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Contributions of adult mortality to declines of Puget Sound Pacific herring

Margaret C. Siple,[1,*] Andrew O. Shelton,[2] Tessa B. Francis,[3] Dayv Lowry,[4] Adam P. Lindquist,[4] and Timothy E. Essington[1]

[1]School of Aquatic and Fishery Sciences, University of Washington, P.O. Box 355020, Seattle, WA 98105, USA
[2]Northwest Fisheries Science Center, NOAA, 2725 Montlake Blvd E, Seattle, WA 98112, USA
[3]Puget Sound Institute, University of Washington Tacoma, 326 E D St, Tacoma, WA 98421, USA
[4]Washington Department of Fish and Wildlife, Marine Fish Science Unit, Olympia, WA, USA

*Corresponding author: tel: +1 (206) 661-8403; fax: +1 (206) 685-7471; e-mail: siplem@uw.edu

Forage fish undergo dramatic changes in abundance through time. Long-term fluctuations, which have historically been attributed to changes in recruitment, may also be due to changes in adult mortality. Pacific herring, a lightly exploited forage fish in Puget Sound, WA, have exhibited shifts in age structure and decreases in spawning biomass during the past 30 years. Here, we investigate changes in adult mortality as a potential explanation for these shifts. Using a hierarchical, age-structured population model, we indicate that adult natural mortality for Puget Sound Pacific herring has increased since 1973. We find that natural mortality has increased for every age class of adult (age 3+), especially age 4 fish, whose estimated mortality has doubled over the survey time period (from $M = 0.84–1.76$). We demonstrate that long-term shifts in mortality explain changes in age structure, and may explain biomass declines and failure to reach management thresholds for two spawning sites in Puget Sound (Cherry Point and Squaxin Pass). Temporal shifts in natural adult mortality could have negative implications for herring and herring predators. We demonstrate that adult mortality, in addition to recruitment variation, is an important driver for forage fish, which face exceptionally high natural mortality compared with other fishes.

Keywords: forage fish, natural mortality, Pacific herring, population dynamics.

Introduction

Population fluctuations are a key feature of marine fishes (Vert-pre et al., 2013). These fluctuations are induced by changes in demographic rates like growth, reproduction or survival. A great deal of effort has been devoted to characterizing recruitment as an important driver of population dynamics for marine fish. However, there is mounting evidence that post-recruitment mortality also plays an important role. In exploited marine populations, the combination of fishing and natural mortality has been hypothesized to magnify population fluctuations (Shelton and Mangel, 2011). Increased natural mortality can increase the importance of short-term fluctuations in determining abundance (Rouyer et al., 2012) and amplify the effects of impaired recruitment (Okamoto et al., 2016). Changes in natural mortality can therefore be important drivers of population dynamics of marine fish.

Small pelagic schooling fish species ("forage fish") like sardines (Sardinella spp.), anchovies (family Engraulidae), and herring (Clupea spp.) are well known for their high-amplitude fluctuations in abundance (Hjort, 1914; Toresen and Østvedt, 2000; Chavez et al., 2003), which occur on both short (interannual) and long (decadal) time scales. Although many studies have focused on the role of recruitment variation—and climatic drivers of recruitment in particular—as the primary driver of forage fish population fluctuations (e.g. Tourre et al., 2007), there is increasing evidence that changes in post-recruitment mortality play an important role in population dynamics. For example,

high-amplitude fluctuations in Pacific herring (*Clupea pallasii*) abundance have been attributed to changes in fishing mortality (McKechnie *et al.*, 2014), environmental conditions (Nagasawa, 2001), predation mortality (Walters *et al.*, 1986) or some combination of the three (e.g. Schweigert *et al.*, 2010). However, the influence of variable natural mortality on population fluctuations is difficult to discern because of the inherent challenge of distinguishing fishing mortality from natural mortality (Hilborn and Walters, 1992).

In the north Pacific, Pacific herring are a key forage species and are heavily fished, providing economic value to large-scale fisheries in Alaska and British Columbia. They are food for predators at multiple life stages, providing a seasonal "pulse" of marine nutrients to marine and terrestrial predators during spawning (Willson and Womble, 2006) and acting as energy conduits from lower trophic levels to piscivorous predators and seabirds throughout their life span (Beaudreau and Essington, 2011; Schrimpf *et al.*, 2012). They are also considered a "cultural keystone species" (Thornton and Kitka, 2015; *sensu* Garibaldi and Turner, 2004) as they are the focus of indigenous harvest practices and cultural traditions. Pacific herring in Puget Sound, WA provide an excellent opportunity to study the importance of natural mortality relative to other drivers like recruitment. In this system, they experience little fishing mortality. Natural mortality is likely high because they are a preferred prey for many species in the food web (Ainsworth *et al.*, 2008; Harvey *et al.*, 2012) including salmonids (Duffy *et al.*, 2010), seabirds (Lance and Thompson, 2005), and marine mammals (Lance and Jeffries, 2006). In contrast to more heavily exploited forage fish populations, including other Pacific herring populations in the Northeast Pacific, Puget Sound herring have supported only a small bait fishery in recent years (2–6% of spawning stock biomass per year between 2003 and 2012) (Stick *et al.*, 2014). Despite very low fishing mortality rates, previous research has suggested a decline in spawning biomass (Siple and Francis, 2016) and a shift in age structure (Stick *et al.*, 2014) in Puget Sound herring. The relatively low fishing mortality provides a unique opportunity to understand variation in natural mortality in a wild forage fish population.

