Anthropocene, it is unlikely that a single driver can be identified as a sole and unequivocal cause for biodiversity declines. Diseases, predation, shoreline and estuary modification, climate change, and the cumulative impacts of watershed development remain viable explanations for Puget Sound Pacific herring, and each is likely to interact with others. The conservation and restoration actions that the widespread decline in Puget Sound herring demands will benefit from fully acknowledging the uncertainty regarding root causes by following robust principles of decision-making under uncertainty (Tulloch et al. 2015; Hemming et al. 2022).

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**Data Availability** All data and source code used to run the analysis are available at <https://github.com/tessington/PS-Herring>.

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