



Historical reconstruction of the Puget Sound (USA) groundfish community

Timothy Essington^{1,*}, Eric J. Ward², Tessa B. Francis³, Correigh Greene²,
Lauren Kuehne¹, Dayv Lowry⁴

¹University of Washington, School of Aquatic and Fishery Sciences, Seattle, WA 98195, USA

²Conservation Biology Division, Northwest Fisheries Science Center, National Marine Fisheries Service, Seattle, WA 98112, USA

³University of Washington Tacoma, Puget Sound Institute, Tacoma, WA 98421, USA

⁴Washington Department of Fish and Wildlife, Olympia, WA 98501, USA

ABSTRACT: We examined historical and contemporary trends for a suite of groundfish species in Puget Sound, Washington, USA, to ask how the groundfish community has responded following shifts in fishing regulations, climate, food web, and a growing human population in the surrounding watershed. We used contemporary data (1990–2017) from a standardized annual bottom trawl survey with historical logbook information (1948–1977) from a research vessel. We standardized data to account for spatial and temporal effects on catch rate by first fitting a Bayesian model to the contemporary data, and then using the posterior distributions of the covariates as prior distributions when fitting models to the historical data. We found that most of the 15 species chosen for analysis had highly variable population dynamics within both time periods, and that patterns of variability were similar in the contemporary and historical time period. Surprisingly, there was little evidence of community-wide recovery following regulations that first limited and then banned commercial bottom trawling in the late 1980s to mid-1990s. Spotted ratfish and English sole dominated catches in both time periods, and species that were common in the historical time period were also common in the contemporary time period. The absence of coherent community changes in response to fisheries regulations and other major social and ecological changes may signal the complex dynamics of an urban estuary that is subject to multiple external drivers, and speaks to the need to consider long-term dynamic behavior of populations and communities when establishing ecological indicators.

KEY WORDS: Estuary · Historical data · Fish assemblages · Conservation · Ecological baselines · Multiple stressors

Resale or republication not permitted without written consent of the publisher

1. INTRODUCTION

Conservation and restoration plans are increasingly using historical information to guide policy and decision making (Swetnam et al. 1999, Samhoury et al. 2011, McClenachan et al. 2012, Engelhard et al. 2016). Historical data can provide much needed context on changes in system state (Kittinger et al. 2013, Van Houtan & Kittinger 2014) and help determine the intrinsic patterns of variability of ecosystem com-

ponents (Schindler et al. 2006). Historical analysis aids conservation planning and policy in 3 ways. First, it provides information on plausible recovery targets for species or ecological processes, which may be set far below levels that ecosystems have historically supported (Pauly 1995, McClenachan et al. 2012) or may be unattainable due to the current ecosystem state (Marsh et al. 2005). Second, historical information allows for better understanding of how anthropogenic and environmental drivers have

*Corresponding author: essing@uw.edu

shaped ecosystems (Tallis et al. 2010). Third, historical analyses are also valuable in detecting slow system or transient dynamics, and in distinguishing long-term trends from low-frequency oscillations (Hastings et al. 2018).

Here we examined patterns in historical and contemporary occurrence and density for groundfish in Puget Sound, Washington State, USA. Puget Sound is one of the largest and most ecologically significant estuaries in the USA. It supports a rich fauna, including over 250 fish species (Pietsch & Orr 2019), and is the second largest estuary complex in the coterminous USA (Ruckelshaus & McClure 2007). Like many US estuaries, the surrounding watersheds support a large human population and several dense urban centers, both of which have grown rapidly in the last century, placing the ecological system under considerable stress. Currently, several fish populations and stocks are considered to be threatened and/or at-risk (Musick et al. 2000, Washington Department of Fish and Wildlife 2008), and there is widespread recognition that Puget Sound marine life is threatened by impairment of habitat and water quality (Levings & Thom 1994, Landahl et al. 1997, Bargmann 1998).

Commercial fisheries for groundfish, anadromous salmon, and Pacific herring *Clupea pallasii* operated for well over a century (Schmitt et al. 1991), and recreational fishing became prominent in the 1970s (Washington 1977, Williams et al. 2010). The only fisheries of commercial significance remaining today are for Pacific salmon (steelhead *Oncorhynchus mykiss*, coho *O. kisutch*, chum *O. keta*, pink *O. gorbuscha*, sockeye *O. nerka*, and Chinook *O. tshawytscha*). While data on a select few species indicate that populations are currently at depressed levels (Drake et al. 2010, National Marine Fisheries Service 2014), a critical outstanding question in the management of the Puget Sound ecosystem is the degree to which the current observed state of the entire marine community differs from earlier states and in particular prior to the initiation of systematic monitoring. In addition, if current and historical states are different, it is unclear whether the differences are the result of large-scale anthropogenic influences, targeted fisheries, or regional environmental influences. A related question important for management is whether there is synchrony in the response of the marine community that may result from a common set of exogenous influences, or whether individual species show unique trends or state changes.

Current efforts to implement action plans to protect and restore the Puget Sound ecosystem are hindered by a paucity of long-term data on species and com-

munity trends (Essington et al. 2011). This is because, unlike other major US estuaries, Puget Sound has not been the subject of routine, standardized monitoring across time scales that would facilitate evaluation of the success or failure of restoration and recovery policies. As a result, current understanding of ecological change comes from comparative analysis of data collected in different decades (Greene et al. 2015) or from time series collected in a geographically restricted area (Essington et al. 2013). Longer time series that incorporate the full geographic and biological extent of the ecosystem are needed to reveal the consequences of anthropogenic and environmental change on fish species in Puget Sound.

We developed a new method that uses contemporary (1992–2016) survey data collected by the Washington Department of Fish and Wildlife to standardize historical (1948–1977) data, and applied that method to reveal patterns (trends and characteristic variability) in the Puget Sound groundfish community. We focused on the groundfish community to fill a gap in understanding about the Puget Sound marine ecosystem as a whole. Species comprising this community are taxonomically diverse, including several species of Chondrichthyes (sharks, rays, and chimaeras) and Teleostei (flatfishes, cods, eelpouts, and others). We first summarize information on anthropogenic and natural drivers of change in Puget Sound and then ask ‘What are characteristic patterns of variability in population and community dynamics?’; and ‘Has there been a wholesale shift in the groundfish community and, if so, can it be linked to specific anthropogenic or natural drivers?’

2. METHODS

2.1. Recent history of Puget Sound

As is true for most coastal ecosystems (Jackson et al. 2001), Puget Sound has a long history of fishing. Commercial fishing for groundfish operated in Puget Sound beginning in the late 1800s and persisted through the bulk of the 20th century. Commercial groundfish fisheries targeted flatfish, gadids, skates, Pacific spiny dogfish *Squalus suckleyi*, and rockfishes (*Sebastes* spp.), primarily using bottom trawls (over 50% of catch), midwater trawls, and various fixed gear (Palsson et al. 1998). Bottom trawling landings reached a peak of ca. 12 250 mt annually in the 1980s. Thereafter, landings declined sharply owing to stock depletion (Palsson et al. 1997, 2009) and a series of regulatory actions that closed large regions of Puget

Sound to state-endorsed trawling in 1989 and banned non-tribal bottom trawling in 1994 (Palsson et al. 2009; Fig. 1). Recreational fishing for groundfish has spanned Puget Sound since the 1950s (Washington 1977, Beaudreau & Whitney 2016), and while total landings were typically <20% of commercial landings (Palsson et al. 1997), recreational landings for some species such as rockfishes exceeded commercial landings and likely contributed to population depletion (Williams et al. 2010). The 1974 Boldt decision that granted salmon harvest rights to Native American tribes resulted in a redirection of non-tribal recreational fishing effort towards groundfish, especially rockfish (Williams et al. 2010). Subsequently, several regulatory actions (e.g. bag limits, marine protected areas, species take prohibitions) were enacted through the late 1980s and early 1990s that diminished the intensity of recreational fishing on groundfish (Palsson 1998). Pacific herring, an important prey species for many groundfish (Harvey et al. 2012), was fished heavily in the 1960s and 1970s, initially for reduction and then in sac-rope fisheries. Today, commercial fishing for herring persists at much lower levels, primarily to provide bait for the recreational salmon fishery

(Stick et al. 2014, Sandell et al. 2019). Commercial and recreational salmon fisheries have operated for decades, with landings peaking (ca. 35 000 mt statewide) in mid-century (Fig. 1). Thus, a combination of regulation and market forces led to distinct periods of high (1960–1980) and low (1995–present) fishing intensity targeting multiple levels of the food web (Fig. 1).

Other anthropogenic and natural changes to Puget Sound may have had important effects on marine life (Fig. 1). Most notably, human population density in the jurisdictions surrounding Puget Sound has grown at an annual rate of nearly 20% per decade (US Census Bureau, www.census.gov), outpacing the US national rate by nearly 2-fold (Fig. 1). This growing human population is associated with numerous ecosystem-level effects, including harmful algal blooms (Anderson et al. 2002, Johnson et al. 2010), toxic contaminant inputs (Hart Crowser Inc 2007, West et al. 2008), and nearshore habitat alteration (Dethier et al. 2017). At the same time, terrestrial organic carbon inputs associated with run-off and logging activities have declined in recent decades (Brandenberger et al. 2008), and the closure of smelting plants has reduced inputs of some combustion-derived pollutants (Louchouart et al. 2012).