In addition to experiencing very low exploitation rates, herring in Puget Sound comprise multiple subpopulations or "stocklets" (Stick *et al.*, 2014; see Siple and Francis, 2016), which are defined by the spawning sites to which they return. This provides the opportunity to examine both temporal and spatial variability in recruitment, adult mortality, and abundance fluctuations. Previous work has shown that time series of spawning biomass in Puget Sound across stocklets are asynchronous, suggesting that local-scale processes might impose distinct mortality regimes (Siple and Francis, 2016). Additionally, two potential mechanisms motivate examining spatial variation in adult mortality in Puget Sound: (i) tissue contaminant concentrations in adult herring, which may have deleterious sublethal effects, vary spatially (West *et al.*, 2008), and (ii) predators may forage more actively in some areas than others (Ward *et al.*, 2012). Spatial variation in natural mortality, including different trends through time, would indicate that local processes are important for determining population dynamics. Understanding spatiotemporal variation in adult natural mortality, therefore, and its links to biomass trends, will help to elucidate the role of local processes in determining population dynamics, and suggest potential management interventions in recovery or conservation situations.

To evaluate spatial variation in natural mortality and the importance of local processes in determining population dynamics over time, we estimate temporal and spatial variation in Puget Sound herring natural mortality rates using time-series models. We then compare models to reveal the role of spatial vs. temporal changes in mortality and use simulations to demonstrate the importance of natural mortality and recruitment variation in a forage fish population.

Methods

We investigated temporal changes in adult mortality in Pacific herring over 36 years (1973–2008), and assessed whether these changes are unique across a set of spatially distinct herring spawning sites (hereafter, we refer to these as "sites" and the populations that spawn at them as "stocklets"). We fitted multiple hierarchical, age-structured models, using herring trawl survey data from eight sites in Puget Sound, then used model fits to evaluate whether there was evidence for temporal and/or spatial variation in mortality. Finally, we used estimated life history parameters (initial age distribution, recruitment, and mortality) to simulate the effects of constant vs. time-varying mortality on Puget Sound Pacific herring biomass, and compared our predictions against observed abundance and management targets.

Study site

Puget Sound is a partially mixed estuarine fjord in western North America, composed of oceanographically distinct basins separated by sills. It is connected to the coastal Pacific Ocean by the Strait of Juan de Fuca. It has a shoreline of ~2000 km, enclosing a water area of 2642 km^2 at mean high water. Tides are the main driving force of physical oceanographic processes in Puget Sound, and tidal range varies nearly twofold between the northern and southern parts of Puget Sound. Its maximum depth is 284 meters and average depth is ~130 m. Subtidal circulation is driven primarily by density gradients, with fresh surface water from rivers interacting with saltier marine water at the mouth of Puget Sound (Babson *et al.*, 2006). Like other large estuaries, Puget Sound has an along-estuary salinity gradient (~2 × 10^{-5} psu m^{-1}; (Sutherland *et al.*, 2011)). The basins in Puget Sound are generally well-oxygenated, although oxygen depletion is a concern in some areas (e.g. Hood Canal; Newton *et al.*, 1995). Pacific herring return to beaches to spawn each winter between January and June, depending on the stocklet.

Data

We used age-specific abundance of Pacific herring in Puget Sound collected intermittently (mostly annually) between 1973 and 2008, at eight spawning sites. Numbers-at-age data were collected by the Washington Department of Fish and Wildlife (WDFW) using a midwater trawl coupled with acoustic surveys targeting prespawning aggregations of Pacific herring, 3–4 weeks before winter spawning in Puget Sound (Stick *et al.*, 2014). Rope trawls were used to collect samples of fish at the peak of prespawner biomass at each site (Burton, 1991). Larger sites with multiple aggregating schools were split into "subareas". Subsamples (N = 100) provided data on mean weight at age a ($\bar{W}_a$) and proportion at age a (by abundance, P_a and by weight, P_{wa}), while acoustic surveys provided data on total biomass (B_{total}). Estimates of numbers at age (N_a) in each subarea were derived as:

$$N_a = \frac{B_a}{\bar{W}_a} \tag{1}$$

$$B_a = B_{total} P_{wa} \tag{2}$$

$$P_{wa} = P_a \frac{\bar{w}_a}{\sum\limits_{i=1}^{n} P_i \bar{W}_i} \tag{3}$$

where B_a is the estimated biomass at age a and n is the number of ages.

For sites with multiple subareas (e.g. Port Orchard and Port Madison), proportions at age were calculated separately for each subarea and then pooled proportionally to their contribution to the total biomass (O'Toole, 1994). Age was determined from scales, with multiple scales read for each fish sampled (Stick *et al.*,

2014). Because proportions at age were not available for every year and every site, we focused our analysis on eight sites for which there are more than 10 years of age-specific abundance estimates (Figure 1). These sites are spatially distributed throughout each of the five Puget Sound basins (Stout *et al.*, 2001) (Figure 1). The trawls used in prespawning surveys only captured adults. In Puget Sound, nearly all age 3 individuals are sexually mature, but the fraction of age 2 individuals captured in the surveys that are sexually mature is unknown (Stick *et al.*, 2014). Therefore, we only used abundance data for herring ages 3 and older.

