

Fishing, environment, and the erosion of a population portfolio

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Abstract. Many organisms exhibit tremendous fluctuations in population abundance and experience unexpected collapse. Conservationists seeking to minimize region-wide variability in resources and reduce extinction risk often seek to preserve a metapopulation portfolio of spatially asynchronous subpopulations connected by dispersal. However, portfolio properties are not necessarily static, and the erosion of a portfolio can fundamentally alter the population dynamics and services a species provides. In the Northeast Pacific, a portfolio of spatially asynchronous herring populations has historically provided regional reliability of herring to mobile predators and commercial fishermen as well as local subsistence and ceremonial harvest. Here, we fit a mechanistic time-series model to herring spawn and catch records from 1950 to 2015 to quantify how population growth, climate, and fishing have contributed to a major shift in the herring portfolio over time. We document the erosion of the herring portfolio and a severe decline in herring population growth. Commercial harvest historically played a key role in herring dynamics, hovering around typical annual exploitation rates (15%) at the archipelago scale, but local harvest rates were much higher when fishing occurred (as high as 65%). Additionally, the Pacific Decadal Oscillation and population growth had equally strong effects on local and regional herring population dynamics. Our results highlight how spatially structured populations can undergo major shifts following disturbance and emphasize how ecological systems do not always rapidly recover and provide services following disturbance. Developing herring management strategies at a finer scale may ensure greater regional resource reliability by recovering previous levels of spatial population asynchrony. However, doing so may require higher implementation and monitoring costs in order to yield higher ecological, social, and economic benefits. Such place-based solutions that match the spatial scale of governance to the spatial scale of ecological dynamics have the potential to improve future management and conservation in an increasingly dynamic world.

Key words: biocomplexity; forage fish; Haida Gwaii; herring; place-based management; portfolio.

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INTRODUCTION

Spatial asynchrony of population abundance and demographic rates is common in numerous taxa, including insects (Ehrlich et al. 1975), plants (Waddle et al. 2019), birds (Ringsby et al. 2002), and fishes (Hilborn et al. 2003). Ecologists and conservation biologists have been increasingly interested in the existence of asynchrony among subpopulations connected through dispersal because it is directly related to metapopulation viability. When populations are connected and highly asynchronous, extinction risk is reduced because abundant subpopulations can re-establish those that have been extirpated (i.e., a rescue effect; Hill et al. 2002). As a corollary, synchronous subpopulations lead to higher likelihood of metapopulation extinction. Therefore, understanding the degree of population asynchrony in wild populations, as well as drivers and patterns of shifts in asynchrony through time, is key to the conservation and management of metapopulations.

Underlying drivers of population asynchrony include genetic or ecological differences in populations across space, spatio-temporal variability in breeding habitat availability, and life-history diversity linked to local environmental drivers. For example, asynchrony across house sparrow populations is driven by local weather conditions that cause variable breeding timing (Ringsby et al. 2002). Similarly, in Pacific salmon (*Oncorhynchus* spp.), spatially asynchronous populations emerge from covariance between life-history diversity (e.g., spawn timing, morphology, egg size, and time spent in sea vs. freshwater) and local environmental variability. The resulting asynchronous population fluctuations generate a population portfolio (similar to financial portfolios; Markowitz 1952), which reduces extinction risk by increasing regional metapopulation stability (Hanski 1998, Leibold et al. 2004, Schindler et al. 2015) and thereby increases the reliability of resources to humans (Nesbitt and Moore 2016) and other predators in the ecosystem (Armstrong et al. 2016).

Importantly, asynchrony is not a fixed, time-invariant attribute of systems. Human impacts, ecological changes, or environmental shifts can decrease spatial asynchrony (Liebhold et al. 2004). This decreased asynchrony can reduce the

viability of the metapopulation and associated ecosystem services. For example, an increase in predators or large-scale environmental impacts can synchronize highly asynchronous populations (Liebhold et al. 2004). Reduced population asynchrony can alter provisioning of cultural and ecosystem services (Luck et al. 2003). In sockeye salmon (*O. nerka*), spatial asynchrony halves variability in annual biomass (Schindler et al. 2010). Increased resource reliability lowers the probability of salmon fisheries closures (Schindler et al. 2010) and is beneficial to mobile predators and riparian ecosystems that are dependent on salmon (Ruff et al. 2011). Consequently, a reduction in the portfolio generated by lower asynchrony can have deleterious effects on the ecological roles and services provided by a species.

Identifying the ecological and environmental drivers of population asynchrony may have important conservation and restoration implications. For example, when a population collapses, identifying which subpopulations might be targeted for restoration to promote population diversity may facilitate regional recovery and system-wide buffering capacity. Here, we explore changes in spatial asynchrony in Pacific herring (*Clupea pallasii*), a species known for boom and bust cycles, important prey for a range of top predators, and the focus of both industrial and indigenous fisheries (Siple and Francis 2015). We make use of a 65-year (1950–2015) spatially explicit data set in Haida Gwaii, British Columbia, Canada, and use it to fit a metapopulation model for 11 local subpopulations of Pacific herring. This approach allows us to ask:

1. What are the relative roles of population growth, climate, and fishing in driving changes in local and regional herring populations?
2. How have local and regional herring populations changed over time?
3. How have patterns of spatial asynchrony in local herring populations changed over time?

METHODS

Study species and system

Pacific herring are an ecologically, commercially, and culturally valuable fish of the North

Pacific (Levin et al. 2016) and are a useful model for examining the causes and consequences of population asynchrony in wild populations. Abiotic and biotic forcing at both local and regional scales drive Pacific herring life-history and population structure (REF), which likely shape population dynamics. Herring recruit to the spawning population at age 3. At age 3 and older (Hay 1985), spawning adults annually migrate from the pelagic environment to inshore habitats to spawn in particular bays along the coast (Floststrand et al. 2009), where they deposit their eggs on shallow subtidal habitats vegetated with algae and eelgrass, *Zostera marina* (Shelton et al. 2014). Larger juvenile herring migrate to deeper waters and individuals from multiple locations are thought to intermix in the coastal ocean, where they experience similar environmental conditions. After maturing, reproductive herring return to spawning beaches and the process repeats. Thus, herring life-history provides the potential to reflect both unique and shared components that may synchronize or desynchronize local populations.

Pacific herring maintain a central node within Northeast Pacific food webs, support top predators (Surma and Pitcher 2015), and are a cultural keystone species for indigenous peoples (Thorn-ton and Kitka 2015). They occur throughout the North Pacific, from the Yellow Sea to coastal California (Love 1996), and local and regional oceanographic conditions have been linked to Pacific herring growth and recruitment (Schweigert et al. 2010).

We focus on herring populations of Haida Gwaii, a remote 300 km long archipelago of ~150 islands (~10,000 km² land area) located at the edge of the continental shelf, 70 km off the north coast of British Columbia, Canada, with a human population of <5000. Haida Gwaii is located at the intersection of the Alaska and California currents, which generates high seasonal oceanographic variability. Throughout the region, system productivity is strongly influenced by upwelling (Crawford 1997).