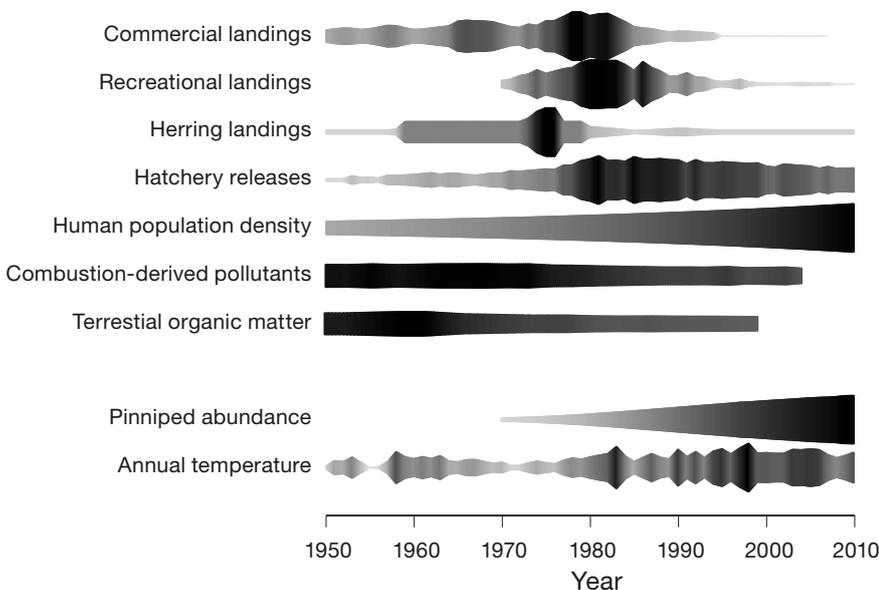


Fig. 1. History of select anthropogenic and environmental drivers on Puget Sound. Commercial and recreational groundfish landings taken from Palsson et al. (1997, 1998), Williams et al. (2010), and Stick et al. (2014). Thickness and color intensity are proportional to the intensity of each driver (each scaled relative to itself for comparison). Hatchery releases of coho and Chinook salmon from www.rmhc.org; human population density from the US Census bureau (www.census.gov). Pollutants and terrestrial organic matter taken from Louchouart et al. (2012) and Brandenberger et al. (2008), respectively. Pinniped abundance is the sum of Steller sea lions, California sea lions, and harbor seals (Chasco et al. 2017a). Annual temperature is scaled annual surface water temperature anomalies from Race Rocks, Washington

Changes in the Puget Sound food web and climate regime over this same time period may also influence groundfish abundance patterns. Hatchery releases of several species of Pacific salmon expanded rapidly in the mid-1970s, reached peak levels in the late 1980s, and have declined since then. Abundance of Pacific salmon in the Salish Sea can range widely on an annual basis and is generally correlated with large-scale environmental factors like the Pacific Decadal Oscillation and El Niño–Southern Oscillation. These broadscale drivers, along with variation in hatchery release schedules, can result in substantial variation in predation and competition effects for resident fish populations (Nelson et al. 2019). Also, densities of pinnipeds (primarily Pacific harbor seals *Phoca vitulina*, but also California sea lions *Zalophus californianus* and Steller sea lions *Eumetopias jubatus*) have increased sharply since the passage of the 1972 Marine Mammal Protection Act (Jeffries et al. 2003, Chasco et al. 2017a; Fig. 1) and the

energetic demands of these populations place predation pressure on pelagic and groundfish prey species (Ward et al. 2012, Chasco et al. 2017b). Declines in herring populations mentioned above may influence groundfish abundances, as well, given their ubiquity in historical and contemporaneous diets of many benthic and pelagic species (Harvey et al. 2012). Meanwhile, the well-documented climate regime shift in the late 1970s from a cold to a warm phase of the Pacific Decadal Oscillation (Mantua et al. 1997) has had detectable influence on Puget Sound oceanographic conditions (Moore et al. 2008a,b), although its effects on species and communities in Puget Sound are complex, species-specific, and not fully established.

In summary, the period of 1950–2010 was one of substantial change in Puget Sound, particularly between 1970 and 1990 when there were large changes in fisheries management regulations, large changes in hatchery salmon production, and an environmental shift from a cold to a warm regime. Meanwhile, throughout the entire period there have been sustained changes in drivers such as human population density and pinniped abundance. Any of these major system changes may have influenced demersal fish communities during this time.

2.2. Data

Our goal was to estimate species-specific trends in Puget Sound groundfish (Table 1) for historical (1948–1977) and contemporary (1990–2016) trawl data sets that vary in sampling location and intensity, survey timing, and survey gear used. The historical dataset, collected opportunistically by the School of Fisheries at the University of Washington, derives from a mix of research projects and class field trips. Logbooks from these research vessels routinely recorded depth, location (often with place names, not coordinates), time, duration, and gear type for each sampling event, along with counts of each species captured. Because each sample was collected for unique reasons, collectively these data do not comprise a survey. However, when standardizing to account for the effects

of sampling location, season, and gear, these data can reveal a fuller picture of changes in the groundfish community.

The contemporary dataset is from a depth- and basin-stratified survey conducted by the Washington Department of Fish and Wildlife to monitor demersal fishes (Blaine et al. 2020). The survey design changed substantially over the time period, from a stratified random survey that visited each basin roughly every 3 yr (1987–2007) to one that visited fixed index sites each year (2008 onwards). Trawl tows were stratified by depth and hydrologic basin, and effort (duration and area swept) was recorded for each tow. Tow duration was usually near 10 min, and swept area was calculated from linear distance traveled and net opening size estimated from sampling depth and trawl wire deployed (mean \pm SD: 9664 ± 3613 m²). Because there is no temporal overlap between the 2 datasets, we cannot directly standardize them to account for differences in gear configuration or vessel.

Table 1. Species included in the analyses, and estimated population vulnerability to fishing based on life history traits. The vulnerability score was calculated using the method of Cheung et al. (2005) with data extracted from fishbase.org on 18 June 2020 (Froese & Pauly 2000)

Common name	Scientific name	Reason for inclusion	Vulnerability score
Flatfish			
English sole	<i>Parophrys vetulus</i>	Common	43
Pacific sanddab	<i>Citharichthys sordidus</i>	Common/fished	35
Northern/ southern rock sole	<i>Lepidopsetta bilineata</i> and <i>L. polyxystra</i>	Common	57
Gadids			
Pacific whiting	<i>Merluccius productus</i>	Common/fished	60
Pacific cod	<i>Gadus macrocephalus</i>	Fished	50
Pacific tomcod	<i>Microgadus proximus</i>	Common	31
Walleye pollock	<i>Gadus chalcogrammus</i>	Common/fished	37
Chondrichthyes			
Spotted ratfish	<i>Hydrolagus colliei</i>	Common	50
Pacific spiny dogfish	<i>Squalus suckleyi</i>	Common/predator/ vulnerable	79
Longnose skate	<i>Beringraja rhina</i>	Common/vulnerable	78
Big skate	<i>Beringraja binoculata</i>	Vulnerable	86
Other species			
Plainfin midshipman	<i>Porichthys notatus</i>	Common	47
Lingcod	<i>Ophiodon elongatus</i>	Predator	63
Shiner perch	<i>Cymatogaster aggregata</i>	Common/prey	17
Blackbelly eel-pout	<i>Lycodes pacificus</i>	Common	47

We only considered 3 sampling methods in the historical logbook records, namely otter trawl, gulf shrimp trawl, and logbook entries that specified 'bottom trawl', but otter trawl was by far the most common sampling method (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m657p173_supp.pdf). The historical data often did not include tow duration and

never included estimates of area swept. For the tows where tow duration was available in the logbook, there was no discernable trend in tow duration through time (Fig. S1).

Approximate tow locations for all of the historical data were estimated based on place names and other location information in logbooks. To account for local-scale influences on catch rate, and thereby minimize the effect of inter-annual changes in sampling locations on the abundance index, we developed a hierarchical spatial classification system, whereby each sample was assigned to a basin and region. Basins are the main geographic divisions of Puget Sound, identified by bathymetric characteristics (Fig. 2: Hood Canal; Whidbey Basin and Skagit Bay; Central Puget Sound; South Puget Sound; San Juan Islands; Strait of Juan de Fuca; Bellingham Bay). Each basin was subdivided into multiple regions, chosen to depict north-south and east-west divisions and to encompass main sampling areas. Although we also designated sites within regions, we were unable to use these designations in the statistical modeling because too few sites were visited multiple times, very few sites could definitively be matched across the 2 data sets, and the historical dataset had a large number of samples with unidentified site.