We estimated natural mortality using an age-structured population model, consisting of a process model to estimate the parameters based on numbers-at-age data, and an observation model that relates observations (data) to the true state of nature. This state-space structure assumes that survey data are observations of an underlying process, in this case the change in age composition over time. The approach allows one to define survey
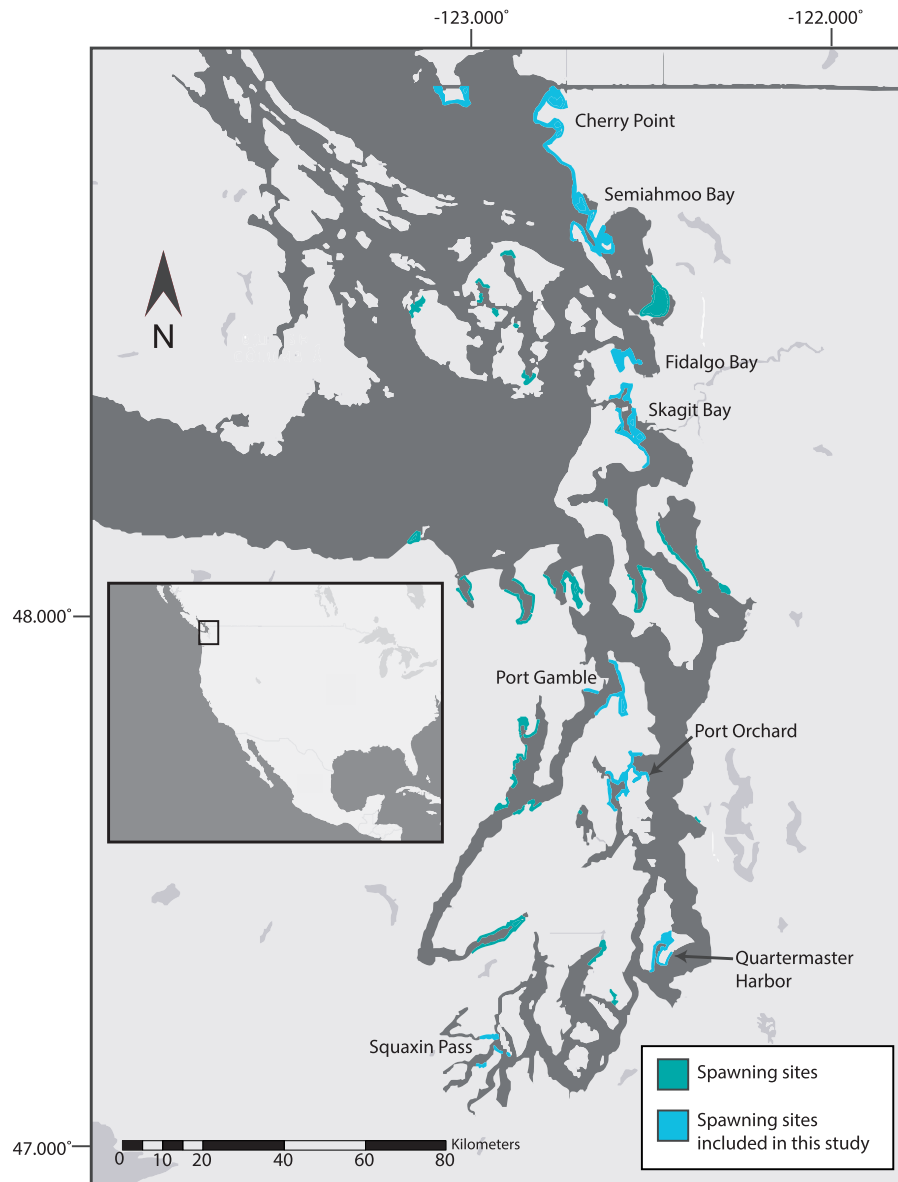
Figure 1. Herring spawning sites in Puget Sound (shaded areas). Sites used in this study are indicated with darker shading and labels. The group of fish returning to each site is referred to as a "stocklet." Map modified from Stick & Lindquist (2014).

data as observations instead of exact values. This way, it is possible to acknowledge and sometimes estimate the amount of measurement error associated with the survey. In the process model, we modelled the numbers of herring in each stocklet as an age-structured population where age-specific mortality rate (M) depends on the time period (described below) or oceanographic basin. Because there are insufficient data to estimate a unique M for the very oldest age classes, we estimated unique mortality rates for ages 3–6, and a shared mortality rate among age 7–9 fish.

The number of age a adult herring in year t, at site s, $N_{a,t,s}$ given natural mortality rate M, is estimated as:

$$N_{a,t,s} = N_{a-1,t-1,s}e^{-M} \qquad (4)$$

We used this general model to explore alternative scenarios in which mortality varies in space and time. We compared seven models: M was the same for all ages, basins, and time periods (null model); M varied only by age (M_a); M varied by age and basin ($M_{a,b}$ and $M_a e^{\beta_b}$, where M_a was modified by a basin effect β_b); M varied by age and time period ($M_{a,p}$ and $M_a e^{\beta_p}$, where M_a was modified by a time period effect β_p); and M varied by basin and time period ($M_a e^{\beta_{b,p}}$; where M_a was modified by a combined basin/time period effect $\beta_{b,p}$). Numbers-at-age data were insufficient to estimate annual shifts in M, so mortality for fish of age a in year t was assumed to have the following form:

$$M_{a,t} = \begin{cases} M_{a,p=1} & if \ t < 1991 \\ M_{a,p=2} & if \ t \geq 1991 \end{cases}$$

where $p = 1$ indicates the first half of the survey time series (1973–1990) and $p = 2$ indicates the second half of the time series (1991–2008). We estimated a value for M in the first and second half of the time series separately, instead of one for each year.

Recruitment to age 3 for Puget Sound herring may vary spatially because of differences in egg loss (Shelton *et al.*, 2014) or exposure of embryos to contaminants (West *et al.*, 2014). We modelled age-3 abundance as a random draw from a lognormal distribution each year, with a different mean for each site. This assumes that recruitment variation is not fully explained by changes in spawning stock biomass (a common assumption for forage fish; Szuwalski and Hilborn, 2015), but allows for spatial variation in recruitment. We assumed that mean recruitment to age 3 (ψ_s) was independent across sites and modelled age-3 abundance as:

$$N_{a=3,t,s} = \psi_s e^{\epsilon} \qquad (5)$$

where $\epsilon \sim N(0, \tau^2)$ represents independent, normally distributed variation around mean recruitment and τ was the same for all

sites. We note that recruitment in forage fish is often described as the number of age-0 or -1 individuals in the population, so the recruitment patterns observed in this study may not be directly comparable to others.