In Haida Gwaii, herring support both commercial and traditional spawn-on-kelp subsistence fisheries (Jones et al. 2010), but major stock declines in 1967 and 1994 resulted in the closure of the commercial fishery (Cleary 2014). Spawn-on-kelp fisheries occur after Pacific herring spawn,

while other fisheries catch pre-spawning adults aggregated in staging areas near spawning sites (Shelton et al. 2014). Predation and commercial fishing cause high mortality in herring adults, juveniles, and eggs during the spring spawn (Schweigert et al. 2010).

Analytical approach

We constructed a Bayesian state-space model to quantify the dynamics of herring at local and archipelago scales in Haida Gwaii. Below, we first describe available data on herring spawn and catch records as well as study locations, then detail our population model and statistical approach.

Data description

We used data from 11 herring subpopulations, geographical units whose boundaries are subdivisions of statistical areas where herring spawn (Hay et al. 2008) in Haida Gwaii (Fig. 1). Subpopulations are identical to sections defined by the Department of Fisheries and Oceans (DFO), but differ from the statistical areas and management areas within which DFO manages herring catch limits (Hay et al. 2008). Currently, DFO manages two separate major stocks. Rennell Sound and Englefield Bay are managed as DFO stock A2W and the south eastern stocks from Cumshewa Inlet (CI) to Louscoone Inset (LI) are managed as a separate area HG.

We used two different data sources to construct our population model for herring subpopulations. First, we used the DFO herring spawn habitat index, an index that estimates the amount of eggs spawned in each subpopulation (the product of the spawn length, spawn width, and scaled by the thickness of spawn layers) measured in units of eggs layers m² (Hay et al. 2008). These data are historically (1950–1987) derived from surface surveys and more recently (1988–2015) from standardized snorkel and SCUBA surveys (Cleary 2014). Though spawn surveys were conducted annually, data were missing for a number of year–subpopulation combinations. Second, we used spatially explicit herring catch records collected by DFO since 1950. Recorded catch (in metric tons) are reported from seine, gillnet, trawl, and open (non-pond) spawn-on-kelp fisheries in each of the subpopulations. Note that the coverage of

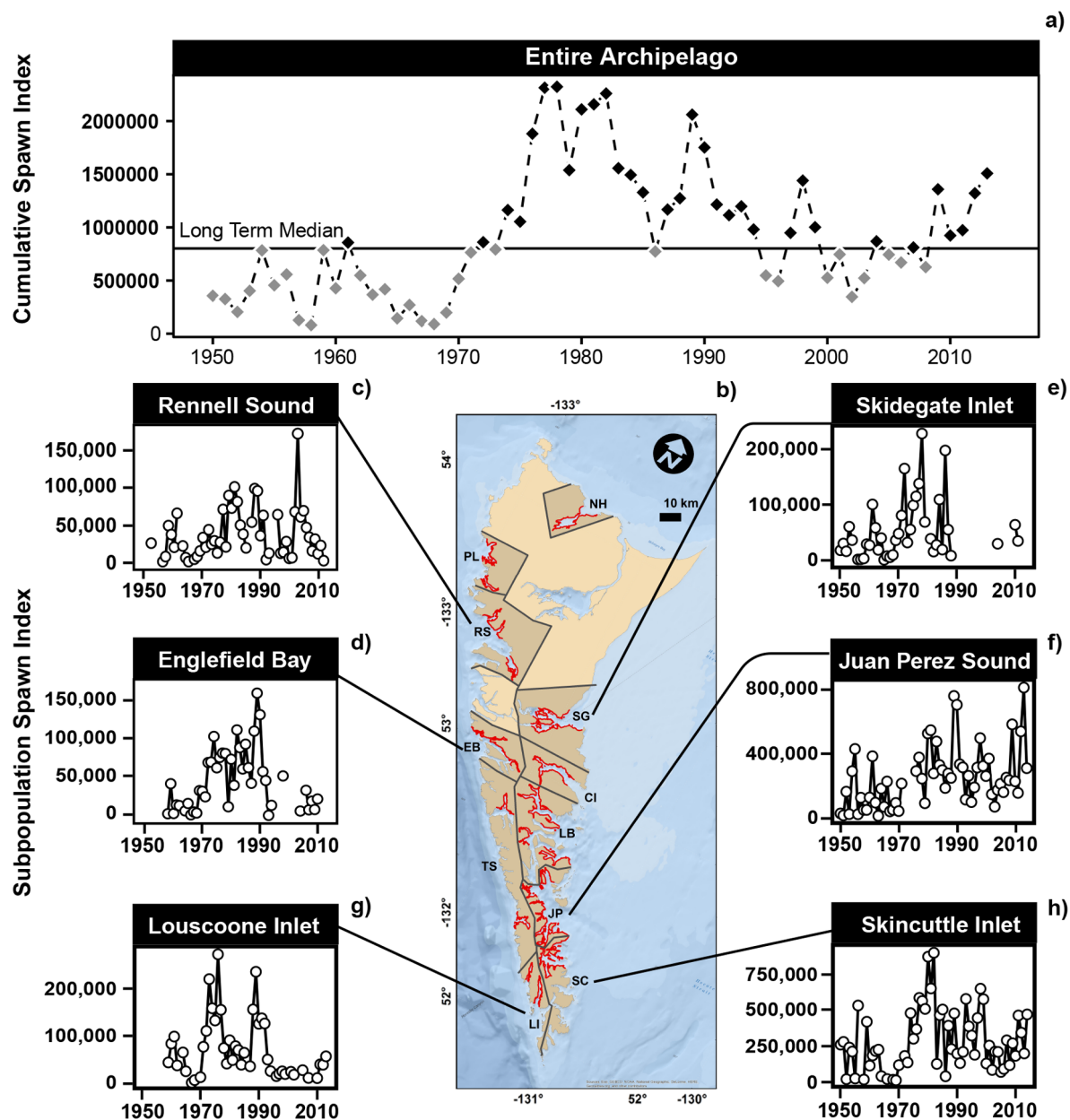


Fig. 1. Spatio-temporal variation in herring spawn in Haida Gwaii. Time-series show cumulative spawn index for entire archipelago (a). Map represents each of 11 subpopulations (b), with coastline surveyed for herring spawn in red. Individual subpopulation spawn index is shown for six focal subpopulations surrounding the archipelago (c–h). Solid line in panel (a) represents the long-term median spawn index, points above the long-term median are black, points below the median are gray.

spawn and catch data were not uniform across space or through time (Appendix S1). Because certain subpopulations were particularly data-poor, we fit the model to all 11 subpopulations

but focused on the model results for 9 data-rich subpopulations, which comprise the vast majority of herring in Haida Gwaii. Importantly, as the fishery targets pre-spawning individuals, catches

occur before spawn surveys occur. While we were confident that catch records and spawn index data points greater than zero were accurate, reports of zero spawn in particular subpopulation–year combinations were considered ambiguous, so they were classified as missing data. While it is possible that the location–year combinations correspond to actual zero observations, in general our understanding of the data suggest that those are primarily missing data, not true zeros. We could add a hurdle component to the model, but we believe that treating the observations as missing is a closer approximation to the truth. In addition, to our knowledge there are almost no examples of true extirpation of local herring stocks along the west coast of North America; there are many examples of populations being pushed to low levels and being difficult to accurately survey, though (Siple and Francis 2015). The structure of our model imposed an assumption that local extinction has not occurred in any of the populations ($B > 0$ at all locations and years). We assume biomass can fall to very low levels but we assume there is always some small number of fish in each modeled area.