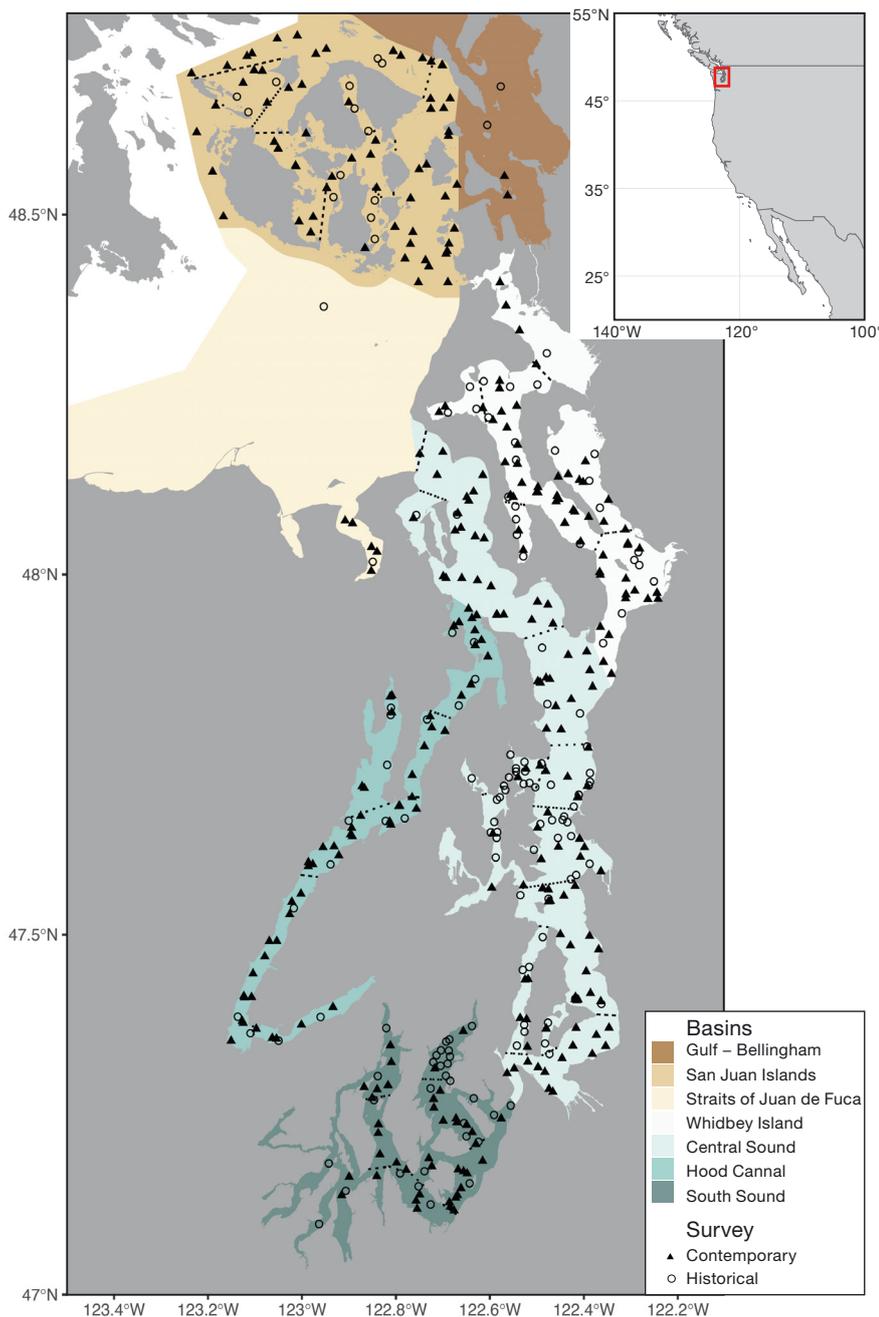


Fig. 2. Tow locations in contemporary and historical data sets. Basins are coded by color, and region delineations are indicated by dotted lines. Historical sampling locations are approximate based on location descriptions in logbooks. Red square in inset map indicates the Puget Sound Region plotted on the left

2.3. Statistical analysis

We used generalized linear mixed effects models (GLMMs) to generate standardized indices of species density and occurrence from the contemporary data, and used the resulting parameter estimates to inform our analysis of the historical data. Essentially, standardization means that we used information in the data on local and regional effects on trawl catches, and then removed those effects to estimate a time series that would be produced if one sampled in a consistent manner (Maunder & Punt 2004). That is, we estimated the effects of covariates such as sampling depth and loca-

tion from fitting models to the contemporary survey data, and used those estimates to standardize the historical data in a Bayesian framework. Analyzing data in such a 2-stage process is one of the advantages of Bayesian inference; non-informative prior probabilities were used in the estimation of models fit to contemporary data, and the resulting posterior probabilities were used as prior probabilities when fitting the same models to the historical data. Moreover, standardization was necessary to quantify temporal trends from the contemporary data because the survey design changed, resulting in different spatial, regional, and temporal coverage.

We restricted our analyses to 15 groundfish (demersal) species, which were selected on the basis of data quantity (commonness among datasets), ecological (e.g. top predators) or economic/fishery (e.g. Pacific cod *Gadus macrocephalus*) importance, and perceived vulnerability (e.g. Chondrichthyes) (Table 1).

We fit a standard delta-GLMM (also sometimes termed a 'hurdle' model) to both contemporary and historical catch data (Thorson et al. 2015). This framework consists of modeling the frequency of occurrence of species in tows and the positive catch rates as a function of covariates. The likelihood for the delta-GLMM is:

$$L(y_i) = \begin{cases} 1 - p_i, & \text{if } y_i = 0 \\ p_i f(y_i | \mu_i, k) & \text{if } y_i > 0 \end{cases} \quad (1)$$

where y_i is the observed catch rate (number/area swept for contemporary data, number/tow for historical data), p_i is the estimated probability of encounter in a tow, μ_i is the predicted average catch rate when a species is present in a tow, and $f(y_i | \mu_i, k)$ is a gamma probability density function with shape parameter k .

The probability of encounter is estimated as a function of fixed effects related to depth and sample date, and random effects related to year, basin, and region where tows were conducted:

$$\text{logit}(p_i) = \mathbf{x}_i \boldsymbol{\beta}_p + \mathbf{t}_i \boldsymbol{\psi}_p + \mathbf{b}_i \boldsymbol{\gamma}_p + \mathbf{r}_i \boldsymbol{\theta}_p \quad (2)$$

where \mathbf{x}_i is the vector of fixed effects covariates for observation i , and \mathbf{t}_i , \mathbf{b}_i , and \mathbf{r}_i are vectors of dummy variables indicating the sampling year, basin, and region, respectively. The vectors $\boldsymbol{\beta}_p$, $\boldsymbol{\psi}_p$, $\boldsymbol{\gamma}_p$, and $\boldsymbol{\theta}_p$ are the fixed and random effects parameters, described below.

In Eq. (1), $f(y_i)$ is a gamma probability density function where the mean is related to fixed and random effects as:

$$\log(\mu_i) = \mathbf{x}_i \boldsymbol{\beta}_y + \mathbf{t}_i \boldsymbol{\psi}_y + \mathbf{b}_i \boldsymbol{\gamma}_y + \mathbf{r}_i \boldsymbol{\theta}_y \quad (3)$$

where the design vectors and parameters are similar to those in the occurrence model (Eq. 2), but we use the subscript p and y to differentiate the 2 equations.

The vectors $\boldsymbol{\beta}_p$ and $\boldsymbol{\beta}_y$ include the fixed effect of intercept (here denoting the long-term expectation over time at average sampling depth), and the effects of depth, season, and gear type (historical data only). We modeled seasonal effects with a Fourier transformation, where we fit coefficients separately for $\cos(d)$ and $\sin(d)$, where d is the day of the year of the sample divided by 365 and multiplied by 2π . We fit several different models to represent alternative ways that depth might dictate encounter probability and catch rate (see Section 2.4).

The random effects of year were modeled as an autoregressive process whereby:

$$\begin{aligned} \Psi_{p,t} &= \rho_p \Psi_{p,t-1} + \varepsilon_{p,t} \\ \Psi_{y,t} &= \rho_y \Psi_{y,t-1} + \varepsilon_{y,t} \end{aligned} \quad (4)$$

where t denotes year, ρ_p and ρ_y are autocorrelation coefficients, and $\varepsilon_{p,t}$ and $\varepsilon_{y,t}$ are normally distributed random variables with mean 0 and standard deviation σ_p and σ_y , respectively. By modeling year effects in this way, we allowed for time-dependent variation without having to *a priori* specify the shape of the trend (e.g. linear, quadratic, asymptotic).

We modeled the effects of basin ($\boldsymbol{\gamma}_p$, $\boldsymbol{\gamma}_y$) and region ($\boldsymbol{\theta}_p$, $\boldsymbol{\theta}_y$) to represent spatial variation in habitat and species distributions. All are assumed to be normally distributed with mean of 0. We assumed $\gamma_p \sim N(0, \sigma_{p,b})$, $\gamma_y \sim N(0, \sigma_{y,b})$, $\boldsymbol{\theta}_p \sim N(0, \boldsymbol{\sigma}_{p,r})$, and $\boldsymbol{\theta}_y \sim N(0, \boldsymbol{\sigma}_{y,r})$ where $\boldsymbol{\sigma}_{p,r}$ and $\boldsymbol{\sigma}_{y,r}$ are vectors of length b (where b is the number of basins), while $\sigma_{p,b}$ and $\sigma_{y,b}$ are scalars. In this way, the model was hierarchical, whereby the variance of regional effects varied by basin.

2.4. Parameter estimation and model selection

We used the contemporary data to test alternative models of which fixed effects to include, while always including the random effects of basin, region, and year. We anticipated that some species would have non-linear responses to depth (e.g. peak density at intermediate depths), and that differences in bathymetry across basins might cause basin-specific relationships between frequency of occurrence/catch rate and depth. To that end, we tested 5 alternative models described in Table 2.

Parameters were estimated numerically using Markov chain Monte Carlo methods, using Stan (Carpenter et al. 2017) with the 'no u-turn sampling' (NUTS) algorithm (Hoffman & Gelman 2014, Stan

Table 2. Alternative fixed effects models tested for each species (see Table 4) fit to contemporary data to evaluate contribution of sampling date, sampling depth, and geographic region (basin)

Model	Parameters
1	$\cos(\text{date}) + \sin(\text{date}) + \text{depth} \times \text{basin} + \text{depth}^2 \times \text{basin}$
2	$\cos(\text{date}) + \sin(\text{date}) + \text{depth} + \text{depth}^2$
3	$\cos(\text{date}) + \sin(\text{date}) + \text{depth} \times \text{basin}$
4	$\cos(\text{date}) + \sin(\text{date}) + \text{depth}$
5	$\cos(\text{date}) + \sin(\text{date})$

Development Team 2017) and ‘rstan’ v 2.19 (Stan Development Team 2017), run in R v 3.5.1 (R Development Core Team 2017). Models were run with 3 chains of 2000 iterations each, using the first 1000 as a warm-up period. This chain length is generally sufficient for the NUTS algorithm (Vehtari et al. 2017), and was confirmed by effective sample sizes and tail sample sizes. Chains were not thinned because autocorrelation was not detected. Model outputs were checked to ensure that few divergent transitions occurred, and convergence was evaluated based on the scale reduction factor \hat{R} (Gelman & Rubin 1992). Posterior predictive checks were visually analyzed to evaluate model fit. To aid in numerical NUTS convergence, i.e. reduce divergences and sampling bias, we used weakly informative priors to constrain parameters with half Cauchy priors for standard deviation parameters (Gelman 2006), and broad Cauchy priors for fixed effects (Table 3). Comparison of posterior densities generated using alternative hyperparameters revealed that the priors had no discernible influence on the estimated posterior probabilities.