We assumed lognormal observation error around numbers at age for each location and year. That is, we assumed a simple observation model:

$$\log(N_{\text{obs} \ a,t,s}) = \log(N_{a,t,s}) + \epsilon_{\text{Obs}} \qquad (6)$$

where ϵ_{Obs} is an independent and normally distributed random variable with mean 0 and standard deviation σ (see prior in Table 1).

Parameter estimation

We fitted model parameters in a Bayesian framework because it allows information to be shared among frequently surveyed sites and those with less data (Punt *et al.*, 2011), and because this hierarchical structure is easier to implement in a Bayesian framework than a maximum likelihood one. A Bayesian approach requires the specification of prior distributions for mortality and recruitment parameters, initial age distribution, and observation error. Parameters for which no prior information was available were given uninformative or diffuse priors (Table 1).

Initial numbers at age were based on recruitment to the first age class and subsequent mortality. We added a penalty to the estimation of initial age structure, based on recruitment and mortality.

The prior mean for adult mortality in this study was based on an estimate of adult Pacific herring mortality outside Puget Sound, along the Pacific coast ($M = 0.6 \, \text{year}^{-1}$; Hourston and Haegele, 1980). Since there was no available information about variation in M, we chose a variance that allowed the prior distribution to be broad and centred around this value.

We obtained posterior probabilities of parameters using Just Another Gibbs Sampler (Plummer, 2003), with three chains and 50 000 simulations, and a burn-in of 10 000 simulations. Results were examined using the R2jags and coda packages in R (Plummer *et al.*, 2006; R Core Team, 2017). We tested Markov Chain Monte Carlo chain convergence using the Gelman-Rubin diagnostic (Gelman and Rubin, 1992) and chain stationarity was assessed using the Geweke statistic (Geweke, 1992). We also visually examined posterior estimates to evaluate cross-correlation between variables, and performed posterior predictive checks of numbers at age to confirm that parameter estimates produced realistic population dynamics. We used Deviance Information Criteria (DIC; Spiegelhalter *et al.*, 2002) to compare fitted models, using DIC.samples() in rjags (Spiegelhalter *et al.*, 2002).

Table 1. Parameters estimated by the age-structured model, their definition, and the priors used to specify their distribution.

Parameter	Definition	Prior distribution
ϵ	Observation error associated with trawl surveys	$\epsilon \sim N(0, \ \sigma)$
σ	Standard deviation of log(Observations)	$\sigma \sim \Gamma(0.5, \ 0.75)$
ψ_s	Mean recruitment to site s	$\psi_s \sim N(11, \ 3)$
ϵ	Recruitment error	$\epsilon \sim N(0, \ \tau)$
τ	Standard deviation of log(Recruitment)	$\tau \sim \Gamma(0.5, \ 0.75)$
M	Mortality rate of herring, where subscripts indicate age (a), time period (p), or basin (b). Prior mean is based on estimates for herring mortality outside Puget Sound ($m = 0.6$; Hourston and Haegele, 1980).	$\ln(M_{a,p}) \sim N(-0.5, \ 0.5)$

The prior for mean recruitment was the same for each site, but was estimated separately for each site.

Model projections

To evaluate the relative influence of adult mortality vs. recruitment variation on observed biomass trends, we used mortality rates estimated by the model above to project herring populations in Puget Sound based on two alternative scenarios for herring mortality: (i) mortality increased halfway through the time series ($M_{a,1}$ changes to $M_{a,2}$ in 1991; "*M* time-varying"), and (ii) mortality was constant throughout the time series (i.e. $M_{a,1} = M_{a,2}$; "*M* constant"). For comparison, we also included two recruitment scenarios, one in which mean recruitment was constant for each stocklet (ψ_s), and one in which mean recruitment varied from year to year. For scenarios where recruitment was variable, we used time series of median recruitment ψ_s and recruitment variability τ drawn randomly from the model. We projected numbers at age for each scenario using estimates of initial age distribution, recruitment variability and mortality from the process model described earlier in Equation (1).

Current management targets for Puget Sound herring are set in terms of adult spawner biomass. To describe herring stocklets in terms of biomass, we used mean weights at age (w_a; determined from trawl surveys at each site; see Supplementary Material) and numbers at age $N_{a,t,s}$ estimated by the model to calculate biomass $B_{t,s}$.

$$B_{t,s} = \sum_{a=1}^{n} N_{a,t,s} w_a \qquad (5)$$

We did not see strong evidence that weight at age varies significantly between sites or over time so w_a was estimated from trawl survey data from all years and sites (Supplementary Figures S3 and S4).

Results

Age truncation and structure of mortality

There was a shared pattern of age truncation (loss of older age classes) and declining biomass for Puget Sound herring over the time period 1973–2012. The maximum age observed in trawl surveys dropped in five of eight stocklets over the course of the WDFW trawl survey (Figure 2) and older fish (>8 years) were not observed in trawl surveys at any spawning site after 2007. Even at sites where spawning biomass appears constant or increasing (e.g. Squaxin Pass), age structure has shifted such that the mean age of Pacific herring has declined over the survey time period (at Squaxin Pass, from 5.98 in 1975 to 2.0 in 2008; Figure 2). The degree to which older age classes were lost varies by spawning site: the proportion of the Squaxin Pass stocklet composed of age 4+ herring declined from 97 to 0% between 1975 and 2008; Cherry Point declined from 90.5 to 0% between 1973 and 2008; and Semiahmoo Bay declined from 7% age 4+ individuals in the 1988 survey to 0% in 2000. All other stocklets experienced little or no change in the number of age 4+ individuals (±0.6–3% since surveys started at each site), but surveys at these sites began in the 1990s, after the percentage of older adults had already declined substantially for Cherry Point and Semiahmoo Bay. On average across all the sites in this study, the proportion of the overall Puget Sound adult herring population composed of age 3 individuals increased from an average of 49% (1973–1990) to 75% (1991–2008); in 2008, the overall Puget Sound herring population was composed of more age 3 herring than all older fish combined (Figure 2).