DFO meticulously applies quality control methods to their reporting of catch and spawn data; however, we acknowledge that long time-series such as this one contain some level of variation among observers. We suggest that this may have contributed to observation error in the spawn index.

We used the Pacific Decadal Oscillation (PDO) Index as a measure of regional oceanographic conditions. The PDO largely reflects ocean temperature and the index is high during anomalously high temperatures and low during anomalously low temperatures. The PDO is a known correlate with increased zooplankton (herring prey) availability, and this increase in zooplankton during anomalously cold productive years is a hypothesized mechanism underlying correlations between the PDO and herring productivity south of Haida Gwaii on the West Coast of Vancouver Island (Ware 1991), and more broadly across the northeast Pacific (Mantua et al. 1997). We calculated the yearly average PDO scores and incorporated them into our population model.

Ideally, we would incorporate information from additional covariates hypothesized to affect herring, such as abundance and consumption rates by predators like pinnipeds or humpback whales (Schweigert et al. 2010). Unfortunately, data on herring predators were not available for the entire time-series. Furthermore, existing predator abundance estimates were aggregated at the archipelago scale and could not be mapped to particular subpopulations that are the focus of this study. In the absence of adequate data on herring predators, we elected to estimate the effects of predator and other unknown biological processes implicitly as a component of the process variability.

Model description

Our model describes annual spawning biomass and population growth rate for the 9 focal subpopulations simultaneously and combines information from the spawn index, catch records, and the PDO index. We first describe our model of herring biology in the process model before detailing the link between our process model and the observed data.

Process model.—We modeled the pre-catch spawning biomass of herring in each subpopulation s and time $t + 1$ (i.e., the sum of the estimated catch ($C_{s,t+1}$) and the estimated post spawning biomass ($B_{s,t+1}$) as a function of the previous year's estimated spawning biomass $B_{s,t}$, the density-independent population growth rate U , a shared regional oceanographic driver (πPDO_t , where π is the coefficient measuring the strength of the PDO effect), and additional process variability $\delta_{s,t}$. Let $Z_{s,t} = B_{s,t} + C_{s,t}$ be the biomass present before the fishery, calculated on the log-scale,

$$\log(Z_{s,t+1}) = \log(B_{s,t}) + U + \pi\text{PDO}_t + \delta_{s,t}. \quad (1)$$

We used a density-independent formulation (linear in log-space) for herring dynamics for two reasons: (1) herring have been heavily exploited by commercial fisheries in the Pacific since at least 1900, allowing us to assume that Pacific herring have been substantially reduced from their pre-fishing abundance and are reasonably well approximated by density-independent dynamics (Vert-pré et al. 2013); and (2) evidence for density-dependent recruitment in Pacific herring in

this region is poor (Zheng 1996). When considered broadly across population viability analyses, density-independent models often serve as reasonable approximations (Sabo et al. 2004). Note that the biomass and population growth at time t predicts the biomass and catch at $t + 1$ collectively because commercial fishing typically occurs each year before herring spawn, whereas abundance surveys occur after spawning. This formulation is appropriate given herring life-history and the shared oceanic environment of adults and is supported by recent genetic and population analysis, suggesting that some population structure exists in herring at fine spatial scales (Siple and Francis 2015).

Climate and fishing are thought to explain much of the variability in herring population dynamics, but other unmeasured processes (e.g., predator abundance or habitat quality) may also be influential. We modeled these other, unspecified processes as $\delta_{s,t}$, a multivariate normal variable with mean 0 and a homogeneous variance across all subpopulations σ^2 . Consequently, this form for the process variability reflects a wide variety of unobserved processes, including consumption by predators, for which we lack adequate data. We initially considered several other model structures, including those with subpopulation-specific differences in growth rates and auto-regressive temporal and spatial formulations; however, gaps in site specific spawn information precluded our capacity to estimate these more complicated dynamics because models would not converge on a solution (Appendix S2).

Observation model.—We did not have direct observations of herring biomass for each subpopulation, so we used the observed spawn index of herring for each subpopulation–year combination, $E_{s,t}$, as our index of herring biomass. We assumed that $E_{s,t}$ scaled proportionally with the true biomass $B_{s,t}$ (Hay et al. 2008) by a factor q_m (catchability), so that

$$\log(E_{s,t}) \sim \text{Normal}(\log(q_m) + \log(B_{s,t}), \tau^2), \quad (2)$$

where τ^2 is the measurement error for the spawn index. We estimated two q for the two survey methods (q_1 for surface surveys and q_2 for SCUBA surveys).

Similar to the spawn index, we assumed that catch data were proportional to the biomass

available before the fishery $Z_{s,t}$ such that

$$\log(C_{s,t}) \sim \text{Normal}((\log(F_{s,t}) + \log(Z_{s,t})), \epsilon^2) \quad (3)$$

where $C_{s,t}$ is the reported catch, $F_{s,t}$ is the estimated proportion of the pre-spawn biomass caught in each subpopulation–year combination, and $Z_{s,t}$ is the pre-spawn biomass in each subpopulation–year combination. Equation 3 only incorporates information from subpopulation–year combinations in which fisheries occurred. We assumed catch was reported accurately and fixed $\epsilon^2 = 0.001$.

Estimation details

Priors.—We used **diffuse non-informative priors** for the majority of parameters. We provided informative priors for q_m (catchability) and τ^2 , the measurement error for the spawn index (Appendix S3).

Estimation.—We implemented our model using JAGS (Plummer 2003), which uses Markov chain Monte Carlo (MCMC) methods to estimate parameters. We ran 4 chains for 500,000 iterations with a burn in of 250,000 iterations and thinned the chains to retain every 10th iteration (Gelman et al. 2014). **Model and code are available as a GitHub repository here <https://github.com/stier-lab/stier-2019-herring-metapop>.**

Below we explored the posterior estimates from these MCMC runs to estimate the biomass (B), archipelago-wide productivity rate (U), contribution of regional ocean conditions (π PDO), effect of fishing (F), and the process variability (δ) on herring population dynamics. For additional detail on posteriors and chains of main parameters, see Appendix S3.

MODEL ANALYSIS

What are the relative roles of population growth, climate, and fishing in driving changes in local and regional population dynamics?