To evaluate the data support of alternative models, we used the Pareto-smoothed importance sampling method described by Vehtari et al. (2017) to approximate leave-one-out cross validation, and calculated stacked Bayesian model weights for each model. Models with the highest Bayesian model weight were assumed to have the most data support. We

evaluated best models separately for the frequency of occurrence (i.e. probability of encounter) and the positive catch rate components of the model.

To fit models to the historical data, we used the best fitting model structure from the contemporary data analysis along with additional terms for gear type (bottom trawl, shrimp trawl, otter trawl). We used the Bayesian posterior probabilities from the analysis of contemporary data as prior probabilities for the depth, day, basin, and regional effects and their variances.

2.5. Post-model analysis

We used the Bayesian model estimates of frequency of occurrence and average catch rate to evaluate dynamics of each species and how they differed between the historic and contemporary period, to address how the overall community dynamics differed between the 2 time periods.

We estimated the average survey catch rate for each year as:

$$\hat{c}_t = \hat{p}_t \hat{\mu}_t \quad (5)$$

where \hat{p}_t and $\hat{\mu}_t$ were calculated assuming otter trawl gear, sampling at the average depth of the contemporary data set, on the average day of the contemporary data set (15 May), for the central basin of Puget Sound (Fig. 1). Estimated catch rates are not directly comparable between historical and contemporary data because different gears and research vessels were used, and the units differed (contemporary data included area swept per tow so y is number per 100 m² swept, while historical data lacked this information so y is number per tow). Thus, when evaluating dynamics of individual species, we standardized each catch rate time series relative to the maximum annual estimate within each data series (this transformation also places each species on the same scale

Table 3. Model parameters, descriptions, and prior probabilities used in fitting to contemporary data. Parameters are defined in Section 2.3

Parameter	Prior distribution	Hyperparameters (location, shape)	Description
$\text{logit}(\rho_p), \text{logit}(\rho_y)$	Normal	0, 1.75	Temporal autocorrelation
β_p, β_y	Cauchy	0, 2.5	Fixed effects
σ_p, σ_y	Half Cauchy	0, 2.5	Interannual variance
$\sigma_{p,b}, \sigma_{y,b}$	Half Cauchy	0, 2.5	Standard deviation in basin effects
$\sigma_{p,r}, \sigma_{y,r}$	Half Cauchy	0, 1.5	Standard deviation in regional effects
k	Uniform	0–100	Shape parameter of gamma probability density function

within an era). We did not make this standardization for frequency of occurrence, because the units of measurement were identical between the 2 periods.

We also used the estimates of yearly catch rate in each time period to examine the extent to which the relative contribution of species to the survey catches varied within and between the 2 time periods. Finally, as a high-level approach to identify species with common variability in catch rates, we calculated the correlation matrix on the catch rate estimates from the 15 species in our analysis. For each species, we first z-scored the time series of unstandardized estimated catch rates, then first-differenced the results. We calculated the multivariate correlation matrix on the first-differenced time series, rather than the not-differenced time series, because the differencing removes any effect of non-stationary processes. In other words, this correlation matrix helps address the question ‘Which species have synchrony in catch rates after removing species-specific trends?’

Data and code are available at https://github.com/tessington/Pugetsound_Groundfish.

3. RESULTS

3.1. Catch rate standardization overview

Frequency of occurrence and positive catch rate were most commonly best explained by the most complex model, where linear and quadratic depth effects varied by basin (Table 4). This was largely due to the San Juan Islands and Hood Canal basins,

where depth effects were steeper than they were in the other basins. Usually, the same fixed effects model provided the best fit to both the frequency of occurrence and positive catch rate, although this varied by species. Model 4 (including date and constant depth effects across basin) was never supported, and Model 5 (including date effect only) was only supported in a single case (Table 4).

3.2. Temporal dynamics by taxonomic group

We begin by summarizing observed patterns of variability in the frequency of occurrence and catch rates. To simplify the summary, we focus on the following types of patterns: (1) overall differences in frequency of occurrence between the historical and contemporary periods; (2) differences or similarities in the variability, and time scales of variability, of catch rates between the 2 time periods; and (3) whether catch rate dynamics in the contemporary period suggest population recovery following cessation of commercial fishing, i.e. monotonically increasing catch rates.

3.2.1. Flatfish

All 3 flatfish groups in our analysis (Pacific sanddab *Citharichthys sordidus*, English sole *Parophrys vetulus*, rock soles *Lepidopsetta* spp.) occurred more frequently in the contemporary survey than in the historical data, and exhibited little interannual variation in frequency of occurrence (Fig. 3). Catch rate (Eq. 5)

Table 4. Bayesian Model weights for 5 alternative fixed effects models (Table 2) fitted to contemporary data. Models with the greatest support are highlighted in **bold**

Species	Frequency of occurrence					Positive catch rate				
	Model 1	Model 2	Model 3	Model 4	Model 5	Model 1	Model 2	Model 3	Model 4	Model 5
English sole	0.80	0.00	0.00	0.20	0.00	0.63	0.21	0.12	0.00	0.04
Spiny dogfish	0.45	0.00	0.52	0.03	0.00	0.65	0.07	0.23	0.00	0.05
Spotted ratfish	0.73	0.00	0.26	0.00	0.02	0.92	0.00	0.00	0.00	0.08
Pacific cod	0.00	0.00	1.00	0.00	0.00	0.77	0.00	0.00	0.23	0.00
Pacific whiting	0.99	0.00	0.00	0.00	0.01	0.70	0.18	0.00	0.00	0.12
Pacific sanddab	0.91	0.01	0.00	0.00	0.08	0.10	0.81	0.00	0.00	0.09
Pacific tomcod	0.88	0.00	0.07	0.00	0.05	0.85	0.00	0.15	0.00	0.00
Walleye pollock	0.97	0.00	0.00	0.00	0.03	0.79	0.00	0.00	0.17	0.04
Plainfin midshipman	0.88	0.00	0.00	0.07	0.05	0.44	0.34	0.22	0.00	0.00
Blackbelly eelpout	0.85	0.00	0.07	0.00	0.08	0.80	0.00	0.12	0.08	0.00
Lingcod	0.00	0.00	0.20	0.00	0.80	0.68	0.04	0.28	0.00	0.00
Shiner perch	0.72	0.00	0.24	0.00	0.04	0.78	0.22	0.00	0.00	0.00
Longnose skate	0.63	0.00	0.36	0.00	0.00	0.64	0.27	0.00	0.00	0.09
Big skate	0.86	0.00	0.00	0.07	0.08	0.00	0.70	0.00	0.00	0.30
Rock sole	0.76	0.00	0.24	0.00	0.00	0.91	0.00	0.00	0.07	0.03

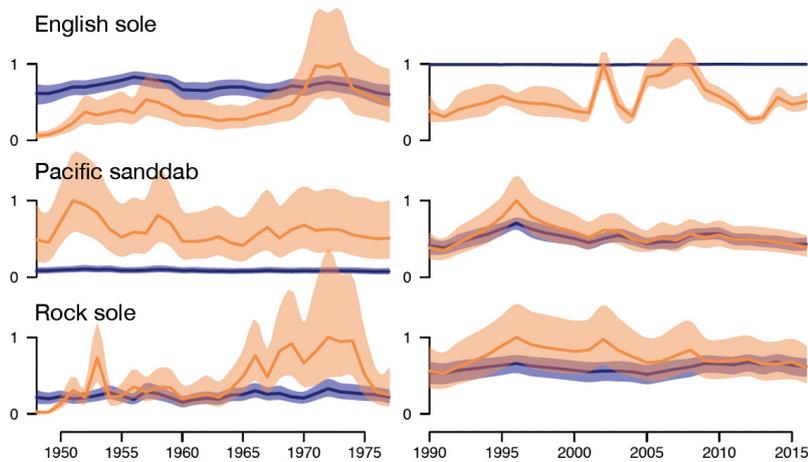


Fig. 3. Estimated annual trends in frequency of occurrence (blue) and catch rate (orange) for 3 flatfish species in Puget Sound. Catch rates are not comparable between the 2 time periods (historical: left column, contemporary: right column) because they are in different units. They are scaled here such that 1 corresponds to the maximum annual catch rate index over each sampling period. Colored areas indicate the 80% credibility interval

was more variable than frequency of occurrence. For example, English sole regularly exhibited pulses of increased abundance lasting several years. In the historical time period, average catch rate increased from the beginning of the time series, until it reached a peak in the early 1970s, and declined slightly thereafter. Catch rates were initially low in the contemporary period and increased to generally higher levels from 2002 to 2010, before declining to lower levels thereafter. The trends in catch rates for Pacific sanddab and rock sole were less clear because they were not sampled as commonly (Fig. 3). In the historic period, there was no discernible trend in Pacific sanddab catch rate, while rock sole exhibited a temporal pattern similar to that of English sole. Both Pacific sanddab and rock sole appeared to have increasing catch rates for the initial portion of the contemporary time series before declining in the latter portion of the time series. None of the flatfish species exhibited a monotonically increasing trend in catch rate during the contemporary period.