There was strong evidence for temporal changes in age-specific mortality but only weak evidence of spatial variation in mortality. The data best supported the model in which M_a varied through time, such that each age experienced a unique temporal shift in M (Age × Period; Table 2). The null model with age-varying mortality alone and the null model with a single M for all basins and time periods were not supported ($\Delta_{\text{DIC}} > 100$). The model where M_a varied spatially and temporally (Age + Basin × Period; $\Delta_{\text{DIC}} = 4$), was less well supported (higher Δ_{DIC}), as was the model where M increased by a common factor β_p for each age class (Age + Period; $\Delta_{\text{DIC}} = 5$). Models where M_a varied spatially (Age + Basin, $\Delta_{\text{DIC}} = 71$; Age × Basin, $\Delta_{\text{DIC}} = 87$) were better than the age-only (Age; $\Delta_{\text{DIC}} = 106$) and null models (single M; $\Delta_{\text{DIC}} = 163$), but still not as well supported as the temporal models (Table 2). Posterior predictive checks confirmed that the best fit model described realistic recruitment dynamics and changes in numbers at age (Figure 3; Supplementary Figure S5).

Observed shifts in herring age structure were consistent with an increase in mortality of herring ages 3–6; and we further found that increases in M varied by age class (Table 2, Figure 4). Since the start of the survey, mean M increased by 35% for age 3 herring, 52% for age 4, 21% for age 5 and 14% for age 6. The model estimated a reduction in Age 7+ mortality (a 95% decline), but we note that the recent time period (1991–2008) mortality estimate is very close to the prior and there are very few data on the oldest age classes for this time period, suggesting that this value reflects the prior instead of the data.

Projections

A substantial fraction of the biomass decline in Puget Sound herring can be attributed to mortality of older age classes (age 3+), vs. variation in recruitment. The scenario with increasing adult mortality and constant recruitment resulted in a nearly one-third decline in total adult biomass in Puget Sound over 36 years compared with scenarios with constant adult mortality (median −28% change in biomass across all sites between 1973 and 2008; Figure 5). The scenario with variable recruitment yielded similar results (median −40% change in biomass; Figure 5). For individual sites, including an increase in adult mortality resulted in biomass estimates that ranged from 2% lower (Cherry Point; 1111 t in 2008) to 58% lower (Squaxin Pass; 119 t in 2008) compared with a constant mortality scenario (Figure 5). Incorporating increased adult mortality resulted in biomass projections that had larger negative changes in biomass, increased variability, and were below the management targets set for Squaxin Pass (119 t of the 880 target) and Cherry Point (1154 t compared with a target biomass of 5000 t; Stick *et al.*, 2014).

Discussion

Recruitment variability, particularly resulting from changes in the environmental conditions experienced by eggs, larvae, or juvenile fish, is often considered a primary driver of forage fish dynamics (Cushing, 1990; Szuwalski and Hilborn, 2015). Our analysis demonstrates that changes in adult natural mortality can drive population dynamics in forage fish. We estimated high natural mortality (M) that increased nearly twofold between 1973 and 2008 (36 years), indicating that adult (age 3+) mortality is high and increasing and offering a potential explanation for profound changes in age structure. Furthermore, our model fits show that an analogous change in recruitment to age 3 could not explain
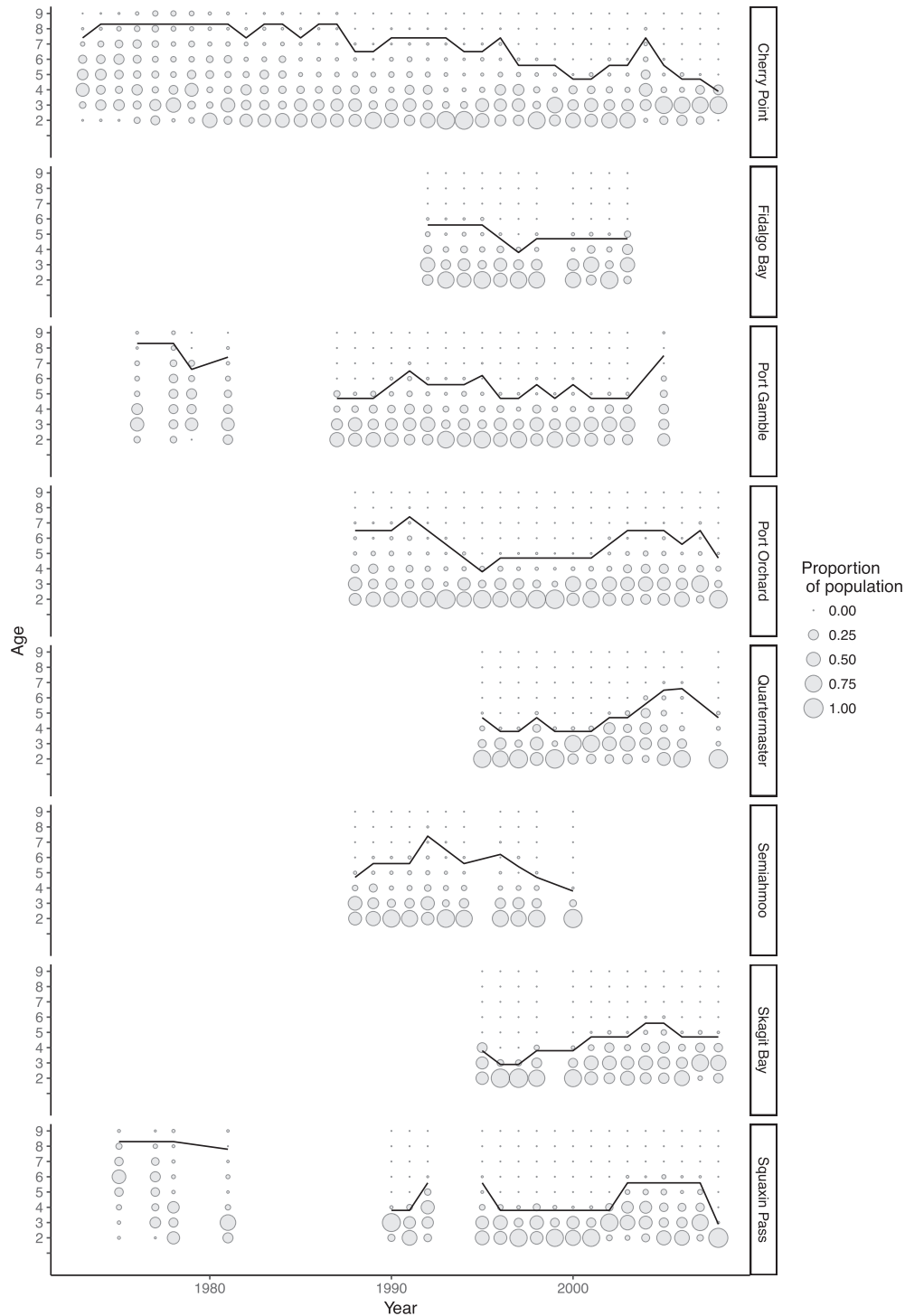
Figure 2. Proportions at age (circles) and the 90th percentile of age (solid line) since the start of the survey.