Our model estimated the contributions of archipelago-wide intrinsic population growth rate, catch rates, and regional oceanographic drivers to herring dynamics. The archipelago-wide intrinsic growth rate, U , was directly estimated in the model. To quantify fishing effects at the subpopulation and archipelago scales, we summarized the proportion catch estimates into three different

response variables: (1) spatial coverage, the proportion of subpopulations with nonzero catch in any given year; (2) archipelago-wide impacts, the average proportion of archipelago-wide biomass caught across all nine focal subpopulations, including the subpopulations where zero catch occurred; (3) subpopulation impacts, the average proportion of biomass caught across focal subpopulations (ignoring the subpopulations where zero catch occurred). We estimated the impacts of ocean temperature by examining the PDO effect (πPDO_t). The contribution of the PDO effect to herring dynamics in any given subpopulation s depends on the relative magnitude of the PDO effect in year t (πPDO_t), the archipelago-wide intrinsic growth rate (U), and the process variability of the subpopulation at time t ($\delta_{s,t}$).

How have local and regional population dynamics changed over time?

The prolonged closure following the 1994 decline suggests there may have been a major shift in herring growth rates. To estimate how herring population growth has changed, we calculated the realized growth rates ($e^{(U+\pi\text{PDO}_t+\delta_{s,t})}$) for each subpopulation–year combination and compared the average realized growth rate of historical subpopulations (1950–1994) to the realized population growth rate during the most recent 15 yr, when archipelago biomass began to slowly rise (1994–2015).

How spatially asynchronous are populations, how strong is the portfolio effect, and have patterns of spatial asynchrony in local herring populations changed over time?

Previous studies linking population asynchrony to metapopulation portfolios have emphasized a basic description of the statistical properties of variance and correlation across abundance time-series (e.g., Moore et al. 2010, Schindler et al. 2010). Here, we first summarize the portfolio of the population for the entire time-series. Secondly, use a 10-year moving window analysis to examine whether the portfolio has changed through time.

To estimate the strength of the portfolio effect and its change through time, we considered four different metrics. First, we examined the ratio of the average temporal coefficient of variation (CV) of the estimated biomass at the

subpopulation scale relative to the CV of the estimated biomass at the archipelago scale (sensu Schindler et al. 2010). Second, we used a method developed by Anderson et al. (2013), which estimates how variable the biomass of the metapopulation is relative to the expected variance based on the variance of the subpopulations. This method accounts for the fact that variance of larger populations often increases nonlinearly with the size of a given subpopulation. Specifically, the portfolio effect is calculated as a linear regression between the log mean and log variance of the estimated biomass of each subpopulation. This relationship is then used to predict the expected interannual variance of the metapopulation in the absence of a portfolio effect. Third, we estimated the community wide asynchrony index proposed by Loreau and de Mazancourt (2013):

$$\psi N = 1 - \frac{\sigma_{NT}^2}{(\sum \sigma_{Ni})^2},$$

where σ_{NT}^2 is the aggregate variance of the total biomass across all subpopulations, and σ_{Ni} is the standard deviation of the biomass of each subpopulation i . The asynchrony index ranges from 1 (perfect asynchrony) to 0 (perfect synchrony). The portfolio effect based on the ratio of the mean subpopulation CV to the metapopulation CV, and mean–variance portfolio effect, and synchrony index were calculated using the *ecofolio* package in R following Anderson et al. (2013). We used each of these three metrics to estimate the portfolio effect for the entire time-series and to characterize changes in the portfolio through time.

Finally, we used a fourth metric which moves beyond these descriptive statistics by examining asynchrony of the realized population growth rates for herring subpopulations, which arises from processes shared among and unique to individual subpopulations. Shared components include both the long-term average population growth rate (U) and common effects of regional oceanographic drivers (PDO_t), whereas the process variability ($\delta_{s,t}$) accounts for additional unmeasured factors and could be similar or divergent across subpopulations. We estimated asynchrony in realized population growth rates among subpopulations by quantifying the pairwise Spearman rank correlation between the

realized growth rates of each subpopulation (i.e., $e^{(U+\pi\text{PDO}t+\delta s,t)}$).

To quantify changes in asynchrony through time (i.e., whether the portfolio is expanding or eroding), we estimated each of the four metrics described above using a 10-year moving window analysis on the median posterior estimates of biomass and process variability from the model. This was a tiered analysis that first examined changes in the portfolio based on the estimated biomass at the subpopulation and metapopulation scale then focused on the process variability for each subpopulation–year combination ($\delta s,t$). This process variability approach removed the constant effects of the archipelago-wide intrinsic growth rate and regional oceanographic conditions, allowing us to examine the process variability terms for each subpopulation and determine how among-subpopulation synchrony changed through time. Specifically, we used a moving window analysis to estimate the 10-year mean cross-correlation for all subpopulation–year combinations. We also examined the average realized population growth rate at the subpopulation scale both before and after each of the most recent population declines in 1994.

RESULTS

Since 1950, herring biomass has varied substantially at both the archipelago and the subpopulation scales (Fig. 2a). At the archipelago scale, herring biomass was relatively high in the 1950s, exhibited a substantial decline in the late 1960s, and then entered an era of high abundance from the 1970s to early 1990s (Appendix S4). A dip below the long-term average led to commercial fishery closures in 1994, after which our analysis suggests the archipelago-wide herring biomass grew above its long-term average. However, subpopulations exhibited a range of dynamics and each showed distinct, asynchronous periods of growth and decline (Fig. 2b,c).

What are the relative roles of population growth, climate, and fishing in driving changes in local and regional population dynamics?

The archipelago-wide intrinsic growth rate, regional ocean conditions, and fishing patterns each contributed to herring spatio-temporal dynamics. Archipelago-wide long-term growth

rates averaged ~6% per year (Fig. 3a). Our analysis emphasizes the importance of temperature as a regional environmental driver of herring dynamics. Herring population growth rates increased in cooler years and decreased in warmer years (Fig. 3b). Thus, changes in temperature that affected all subpopulations collectively introduced some similarity in population dynamics. The contribution of regional oceanographic conditions to herring population growth was temporally autocorrelated, with strings of cool (high productivity) and warm (low productivity) years (Appendix S5). Due to the oscillation between warm and cold oceanographic regimes, the time-averaged effect of regional oceanographic conditions from 1950 to 2015 was small (a ~1.5% increase). However, the estimated contribution of the PDO effect in some years exceeded that of the archipelago-wide population growth rate (Fig. 3), supporting our choice to use a density-independent but environmentally driven population model.

Strong differences in the timing and location of commercial fisheries harvest further contributed to herring dynamics (Fig. 4). In an average year, herring were caught from 25% of the subpopulations, with a high of 50% for the spatial coverage of fisheries in the mid-1960s and a low of 0% during closure periods (Fig. 4a). Historically, fishing effort was clustered on the eastern and southern part of the archipelago, with Skincuttle Inlet, Juan Perez Sound, and Skidegate Inlet fished most frequently (in more than 40% of years; Fig. 1).