3.2.2. Chondrichthyes

Unlike the flatfish, differences in frequency of occurrence between the 2 time periods were less consistent across the cartilaginous fish species. Fre-

quency of occurrence was lower in the contemporary data than historical data for Pacific spiny dogfish, was higher in the historical data for both skate species, and was high in both data sets for spotted ratfish *Hydrolagus colliei* (Fig. 4). Catch rate was more variable, especially for spiny dogfish and longnose skate *Beringraja rhina*. Spiny dogfish catch rates exhibited an increasing trend that persisted for nearly the entire historical time period, but a decreasing trend throughout the entire contemporary time period (Fig. 4). Spotted ratfish fluctuated with no discernible trend in both time periods, yet appeared to have a sustained 15 yr period of enhanced catch rates in the contemporary time period from 1995 to 2010, before declining to lower levels

(Fig. 4). Longnose skate catch rates exhibited a pulse of high abundance at the beginning of the historical time period before declining to very low levels from 1960 onwards (Fig. 4); there was little trend in catch rates in the contemporary time period. Big skate *B. binoculata* catch rates fluctuated without a discernible pattern in both time periods. As with the flatfish, none of the species exhibited a monotonically increasing catch rate in the contemporary time period.

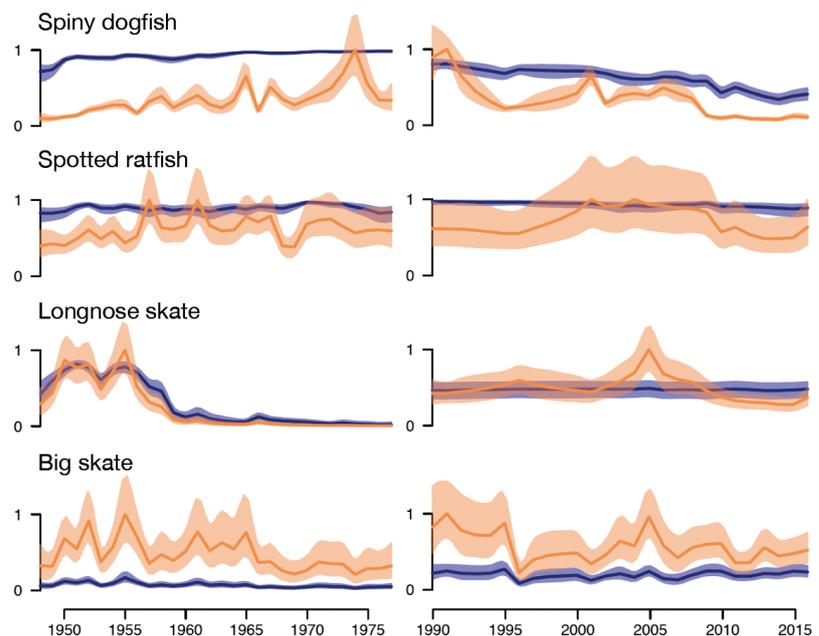


Fig. 4. Estimated annual trends in frequency of occurrence (blue) and catch rate (orange) for the most common species of Chondrichthyes. Other details as in Fig. 3

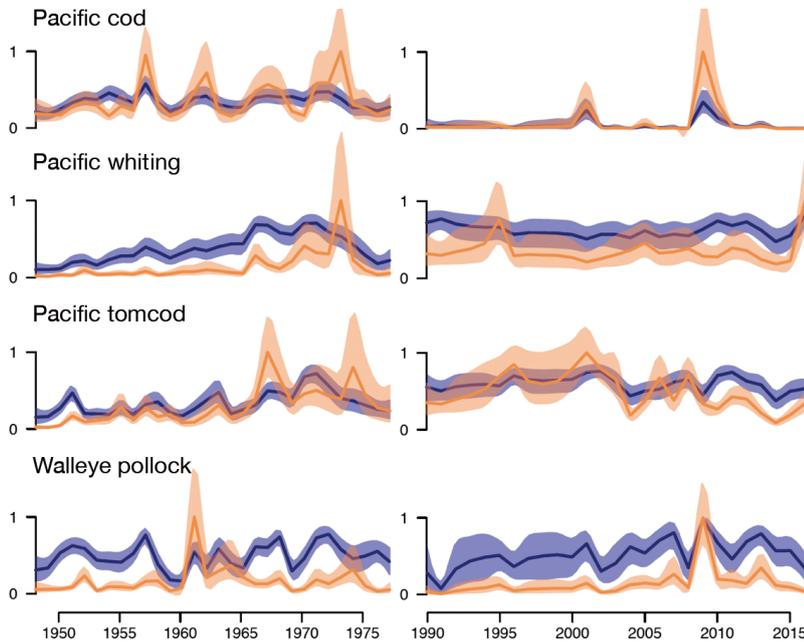


Fig. 5. Estimated annual trends in frequency of occurrence (blue) and catch rate (orange) for the most prevalent gadid species. Other details as in Fig. 3

3.2.3. Gadids

Contemporary frequency of occurrence of Pacific cod was substantially lower than the historical frequency of occurrence (Fig. 5). In the historical period, estimated annual frequency of occurrence averaged 34%, compared to 5% in the contempo-

rary period, and only 2 years had frequency of occurrence that exceeded the lowest levels seen in the historical time period. Frequency of occurrence of Pacific whiting *Merluccius productus* and Pacific tomcod *Microgadus proximus* was generally higher in the contemporary than the historical dataset, while frequency of occurrence of walleye pollock *Gadus chalcogrammus* was not noticeably different across the 2 time periods. Within each time series, only historical Pacific whiting and Pacific tomcod exhibited any notable temporal trend in frequency of occurrence (Fig. 5). Estimated catch rates of all gadid species were highly dynamic at inter-annual time periods, likely reflecting recruitment events (Fig. 5). Annual catch rates of Pacific whiting and Pacific tomcod were greater at the end of the historical time period than the beginning, while catch rates of Pacific tomcod were lower at the end of the contemporary time period than at the beginning. Catch rates of other species fluctuated without discernable trends (Fig. 5). None of the gadid species catch rates exhibited monotonically increasing trends in the contemporary time period.

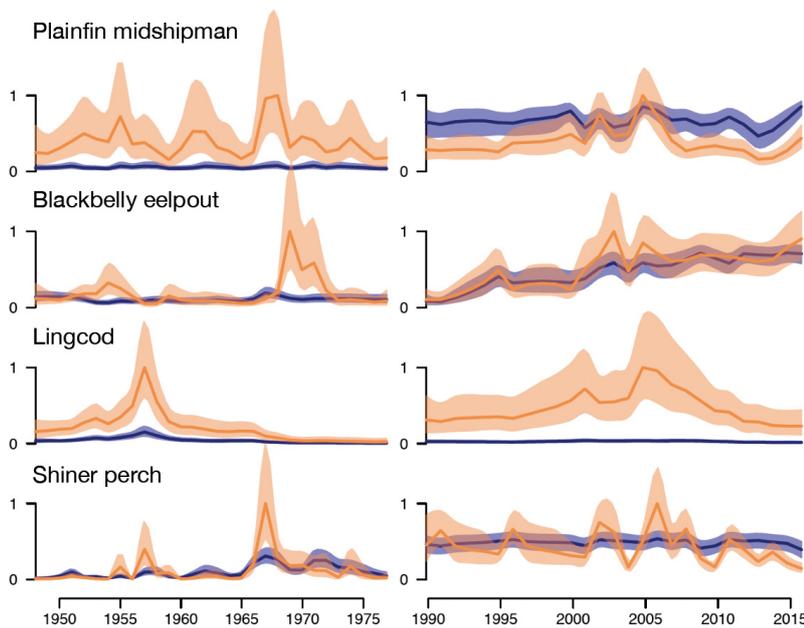


Fig. 6. Estimated annual trends in frequency of occurrence (blue) and catch rate (orange) for several additional encountered species. Other details as in Fig. 3

3.2.4. Other species

All other species except lingcod *Ophiodon elongatus* had higher average frequency of occurrence in the contemporary than in the historical time period (Fig. 6). Blackbelly eelpout *Lycodes pacificus* frequency of occurrence increased consistently throughout the contemporary time period, while that of other species did not exhibit pronounced trends in either time period. Catch rates were more dynamic among these species (Fig. 7). Lingcod exhibited pulses of high catch rates in both the historical and contemporary time series, while blackbelly eelpout catch rates increased nearly linearly throughout the contemporary time period. Shiner perch *Cymatogaster aggregata* and plainfin midshipman *Por-*