the changes in age structure observed in Puget Sound herring (Supplementary Table S1), excluding the possibility that depressed recruitment alone could drive herring populations.

Puget Sound herring stocklets are presently below management targets, and our results suggest that both high and increasing adult mortality and changes in recruitment may be limiting their ability to recover. Our simulations showed that an increase in natural mortality could account for up to a 28% decline in

total biomass of herring across Puget Sound. When model-estimated recruitment variation was included, the increase in mortality caused a ∼40% decline in biomass. Importantly, our simulations suggest that even if mortality had not increased, biomass at Cherry Point and Squaxin Pass—the two stocklets with management-defined spawning biomass targets—would be unlikely to reach those targets. Simulated 2008 biomass under constant mortality was well below management targets, suggesting

that either estimated mortality at the beginning of the time series was already too high to allow recovery to target levels, or that reduced mortality alone is insufficient for recovery, and improved recruitment is also necessary. It is important to note that biomass targets include all spawning ages, which includes some unknown fraction of age-2 spawners that are not incorporated in our model. Our results illustrate the general challenge that using historical biomass targets for conservation may be problematic under changing environmental conditions. It may be impossible to reach historical abundances without correctly identifying the drivers of biomass change. This is particularly important for forage fish populations, whose historical abundances are often poorly understood in the first place.

We predict that the truncated age structure in herring could have major implications for population dynamics going forward, for three main reasons. First, age truncation can remove the buffering effect of older age classes on years with poor growth or recruitment, causing population variability to more closely follow high-frequency environmental signals (Warner and Chesson, 1985). In an urbanized estuary like Puget Sound where nearshore conditions are highly diverse on small spatial scales (Simenstad *et al.*, 2011), temporal and spatial changes in environmental drivers of recruitment may become even more influential to a population dominated by younger individuals. Second, age truncation may also have behavioural impacts: in a study of Pacific herring in on the British Columbia coast, Hourston (1959) found more consistent homing in fish tagged as adults than fish tagged as juveniles (82% of adults returned to spawning beaches where they were tagged after 2 years at large, compared with 52% of herring tagged as juveniles, after adjusting for natural mortality). "Learned migration" was proposed by McQuinn (1997) to explain how herring migration patterns change or disappear under fishing. If homing behaviour in Puget Sound Pacific herring is similarly influenced by older fish, age truncation could lead to unexpected shifts in future spawn timing or location (Francis et al. *unpublished data*). Recruitment made more variable by these changes would compound the effects of age truncation on older age classes, causing population dynamics to track an increasingly variable set of environmental signals.

The absence of spatial effects indicates that drivers of adult mortality operate at an across-basin scale, and that asynchronous biomass dynamics among sites may be driven by differences in recruitment (as in Thorson *et al.*, 2014) or growth instead of adult mortality. Thus, asynchronous biomass dynamics observed at a local (spawning site) scale shown by Siple and Francis (2016) are likely due to spatial differences in other demographic rates like juvenile survival, instead of differences in *M*. Spatial differences in

Table 2. Comparison of life history models with spatial and temporal differences in adult mortality.

Model	Form	ΔDIC
Age × Period	$M_{a,p}$	0
Age + Basin × Period	$M_a e^{\beta_{b,p}}$	4
Age + Period	$M_a e^{\beta_p}$	5
Age + Basin	$M e^{\beta_b}$	71
Age × Basin	$M_{a,b}$	87
Age	M_a	106
Null	M	163