Over the 65-yr time-series, the estimated archipelago-wide proportion of herring caught was low (4%). However, the archipelago-wide impact of fishing exhibited substantial interannual variability, including years with full closures (zero catch) and years in which >20% of the spawning biomass was processed by the commercial fisheries (Fig. 4).

In contrast, at the subpopulation scale, fishing pressure was often high and unevenly distributed in time. Excluding subpopulation–year combinations when fishing did not occur, the average subpopulation exploitation was 15% caught and ranged from 0% to 48% (Fig. 4b). The subpopulation-specific fishing impact varied spatially, with certain populations experiencing exploitation rates as high as 65% of

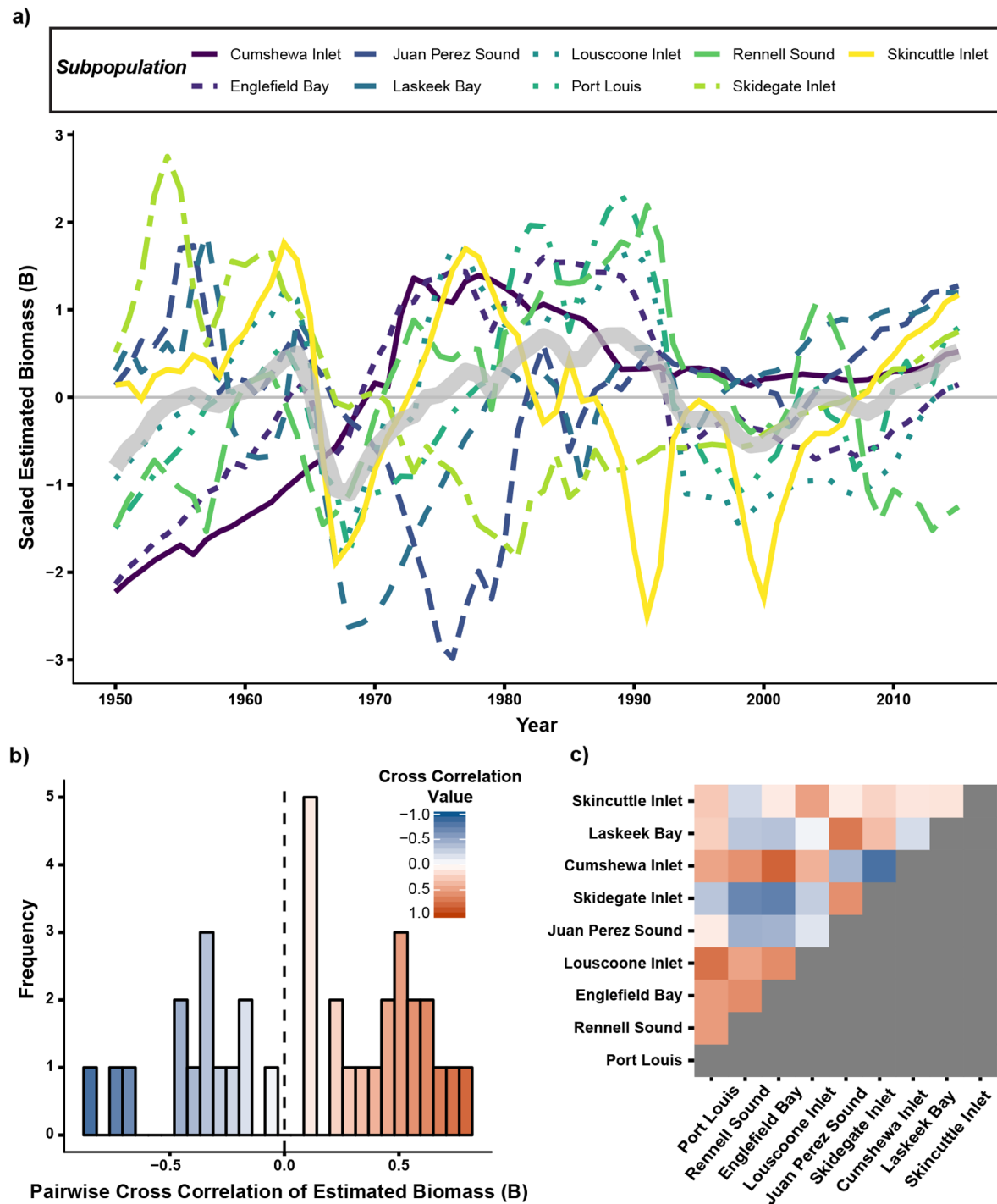


Fig. 2. Temporal variation of scaled herring biomass in Haida Gwaii. Archipelago biomass and each subpopulation's biomass were scaled to mean zero (horizontal gray line) (a). Thick gray line represents average scaled estimated archipelago spawning biomass. Colored lines represent scaled estimated biomass for 9 focal subpopulations. Estimated frequency distribution of similarity of dynamics of all subpopulations (a), and pairwise cross-correlation of each of the estimated biomass of each of the 9 focal subpopulations (b).

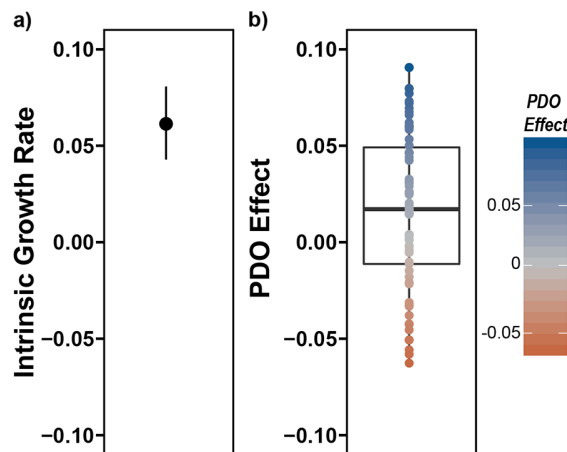


Fig. 3. Estimated average population growth rate for the entire archipelago (a). Point and error bars represent median and 95% credible interval. Boxplot and interquartile range of the PDO effect (πPDO_t) from 1950 to 2015 (b). The PDO effect is calculated as πPDO_t , where π is the coefficient measuring the strength of the PDO effect and PDO is the Pacific Decadal Oscillation Index. Individual points represent the PDO effect in any given year (blue, cold productive years; red, warm low productivity years).

subpopulation biomass (Appendix S6). Thus, our analyses demonstrated that the major decline of herring in Haida Gwaii in the 1990s was associated with unfavorable climatic conditions and high subpopulation-specific fishing mortality.

How have local and regional population dynamics changed over time?

Prior to the closure in 1994, the archipelago-scale herring growth rate was greater than the long-term average in 14 of 17 yr; in contrast, it only exceeded the long-term average in two of the past 20 yr. Indeed, estimates of recent realized population growth suggest that 7 of 9 focal subpopulations have exhibited major declines in population growth since 1994, the year in which the current and prolonged fishery closure began (Fig. 5).