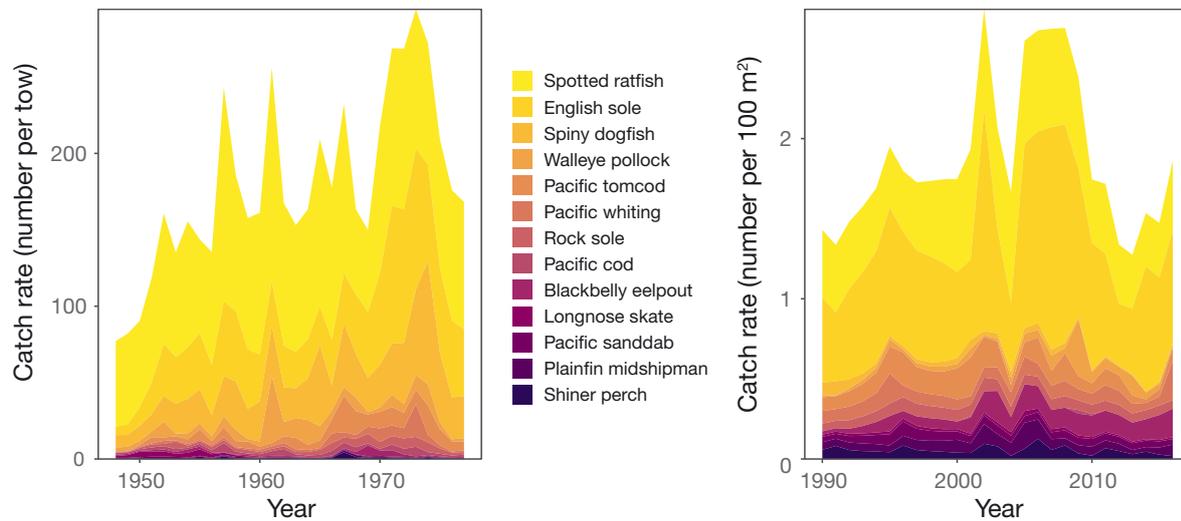


Fig. 7. Dynamics of estimated community composition in the historical time period (left) and contemporary time period (right). Catch rate units are numbers per tow for the historical time period, and numbers per 100 m² in the contemporary time period. Big skate and lingcod are not plotted in this figure because their catch rates were low compared to other species

ichthys notatus tended to exhibit interannual fluctuations with no trend (Fig. 5).

3.3. Groundfish community composition and dynamics

Spotted ratfish and English sole dominated catch rates in both time periods, together accounting for 70 and 65% of the total catch in the historical and contemporary time periods, respectively (Fig. 7). Spotted ratfish were most dominant in the historical time period, accounting for 30–72% of annual catch rate (averaging 50%). In comparison, English sole contribution increased from an average of 20% in the historical period to 38% of the catch rate in the contemporary time period (Fig. 7). Spiny dogfish were a much larger component of the historical catch rate, accounting for, on average, 15% of the catch rate in the historical data but only 1.7% in the contemporary data (Fig. 7). Pacific cod were always a small component of the numerical catch, but declined from 1.23% in the historical time period to 0.09% in the contemporary time period. Blackbelly eelpout was a more important part of the contemporary catch, increasing from 0.7% in the historical time period to 5% in the contemporary time period. Overall community catch rates increased throughout the historical time period (when commercial fishing was active). During the contemporary period when commercial fishing had ceased, the catch rates increased for the first 15 yr, but declined thereafter to levels similar to the start of the time series (Fig. 7).

In both time periods, synchrony between species pairs was more common than anti-synchrony (Fig. 8). In the historical data set, there were 18 significant ($p < 0.05$) positive correlations compared to 3 significant negative correlations. In the contemporary data set, there were 23 significantly positive correlations and 10 significantly negative correlations. However, few of these significant correlations were common across the 2 data sets. Only 1 species pair had significant negative correlations in both time periods, and only 5 species pairs had significant positive correlations in both time periods. Further, the correlation between plainfin midshipman and Pacific spiny dogfish was significantly positive in the historical data set and significantly negative in the contemporary data set (Fig. 8).

4. DISCUSSION

To our knowledge, this study is one of the first to combine historical data with contemporary survey data to evaluate long-term dynamics of a groundfish community in a large estuary. Estuaries are subject to numerous human influences (Fig. 1), and we therefore expected that dynamics, particularly of vulnerable species, would vary markedly between the 2 time periods, similar to the findings of Greenstreet & Hall (1996). Because there was no temporal overlap between the 2 data sets, we are unable to unequivocally conclude that any species became more or less common or abundant, and because many changes

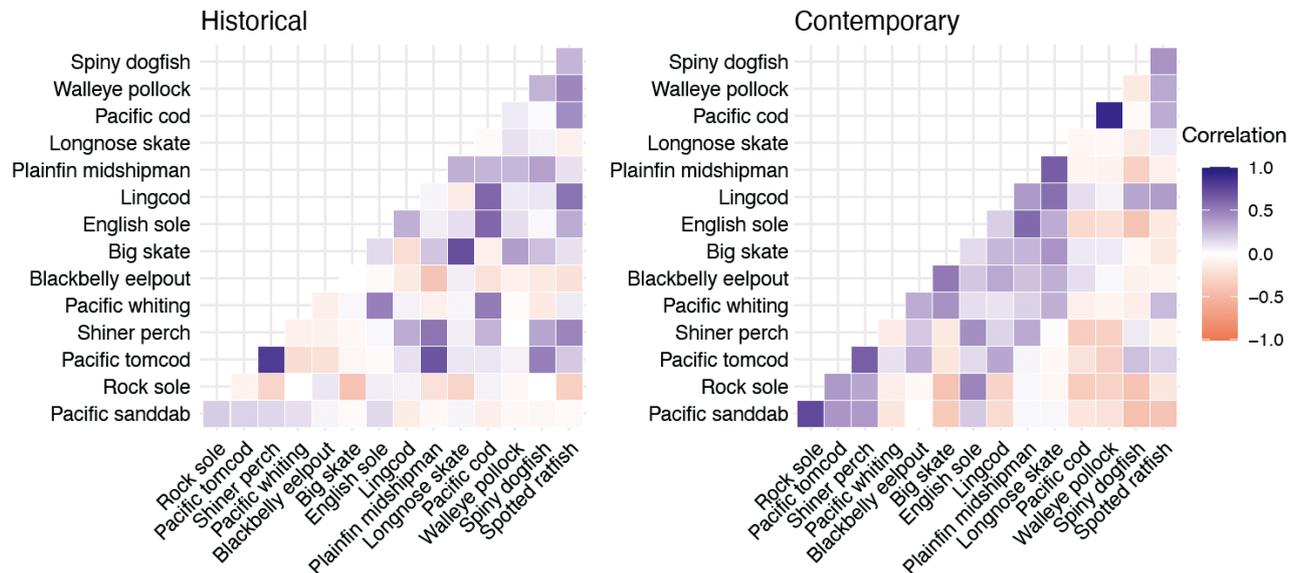


Fig. 8. Estimated correlation matrix of catch rates for the historical (left) and contemporary (right) groundfish data. The catch rates were standardized and first-differenced to remove non-stationary trends

occurred simultaneously, we are unable to link dynamics to specific causes. Despite those limitations, we found that the population dynamics of groundfish were broadly similar across the 2 time periods, and many species that were common in the historical record remained common in the contemporary sampling, with some exceptions. All flatfish species, plainfin midshipman, blackbelly eelpout, and shiner perch were consistently more common in the contemporary than historical data, while Pacific spiny dogfish and Pacific cod were substantially less common in the contemporary data. These shifts may be due to differences in catchability associated with the sampling gear, or may reflect shifts in population abundances and distribution. At a community level, the composition was dominated by the same 2 species (English sole and spotted ratfish) in both time periods. Our combination of historical and contemporary data revealed that many populations undergo low-frequency oscillations in abundance, which has important implications for information needs when setting ecologically relevant baselines and recovery targets for restoration and other management action.

4.1. Insights from historical analyses

This work demonstrates the value of applying historical data to assess the status of marine resources (Van Houtan & Kittinger 2014) in 2 ways. First, our work detected sharp reductions in the frequency of occurrence of Pacific cod between the historical and

contemporary time period, which has been previously described using a combination of fishery and scientific monitoring data but not directly quantified, due to gaps in such data. Pacific cod supported recreational and commercial fisheries from the 1940s to the late 1980s, with annual landings fluctuating around 900 mt (Palsson 1990, Gustafson et al. 2000). Prior work was unable to make firm conclusions regarding its population status because of the paucity of surveys and the reliance on catch data to infer population trends. Gustafson et al. (2000) used data from 1987–1997 to conclude that there was no sustained trend or change in catch rate of Pacific cod, although that study was conducted after regulations imposed in 1987 that ceased most directed fishing towards Pacific cod. In comparison, we found a reduction of approximately 5-fold in the frequency of occurrence between the historical time period and the contemporary time period. Granted, catch rate metrics are not directly comparable as the 2 data periods used different vessels, different net configurations, and different sampling designs; however, for most species the frequency of occurrence was greater in the contemporary time series, with only Pacific cod and Pacific spiny dogfish exhibiting consistently lower frequency of occurrence in the contemporary time period (and the latter reduction was much smaller than that seen for Pacific cod). The shift in the Pacific Decadal Oscillation (Fig. 1) from a cold to a warm phase may be responsible for this decline, as Puget Sound is near the southern edge of the geographic range for

Pacific cod (Ketchen 1961). The interactive effect of warming waters and a concomitant drop in productivity combined with sustained fishing pressure (Pinsky & Byler 2015) may have severely depleted the local stocks.

Second, the longer-term view afforded by the historical reconstruction provides an improved understanding of the temporal scales of population variability in Puget Sound groundfish. For example, the increase in English sole catch rates in the initial phases of the contemporary period might reasonably be interpreted as a response to fishing regulations. However, the historical and contemporary time series show similar time scales of population fluctuations, presenting the possibility that the population response in the 1990s was unrelated to fishing restrictions and was instead driven by interactions between species life history and environmental fluctuations (Botsford et al. 2014). These irregular population dynamics (*sensu* Spencer & Collie 1997) are likely induced by complex interactions of species life history (e.g. longevity, age at maturation), environmentally mediated recruitment, low-frequency environmental dynamics, and species interactions. Low-frequency, irregular dynamics can also explain the lack of consistency in shared temporal dynamics among members of the groundfish community. That is, low-frequency population dynamics can create the appearance of synchrony or asynchrony of species dynamics when time series are relatively short, despite the absence of any long-term relationship (Siple et al. 2020). Short-term observations can give the impression of tending towards an asymptotic state, when in fact the dynamics are transient (Hastings et al. 2018). Our results show that baseline analysis should not consider only the 'average' state, but also the baseline dynamic behavior of populations and communities.