e indicates the base of the natural logarithm (ΔDIC is the difference in Deviance Information Criterion; DIC; between each model and the best fit model).
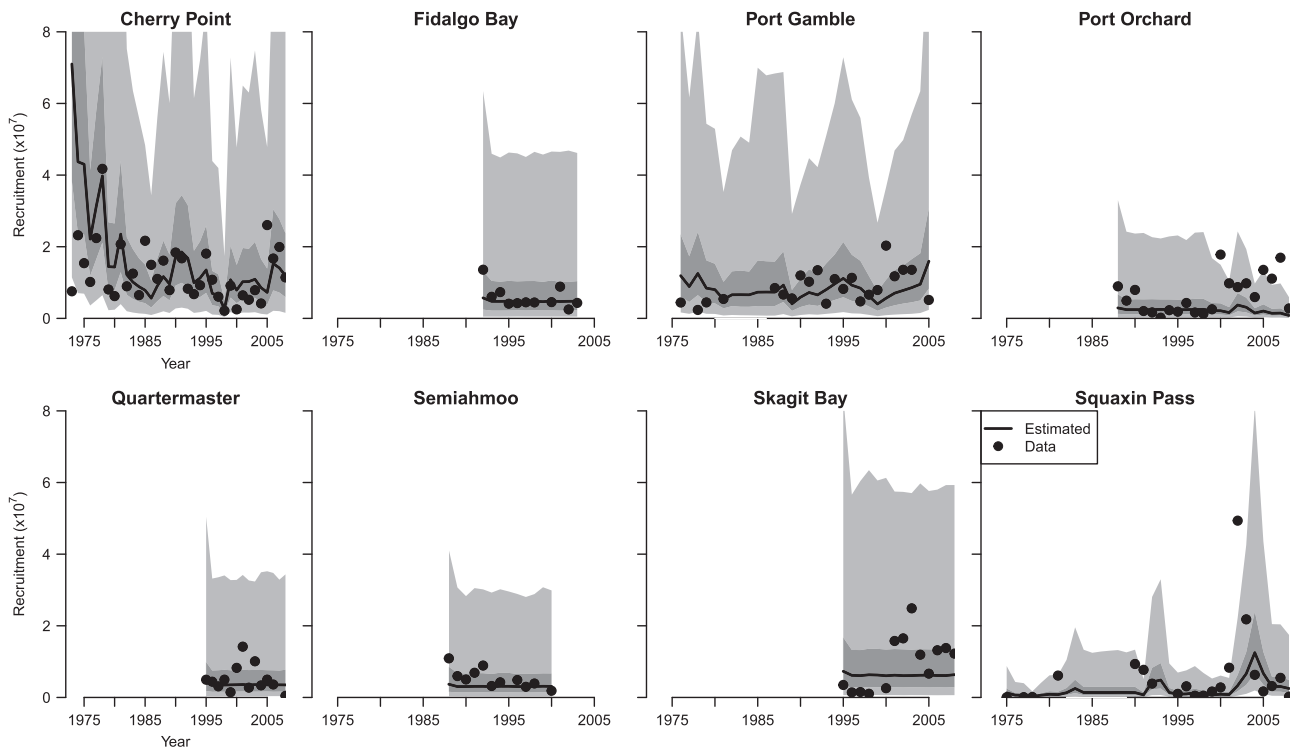

Figure 3. Recruitment to age 3 estimated by the best fit model (median, black line; with 50% and 95% credible intervals shaded) and observed recruitment to age 3 (points) at each site.

adult mortality are still an important consideration, but require higher resolution survey data to detect.

Although we found adult mortality to be a dominant driver of population dynamics in herring, we expect survival through early life history to be important in Puget Sound during other regimes. Forage fish experience large swings in productivity based on the availability of planktonic food sources for newly emerged larvae (Cushing, 1990), the retention of larvae and transport to areas

with planktonic prey (e.g. in the Kuroshio Current Ecosystem; Yatsu *et al.*, 2013), and changes in sea surface temperature that affect growth and recruitment. Herring recruitment, influenced by environmental conditions, is often the source of large fluctuations in productivity as well (Saetre *et al.*, 2002). Finally, age 0–3 herring experience high and variable natural mortality, which can dampen or exacerbate changes in year-class strength (de Barros and Toresen, 1998). In our model, recruitment occurs to age 3, so the "recruitment" estimated by the model includes both environmental impacts on early life history (predation and starvation during first feeding larval and early juvenile stages) as well as effects on age-1 and -2 mortality. A dependency on recruitment may appear as spatial differences in population dynamics; in Puget Sound, predation on herring eggs (Anderson *et al.*, 2009) and juvenile herring (Beaudreau and Essington, 2011) generate spatial difference in early life history survivorship. Therefore, age truncation may give way to spatial differences in early life history survival if this pattern persists.