How spatially asynchronous are populations, how strong is the portfolio effect, and have patterns of spatial asynchrony in local herring populations changed over time?

Our model output suggests distinct changes in population dynamics for Haida Gwaii herring

through time. The nine focal herring subpopulations were characterized by spatially asynchronous dynamics (Fig. 2). This asynchrony (e.g., an above-average year in the biomass of one subpopulation coinciding with a below-average year for another) was revealed by the variable contribution of each subpopulation to archipelago biomass over time (Fig. 2). For example, Skidegate Inlet was a major contributor to archipelago biomass in the 1950s, but had declined in relative importance since the 1960s (Fig. 2). On average, the subpopulations were highly asynchronous with an asynchrony index of 0.78 over the full time-series (Fig. 6c) and pairwise Spearman correlation between subpopulations varying from -0.8 to 0.8 (Fig 6b). The spatially asynchronous dynamics among subpopulations produced a portfolio effect, where the CV of the metapopulation ($\text{CV} = 0.82$) was more than double the average CV of the subpopulation ($\text{CV} = 0.37$; Fig. 6d). The mean-variance portfolio analysis suggested that the population was 2.1 times more stable than a homogenous population. However, over the full time-series, synchrony among subpopulations has increased by $>60\%$ for the realized population growth rate (i.e., mean pairwise Spearman correlation in 1950–1994 was 0.17, 1995–2015 was 0.28; Fig. 6b).

Interactions among fishing effects, the long-term population growth rate, and regional oceanographic conditions all contributed to low synchrony among herring subpopulations. Process variability, which estimates the effect of factors not accounted for explicitly in our model (e.g., habitat quality and predation), revealed unexpected patterns over the past 65 yr. First, the archipelago-wide average value of process variability (δ) had declined from slightly positive during the 1950s and 1960s to negative during the past 20 yr (Fig. 6 a), indicating that Haida Gwaii herring populations have recently experienced lower population growth. Second, the realized among-subpopulation variation declined over the time-series (Fig. 6 a), suggesting lower variation in growth rates in recent years (among-subpopulation variance in process variability δ_{σ}^2 : $\delta_{1950-1968}^2$, 0.08; $\delta_{1969-1995}^2$, 0.04; $\delta_{1996-2015}^2$, 0.01). Together, these patterns suggest a systematic, gradual, but unexplained shift in the coastal ocean ecosystem around Haida Gwaii that is evident even after accounting for fisheries catch and regional oceanography.

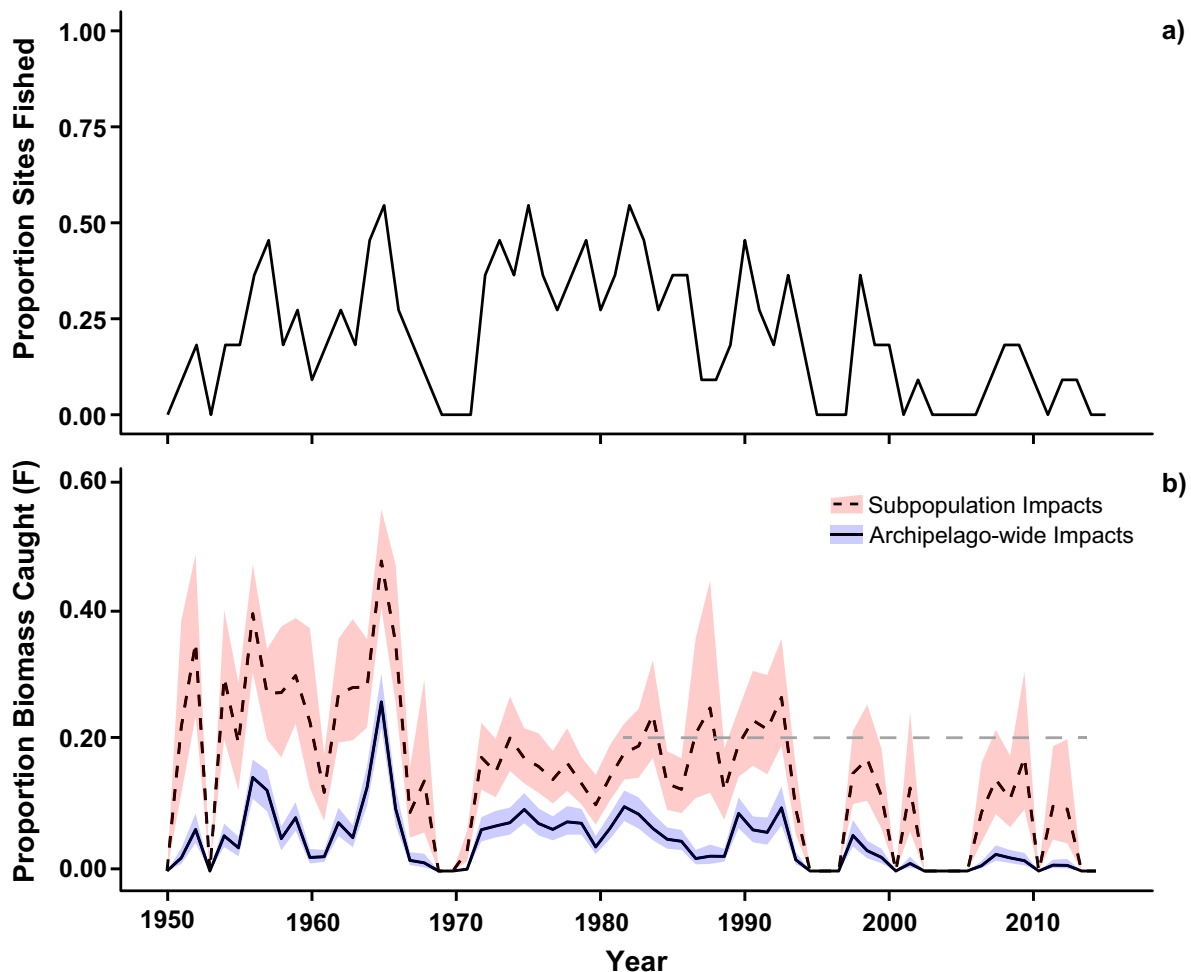


Fig. 4. Variation in fishing impacts through time. Spatial coverage, (a) the proportion of subpopulations (out of nine) with nonzero catch in any given year (right axis). The spatially averaged median fishing effect for the entire archipelago (b). Dashed line with red halo represents subpopulation impacts: the average proportion of biomass caught across focal subpopulations, ignoring the subpopulations where zero catch occurred. Solid line with blue halo represents archipelago-wide impacts: The average proportion of biomass caught across focal subpopulations, including subpopulations where zero catch occurred. Archipelago and subpopulation impacts (blue and red lines) are measured in proportion catch (F). Gray dashed line represents DFO maximum allowable herring fishing effort since 1983, shaded areas represent 95% credible intervals.