Taken together, these observations speak directly to the selection and interpretation of ecological indicators, limits, and targets for these indicators as used in decision making (Rice & Rochet 2005). Recently, groundfish (specifically 'benthic marine fish') have been listed as one of 6 'vital sign' indicators to assess progress towards meeting the recovery goal of 'Thriving Species and Food Webs' (<https://vitalsigns.pugetsoundinfo.wa.gov/About>) for the State of Washington. Our results suggest that target and limit levels for these species will be difficult to assign using contemporary data alone. Semi-quantitative trend indicators, or composite indicators (e.g. total groundfish biomass, biomass by functional group)

may prove more useful than species-level indicator targets (Samhuri et al. 2011).

4.2. Responses to fishing restrictions

We had expected that regulations restricting bottom trawling, which began in the late 1980s as area restrictions and were finalized in 1994 with a complete ban, would have fostered population recovery of targeted and other vulnerable species within the contemporary period, as has been witnessed in several areas when fishing has been radically diminished (Halpern & Warner 2002, Neubauer et al. 2013). We expected this recovery to appear as monotonically increasing trends in catch rates in the contemporary time period, yet few species had catch rate dynamics that matched this expectation. Several species (English sole, rock soles, lingcod, longnose skate) exhibited increased catch rate trends in the early part of the contemporary time series, only to decline in the latter portion of these time series. Only blackbelly eelpout exhibited sustained increases throughout the sampling period, although there is not much indication that eelpouts are particularly vulnerable to fishing (based on life history traits; Table 1) and this species was never a specific target of commercial trawl fishing. At the same time, Pacific spiny dogfish exhibited reduced frequency of occurrence and declining catch rate after the cessation of bottom trawling, despite having a life history that makes it more vulnerable to fishing mortality (Table 1).

The absence of a pronounced signal from fishing restrictions may also indicate that fishing intensity was not sufficiently strong to significantly deplete these populations, in light of other drivers of population dynamics. Also, the trawl gear used here did not effectively sample vulnerable rockfish species that are known to have been heavily impacted by fishing (Palsson et al. 2009), so we could not include them in our analysis. Alternatively, the initial regulatory changes that began in the late 1980s may have allowed some species to recover prior to the onset of the contemporary sampling period. If this were true, then it would explain why many species had higher frequency of occurrence in the contemporary data set. The absence of substantial community changes in response to fisheries regulations may also signal the complex dynamics of an urban estuary that is subject to multiple external drivers. During the same time that fishing regulations restricted and then banned bottom trawling, recreational fishing for groundfish increased (largely targeting rockfish and

lingcod) and then decreased, the northeastern Pacific Ocean shifted climatic regimes, piscivorous pinniped populations continued to increase, and the forage base, in Pacific herring, continued to decline. Predicting population-level consequences to cumulative drivers is already challenging (Hodgson et al. 2019), and is even more difficult at a community or food web level because of uncertainty regarding species interactions (Yodzis 2000) combined with time-lagged, non-equilibrium, and non-linear dynamics (Sugihara et al. 2012, Shelton et al. 2013, Ye et al. 2015). For example, restoration strategies that are limited to targeting only a segment of the food web are less likely to be successful than strategies that target both predators and prey (Samhuri et al. 2017). Within our groundfish community are piscivorous fish (spiny dogfish, Pacific cod, lingcod), whose dynamics may have affected smaller-bodied groundfish. Indeed, the lack of persistent correlations of species dynamics that we observed is consistent with the hypothesis of a high-dimensional system with multiple interacting components.

4.3. Comparison to pelagic species

The absence of sustained directional change in the groundfish community stands in rather stark contrast to changes in the pelagic community. While each Pacific salmon run has a unique temporal pattern of smolt and smolt-to-adult survivorship, overall, coho and steelhead salmon have experienced a notable decline from the late 1970s to the present day (Zimmerman et al. 2015, Kendall et al. 2017). Chinook salmon survivorship exhibits less of a pattern (Ruff et al. 2017), but this may reflect the fact that reliable and spatially comprehensive data are not available for the late 1970s when other salmon showed declines. At the same time, pink and chum salmon have experienced increased survival and have become more abundant since the mid-1990s (Sobocinski et al. 2018, Losee et al. 2019). Greene et al. (2015) documented increased frequency of large jellyfish catch events in pelagic surveys in the 2000s compared to the 1970s and 1980s, and also documented declines in Pacific herring catch rates, consistent with the State of Washington Pacific herring spawning biomass surveys (Stick et al. 2014, Siple et al. 2018). Degradation of critical freshwater habitat for anadromous salmonids plays an important role in limiting the productivity of these species, and the outsized influence of this stressor on population trends, plus the somewhat limited time spent in the estuary by many salmon

species, could explain the relatively stronger signal in comparison to the resident benthic species evaluated here. Pacific herring were subject to a major fishery that reduced their abundances dramatically, which, in combination with their dependence on near-shore habitats that are largely degraded, declining recruitment and adult survivorship (Siple et al. 2018), and predation by pinnipeds, could explain why these declines are so clearly detected.

4.4. Caveats and limitations

Our analysis method required that we made several assumptions that may have affected the precision and accuracy of our standardization methods. First, there was no overlap in sampling between the historical data record and the contemporary survey period, and little information is available on the specific configuration of historical trawl gears. Consequently, we cannot fully reconstruct long-term dynamics, but instead could only ask whether the characteristics of populations and community dynamics were similar across the time periods. Second, in our standardization method, we assumed that yearly dynamics were shared across all Puget Sound basins, yet it is likely that individual basins experience localized fluctuations related to recruitment and settlement processes. Third, the locations of the historical sampling records had to be inferred from logbook notes, limiting our ability to fully account for localized effects on catch rates. Fourth, the historical data from logbooks contained limited information on tow duration and no information on area swept, and involved 3 separate fishing gears. Differences in fishing effort can confound frequency of occurrence and catch rate (numbers per tow). The effects of fishing gear on frequency of occurrence and catch rate were often substantial (Table S1), but were species-specific, and most of the samples in the historical period were collected with otter trawls (Fig. S1).

4.5. Conclusions

Currently, many efforts are underway to restore, recover, and protect Puget Sound functioning and the benefits it provides to people (Puget Sound Partnership 2010). The main proximate threats include shipping, toxic contaminants, harmful algal blooms, loss of nearshore habitats, and non-point source pollution from an increasingly urbanized watershed. At the same time, oxygen depletion, ocean acidification,

and ocean warming pose long-term threats to aquatic life. Despite these threats, we found little evidence that these have had detectable and marked influence on some of the most common and historically exploited groundfish populations in this ecosystem over the time periods evaluated in the study. Our results suggest that these populations are insensitive to these threats, that other environmental drivers are counteracting the stressors we identified here, or that the community response is challenging to detect given the limitations of our data.

Acknowledgements. We thank Bruce Miller for his careful stewardship of the historical logbooks; the Washington Department of Fisheries and Wildlife data managers for prompt access to data and responding to data requests; and the research vessel captains who maintained detailed catch records for decades. We also thank several reviewers for helpful comments that improved the manuscript, and Elizabeth Ng for managing and collating the data and generating maps. This work was funded in part by a grant from Washington Sea Grant, University of Washington, pursuant to National Oceanic and Atmospheric Administration Award No. NA14OAR4170078. The views expressed herein are those of the authors and do not necessarily reflect the views of NOAA or any of its sub-agencies. The work was also funded by a grant from Washington Sea Grant, and the digitization process was supported by a grant from the SeaDoc Society. Ongoing support for the Washington Department of Fish and Wildlife bottom trawl survey is provided by appropriations from the Washington State General Fund.