Our results demonstrate that adult herring in Puget Sound have high and increasing rates of natural mortality. Higher susceptibility of older adults to pathogens and bioaccumulation of contaminants are two plausible sources of mortality for older herring in Puget Sound. Older herring are more susceptible to certain infectious diseases and parasites; e.g. *Ichthyophonus hoferi* infection rate and parasite load both generally increase with age (Hershberger *et al.*, 2015). Diseases can also act synergistically, exacerbating the effects of other stressors (Hershberger *et al.*, 2006). Lipophilic contaminants such as PCBs, which tend to bioaccumulate in older individuals, are particularly relevant in highly urbanized estuaries like Puget Sound. Tissue PCB concentrations are higher for Puget Sound resident fish (in this case, Chinook salmon) than oceanic migrants (West *et al.*, 2008; O'Neill and West,
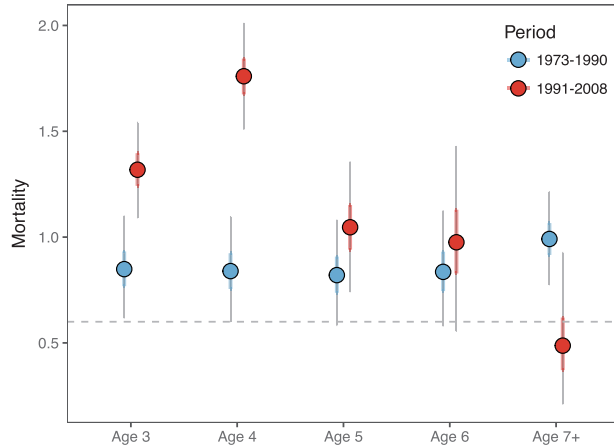
Figure 4. Posterior distributions of $M_{a,p}$ where p represents the time period (first or second half of the survey time series) and a represents age. Vertical bars indicate 50% and 95% quantiles. The average M previously estimated for Pacific herring on the Pacific Coast, and the mean of the prior used for all $M_{a,p}$ ($M = 0.6$; Hourston and Haegele, 1980) is represented by a dashed line.
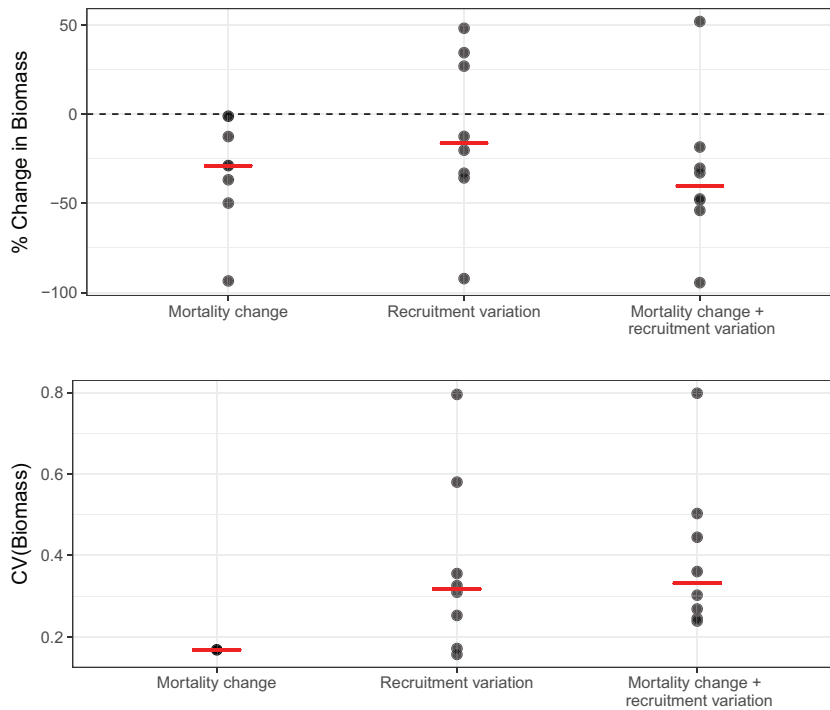
Figure 5. Simulated percent change in biomass and CV(Biomass) over the survey time period, based on simulations with mortality changes and recruitment variation estimated from the model. Each point represents one site; bars indicate the median across all sites.

2009) and have not declined in Puget Sound Pacific herring since 1990 (West and O'Neill, 2007). Contaminants and disease may also make herring more susceptible to other sources of mortality such as predation via sublethal effects. Age truncation occurred across sites, suggesting that the observed changes were not simply due to movement of adults between sites. This is supported by genetic evidence, which indicates little or no mixing of spawning adults between Washington and British Columbia stocks (Beacham *et al.*, 2008).

There is conflicting evidence that the observed increase in adult mortality could have resulted from increased predator abundance. Abundances of some herring predators in Puget Sound are not consistent with this possibility: Chinook salmon, e.g. have declined to less than half of their estimated historical run size (Good *et al.*, 2005), and several species of seabirds that consume adult herring are also in decline (Western grebes have declined by 95% in Puget Sound since 1975; surf scoters at some locations have declined by 97.5%; Puget Sound Action Team, 2007; Pearson and Hamel, 2013). Exceptions to this general decline in seabird abundance are double-crested and pelagic cormorants, which are main seabird predators of herring in Puget Sound and have increased 97 and 87%, respectively, between 1978 and 2005 (Bower, 2009). In contrast, pinniped populations (sea lions and harbour seals) regularly consume herring (NMFS, 1997) and have increased exponentially in abundance (harbour seal abundance increased seven- to tenfold between 1970 and 2003; Jeffries *et al.*, 2003; Steller sea lions increased three- to fourfold between 1979 and 2010; Wiles, 2015). If the high consumption rates of Chinook salmon by pinnipeds (Chasco *et al.*, 2017) are comparable to predation pressure on herring, predation mortality could be an important factor.

Incorporating changes in vital rates into population assessments will be an ongoing challenge to managing fish and wildlife in a changing climate. For exploited fish populations, accurately identifying temporal changes in natural mortality influence is essential to understanding drivers of abundance (e.g. Predator-driven Allee effects; Kuparinen and Hutchings, 2014; Swain and Benoît, 2015) and accurately assessing population status (Johnson *et al.*, 2015; Thorson *et al.*, 2015). Changes in natural mortality have also been documented in Atlantic cod (Swain, 2011), winter skates (Swain *et al.*, 2009), and white hake (Benoît *et al.*, 2011). Our findings add to the growing body of evidence that changes in natural mortality are an important consideration for assessing population trends and ecology. Although high natural mortality is expected for forage fish relative to other marine fishes because of predation, the pattern of increasing *M* with age is contrary to most models of mortality in marine fish, which often assume that survival increases with size because predators are gape-limited (Sogard, 1997). In most fished populations, fishing mortality increases with age, but the bait fishery for Puget Sound herring selects younger individuals, so fishing mortality does not explain the differences in *M* observed here. Increases in natural mortality can remove the buffering effect of adult survival on population size, making fish populations more sensitive to recruitment variation. Here we demonstrate temporal changes in natural mortality in a key forage species. These changes are sufficiently large to cause long term declines in biomass, in combination with other demographic changes. Long-term shifts in adult mortality, although challenging to detect in heavily exploited populations, should be considered a possibility for forage species and incorporated in population assessments, as should particularly high rates of adult mortality.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the article.

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