DISCUSSION

Many organisms exhibit noisy population dynamics and experience unexpected collapses (Anderson et al. 2017). After a major stock decline, a common assumption is that it will rebound with similar properties. Our study highlights how spatially segregated populations can undergo major shifts in population dynamics

and the degree of asynchrony during a period of major population decline. Such dramatic shifts can fundamentally alter resource abundance and reliability, having major consequences for ecosystem services provided by harvested organisms. Herring subpopulations exhibited a region-wide decline in population growth and an erosion of the metapopulation portfolio defined by decreased process variation asynchrony and a

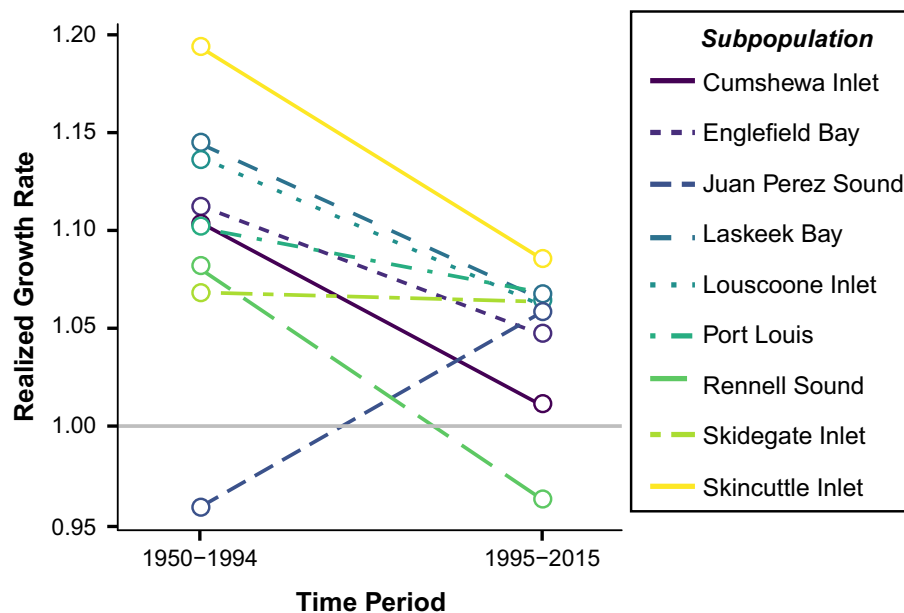


Fig. 5. Subpopulation-specific realized growth historically (1950–1994) and since the most recent fishery closure (1995–2015). Endpoints of lines represent average realized population growth for each subpopulation (represented by line type and color). Realized growth is calculated as: $e^{(U+\pi\text{PDOT}+\delta s, t)}$.

suite of metrics of population asynchrony and portfolio effects. While fishing rates were historically very high, these major shifts in population dynamics have occurred during an era of long commercial fishery closures. We present evidence suggesting that historically high harvest rates may be important to understanding earlier major stock declines, but may not hold the answer to questions about stalled recoveries in certain areas or the collapse of the portfolio. Given the decline in population growth rate and the decrease in population asynchrony that maintains the portfolio, herring may now have a more limited capacity to rebound from future exploitation events.

Potential mechanisms underlying changes in subpopulation asynchrony

Increasingly similar realized population growth rates likely underlie the increasingly similar dynamics among the subpopulations. While the drivers of these increasingly similar growth rates are unclear, ecological theory describes at least three, non-mutually exclusive drivers that may explain the observed decrease in spatial asynchrony in spatially segregated populations: (1)

shared large-scale environmental drivers, (2) increased dispersal among populations, and (3) predators focusing on areas where prey are disproportionately abundant (Liebhold et al. 2004). Our results highlight that climate can be as influential as the intrinsic population growth rate when it comes to population fluctuations in herring. Yet, widespread environmental disturbance is an unlikely mechanism because herring populations have, until recently, been experiencing favorable cold and productive environmental conditions, making it difficult to implicate a major climatic shift as the cause of reduced population growth (even if it could produce decreased asynchrony). Similarly, while high dispersal rates among local populations can homogenize their dynamics, there is currently no evidence that connectivity among herring subpopulations has increased rapidly in recent decades.

Mortality from disease, predators, and parasites is a known driver of synchrony among spatially distinct prey populations (Rohani et al. 1999, Cattadori et al. 2005, Vasseur and Fox 2009). We argue that mortality (from predation or harvest) is the most likely explanation for reduced asynchrony in Pacific herring

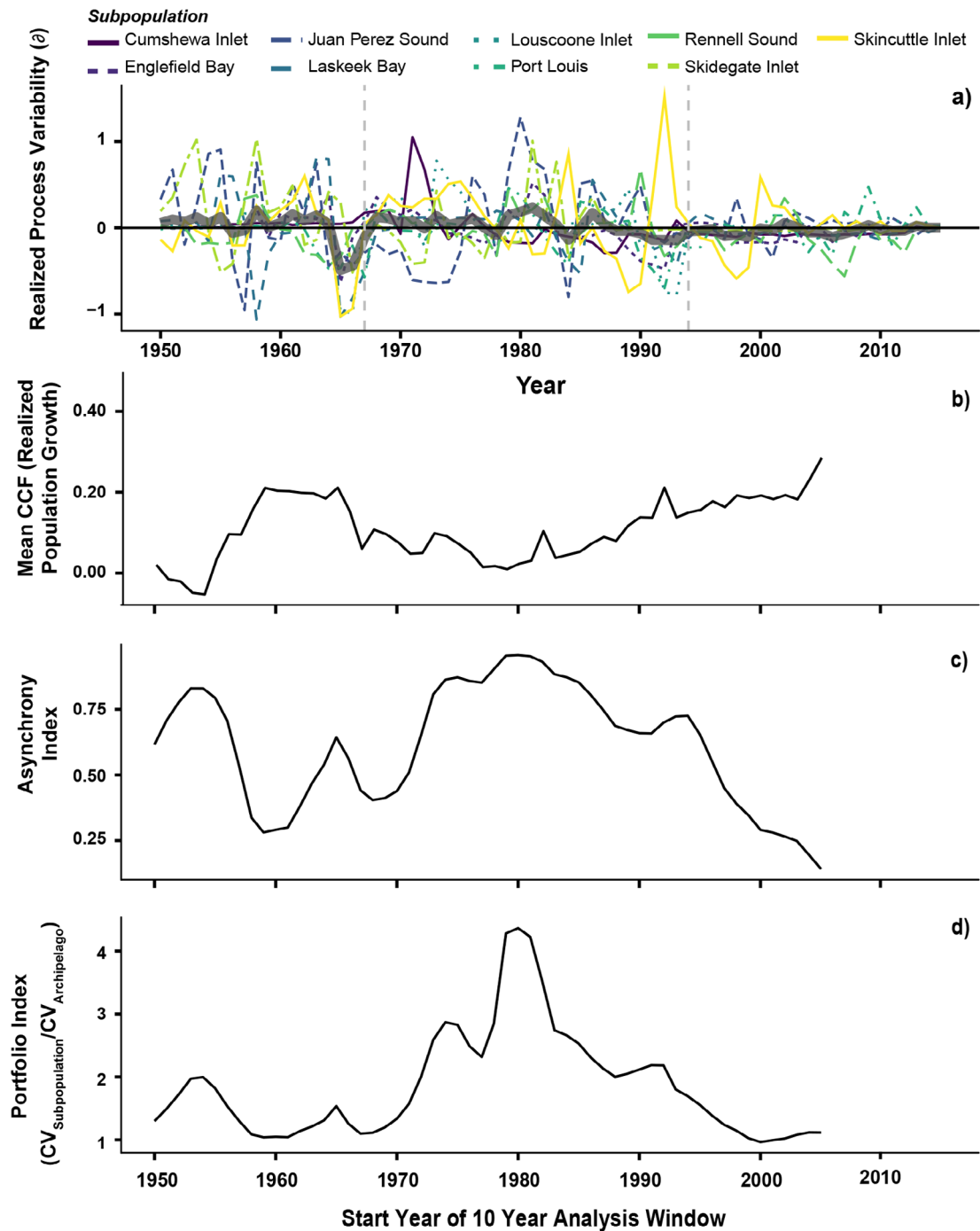


Fig. 6. Process variability (δ) representing the detrended population growth rate shifts not unaccounted for by intrinsic growth (U) and the effect of climate (π PDO). Mean (δ) across all subpopulations is plotted as a thick gray line. Individual subpopulation deltas are plotted by color and line type. Three different measures of synchrony based on estimated subpopulation and archipelago biomass are plotted: (a) mean pairwise cross-correlation in realized population growth rate, (b) asynchrony index, and (c) the portfolio effect (ratio of the CV of the subpopulation to the archipelago).

subpopulations. Highly mobile and efficient commercial fisheries often seek herring hot spots and likely distribute effort accordingly (Gillis and Peterman 1998). This higher proportionate fishing effort on subpopulations that historically generated asynchrony can lead to reduced asynchrony in dynamics of spatially distinct subpopulations. Our model demonstrates that regional catch limits were often exceeded at the subpopulation scale, and that fishing has not been distributed homogeneously. Historically, commercial harvest rates at subpopulation scale were quite high (as much as 65% of the spawning biomass). The consequences of such high local harvest rates for metapopulation dynamics will depend strongly upon additional biological details that remain unknown for herring (primarily on adult migration rates and homing rates of juveniles) and are beyond the scope of this paper. Moreover, unless reduced herring asynchrony is due to carryover effect from historically high fishing rates, additional sources of mortality through natural predators would likely be required to drive the current erosion of the portfolio.

The recovery of marine mammals (e.g., humpback whales) that prey on herring may underlie declines in herring population growth and reduced asynchrony. This marine mammal recovery is often considered the mechanism of increased natural mortality of herring in Haida Gwaii, particularly in the southern subpopulations where mortality has approximately doubled from 1973 to 2008 (Schweigert et al. 2010). In other systems, predation can reduce spatial asynchrony if predators are highly mobile relative to local prey populations (Ims and Andreasen 2000). In British Columbia, humpback whale populations have been rapidly increasing due to legal protection (Ford 2009). Humpback whales can also move quickly over great distances to feed on multiple herring subpopulations, potentially having a strong influence on the observed reduction in herring asynchrony. The combination of high historic catch rates and more recent increases in natural mortality potentially induced by predator recoveries may underlie the decline in population growth rates. Indeed, ecosystem recoveries where predators recover before their prey can be highly inefficient (Samhouri et al. 2017). Similar examples of double jeopardy associated with multiple impacts are present in other

systems and can affect ecosystem services (Marshall 2008).

Our model is an initial step toward understanding how fishing and climate drive spatio-temporal herring population dynamics. Additional research on predator-prey interactions, connectivity, and environmental impacts will benefit our mechanistic understanding of recent shifts in population dynamics, including the recent erosion of the herring portfolio. For example, future models might consider explicitly estimating the impacts of wide-ranging humpback whales, central place foraging predators such as seals and sea lions (Cook et al. 2015), and predation by groundfishes such as arrowtooth Flounder and Pacific halibut (Barnes et al. 2018). Similarly, our model links climate shifts to herring population dynamics, but does not explore links between environmental fluctuations, age structure, and density-dependent recruitment. Such interactions have been identified in the eastern Pacific for other forage fish species (e.g., sardines and anchovies; Lindegren et al. 2013), suggesting a deeper exploration of environmental impacts on Pacific herring might yield greater insight into recent low population growth rates.

Implications for sustainable harvest and conservation

Forage fish such as Pacific herring both directly and indirectly support some of the largest fisheries in the world. Yet, the high sensitivity of these stocks to environmental conditions and fishing pressure continues to challenge sustainable management and conservation efforts (Essington et al. 2015). Our study adds to a growing literature documenting spatially asynchronous population dynamics in marine systems (e.g., southern Pacific herring populations, Siple and Francis 2015; Atlantic herring, *Clupea harengus*, Secor et al. 2009; groundfish, Thorson et al. 2018; sockeye salmon, Moore et al. 2010; steelhead, *Oncorhynchus mykiss*, Moore et al. 2014; and Chinook salmon, *O. tshawytscha*). High spatial asynchrony produces a population portfolio that can increase resource resiliency and reduce the risk of fishery closures (Schindler et al. 2010). The erosion of population portfolios maintaining key marine resources have rarely been described (but see Carlson et al. 2011, Satterthwaite and Carlson 2015, Freshwater et al.

2017, Oken et al. 2018), yet may lead to resource volatility, and theoretically can destabilize the surrounding food web (Rooney et al. 2006, Oken et al. 2018) filled with key species of commercial and conservation concern (Stier et al. 2017).

Understanding spatial differences in population dynamics and changes in this structure through time is likely to improve our ability to achieve sustainable solutions for marine, terrestrial, and aquatic systems as well as the food webs and cultures that depend upon them. Our results document sustainable fishing rates at the regional scale that masked relatively high fishing rates at local scales. Such heavy local fishing pressure has the potential to disrupt socially learned migration behavior where older individuals in populations facilitate the migration of younger generations (MacCall et al. 2019). Developing herring management strategies at a finer spatial scale may significantly improve herring management (Punt et al. 2018, Voss et al. 2018, Okamoto et al. 2020), thereby ensuring greater regional resource reliability—though doing so may require higher implementation and monitoring costs in order to yield greater ecological, social, and economic benefits. Resource managers are becoming increasingly aware that sustainable management of common-pool resources may require place-based solutions (Turner et al. 2003) that match institutional and ecological scales (Leslie et al. 2015). Such considerations have the potential to improve future management and conservation in an increasingly dynamic world.

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