LITERATURE CITED

- Anderson DM, Glibert PM, Burkholder JM (2002) Harmful algal blooms and eutrophication: nutrient sources, composition, and consequences. *Estuaries* 25:704–726
- Bargmann G (1998) Puget Sound groundfish management plan. Washington Department of Fish and Wildlife, Olympia, WA
- Beaudreau AH, Whitney EJ (2016) Historical patterns and drivers of spatial changes in recreational fishing activity in Puget Sound, Washington. *PLOS ONE* 11:e0152190
- Blaine J, Lowry D, Pacunski R (2020) 2002–2007 WDFW scientific bottom trawl surveys in the southern Salish Sea: species distributions, abundance, and population trends. Washington Department of Fish and Wildlife, Olympia, WA
- Botsford LW, Holland MD, Field JC, Hastings A (2014) Cohort resonance: a significant component of fluctuations in recruitment, egg production, and catch of fished populations. *ICES J Mar Sci* 71:2158–2170
- Brandenberger JM, Creclius EA, Louchouart P (2008) Historical inputs and natural recovery rates for heavy metals and organic biomarkers in Puget Sound during the 20th century. *Environ Sci Technol* 42:6786–6790
- Carpenter B, Gelman A, Hoffman MD, Lee D and others (2017) Stan: a probabilistic programming language. *J Stat Softw* 76:1–32
- Chasco B, Kaplan IC, Thomas A, Acevedo-Gutiérrez A and others (2017a) Estimates of Chinook salmon consumption in Washington State inland waters by four marine mammal predators from 1970 to 2015. *Can J Fish Aquat Sci* 74:1173–1194
- Chasco BE, Kaplan IC, Thomas AC, Acevedo-Gutiérrez A and others (2017b) Competing tradeoffs between increasing marine mammal predation and fisheries harvest of Chinook salmon. *Sci Rep* 7:154389
- Cheung WWL, Pitcher TJ, Pauly D (2005) A fuzzy logic expert system to estimate intrinsic extinction vulnerabilities of marine fishes to fishing. *Biol Conserv* 124:97–111
- Dethier MN, Toft JD, Shipman H (2017) Shoreline armoring in an inland sea: science-based recommendations for policy implementation. *Conserv Lett* 10:626–633
- Drake JS, Berntson EA, Cope JM, Gustafson RG and others (2010) Status review of five rockfish species in Puget Sound, Washington: bocaccio (*Sebastes paucispinis*), canary rockfish (*S. pinniger*), yelloweye rockfish (*S. ruberrimus*), greenstriped rockfish (*S. elongatus*), and redstripe rockfish (*S. proriger*). NOAA Tech Memo NMFS-NWFSC-108. US Department of Commerce, Seattle, WA
- Engelhard GH, Thurstan RH, MacKenzie BR, Alleway HK and others (2016) ICES meets marine historical ecology: placing the history of fish and fisheries in current policy context. *ICES J Mar Sci* 73:1386–1403
- Essington TE, Klinger T, Conway-Cranos T, Buchanan J and others (2011) The biophysical condition of Puget Sound. In: Ruckelshaus M (ed) Puget Sound science update. Puget Sound Partnership, Olympia, WA, p 205–423
- Essington TE, Dodd K, Quinn TP (2013) Shifts in the estuarine demersal fish community following a fishery closure in Puget Sound, Washington. *Fish Bull* 111:205–217
- Froese R, Pauly D (2000) FishBase 2000: concepts, design and data sources. ICLARM, Los Baños, Laguna
- Gelman A, Rubin DB (1992) Inference from iterative simulation using multiple sequences. *Stat Sci* 7:457–511
- Gelman A (2006) Prior distributions for variance parameters in hierarchical models (comment on article by Browne and Draper). *Bayesian Anal* 1:515–534
- Greene C, Kuehne L, Rice C, Fresh K, Penttila D (2015) Forty years of change in forage fish and jellyfish abundance across greater Puget Sound, Washington (USA): anthropogenic and climate associations. *Mar Ecol Prog Ser* 525:153–170
- Greenstreet SPR, Hall SJ (1996) Fishing and the ground-fish assemblage structure in the north-western North Sea: an analysis of long-term and spatial trends. *J Anim Ecol* 65: 577–598
- Gustafson RG, Lenarz WH, McCain BB, Schmitt CC, Grant WS, Builder TL, Methot RD (2000) Status review of Pacific hake, Pacific cod, and walleye pollock from Puget Sound, Washington. NOAA-NWFSC Tech Memo 44. Northwest Fisheries Science Center, Seattle, WA
- Halpern BS, Warner RR (2002) Marine reserves have rapid and lasting effects. *Ecol Lett* 5:361–366
- Hart Crowser Inc (2007) Control of toxic chemicals in Puget Sound Phase 1: Initial estimate of loadings. Washington Department of Ecology, Olympia, WA
- Harvey CJ, Williams GD, Levin PS (2012) Food web structure and trophic control in central Puget Sound. *Estuaries Coasts* 35:821–838
- Hastings A, Abbott KC, Cuddington K, Francis T and others (2018) Transient phenomena in ecology. *Science* 361: eaat6412
- Hodgson EE, Halpern BS, Essington TE (2019) Moving

- beyond silos in cumulative effects assessment. *Front Ecol Evol* 7:211
- Hoffman MD, Gelman A (2014) The No-U-Turn Sampler: adaptively setting path lengths in Hamiltonian Monte Carlo. *J Mach Learn Res* 15:1593–1623
- Jackson JBC, Kirby MX, Berger WH, Bjorndal KA and others (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–637
- Jeffries S, Huber J, Calambokidis J, Laake J (2003) Trends and status of harbor seals in Washington state: 1978–1999. *J Wildl Manag* 67:207–218
- Johnson PTJ, Townsend AR, Cleveland CC, Glibert PM and others (2010) Linking environmental nutrient enrichment and disease emergence in humans and wildlife. *Ecol Appl* 20:16–29
- Kendall NW, Marston GW, Klungle MM (2017) Declining patterns of Pacific Northwest steelhead trout (*Oncorhynchus mykiss*) adult abundance and smolt survival in the ocean. *Can J Fish Aquat Sci* 74:1275–1290
- Ketchen KS (1961) Observations on the ecology of the Pacific cod (*Gadus macrocephalus*) in Canadian waters. *J Fish Res Board Can* 18:513–558
- Kittinger JN, Houtan KSV, McClenachan LE, Lawrence AL (2013) Using historical data to assess the biogeography of population recovery. *Ecography* 36:868–872
- Landahl JT, Johnson LL, Stein JE, Collier TK, Varanasi U (1997) Approaches for determining effects of pollution on fish populations of Puget Sound. *Trans Am Fish Soc* 126:519–535
- Levings CD, Thom RM (1994) Habitat changes in Georgia Basin: implications for resource management and restoration. *Can Tech Rep Fish Aquat Sci* 1948:330–349
- Losee JP, Kendall NW, Dufault A (2019) Changing salmon: an analysis of body mass, abundance, survival, and productivity trends across 45 years in Puget Sound. *Fish Fish* 20:934–951
- Louchouart P, Kuo LJ, Brandenberger JM, Marcantonio F, Garland C, Gill GA, Cullinan V (2012) Pyrogenic inputs of anthropogenic Pb and Hg to sediments of the Hood Canal, Washington, in the 20th century: source evidence from stable Pb isotopes and PAH signatures. *Environ Sci Technol* 46:5772–5781
- Mantua NJ, Hare SR, Zhang Y, Wallace JM, Francis RC (1997) A Pacific interdecadal climate oscillation with impacts on salmon production. *Bull Am Meteorol Soc* 78:1069–1079
- Marsh H, De'ath G, Gribble N, Lane B (2005) Historical marine population estimates: triggers or targets for conservation? The dugong case study. *Ecol Appl* 15:481–492
- Maunder MM, Punt AE (2004) Standardizing catch and effort data: a review of recent approaches. *Fish Res* 70:141–159
- McClenachan L, Ferretti F, Baum JK (2012) From archives to conservation: why historical data are needed to set baselines for marine animals and ecosystems. *Conserv Lett* 5:349–359
- Moore SK, Mantua NJ, Newton JA, Kawase M, Warner MJ, Kellogg JP (2008a) A descriptive analysis of temporal and spatial patterns of variability in Puget Sound oceanographic properties. *Estuar Coast Shelf Sci* 80:545–554
- Moore SK, Mantua NJ, Kellogg JP, Newton JA (2008b) Local and large-scale climate forcing of Puget Sound oceanographic properties on seasonal to interdecadal timescales. *Limnol Oceanogr* 53:1746–1758
- Musick JA, Harbin MM, Berkeley SA, Burgess GH and others (2000) Marine, estuarine, and diadromous fish stocks at risk of extinction in North America (exclusive of Pacific salmonids). *Fisheries* 25:6–30
- National Marine Fisheries Service (2014) Endangered and threatened wildlife; final rule to revise the code of federal regulations for species under the jurisdiction of the National Marine Fisheries Service. *Fed Reg* 79:20802–20817
- Nelson BW, Shelton AO, Anderson JH, Ford MJ, Ward EJ (2019) Ecological implications of changing hatchery practices for Chinook salmon in the Salish Sea. *Ecosphere* 10:e02922
- Neubauer P, Jensen OP, Hutchings JA, Baum JK (2013) Resilience and recovery of overexploited marine populations. *Science* 340:347–349
- Palsson WA (1990) Pacific cod (*Gadus macrocephalus*) in Puget Sound and adjacent waters: biology and stock assessment. Washington Department of Fish and Wildlife, Olympia, WA
- Palsson WA (1998) Monitoring the response of rockfish to protected areas. In: Yoklavich MM (ed) Marine harvest refugia for West Coast rockfish: a workshop. NOAA Tech Memo NMFS NOAA-TM-NMFS-SWFSC-255, p 64–71
- Palsson WA, Hoeman JC, Bargemann GG, Day DE (1997) 1995 Status of Puget Sound bottomfish stocks (revised). Washington Department of Fish and Wildlife, Olympia, WA
- Palsson WA, Northrup TJ, Barker MW (1998) Puget Sound groundfish management plan. Washington Department of Fish and Wildlife, Olympia, WA
- Palsson WA, Tsou TS, Gargmann G, Buckley RM and others (2009) The biology and assessment of rockfishes in Puget Sound. Washington Department of Fish and Wildlife, Olympia, WA
- Pauly D (1995) Anecdotes and the shifting base-line syndrome of fisheries. *Trends Ecol Evol* 10:430
- Pietsch TW, Orr JW (2019) Fishes of the Salish Sea: Puget Sound and the Straits of Georgia and Juan de Fuca (3-volume set). University of Washington Press, Seattle, WA
- Pinsky ML, Byler D (2015) Fishing, fast growth and climate variability increase the risk of collapse. *Proc R Soc B* 282:20151053
- Puget Sound Partnership (2010) Strategic science plan. Puget Sound Partnership, Olympia, WA
- R Development Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Rice J, Rochet M (2005) A framework for selecting a suite of indicators for fisheries management. *ICES J Mar Sci* 62:516–527
- Ruckelshaus M, McClure MM (2007) Sound science: synthesizing ecological and socioeconomic information about the Puget Sound ecosystem. US Dept. of Commerce, National Oceanic and Atmospheric Administration, NMFS, Northwest Fisheries Science Center, Seattle, WA
- Ruff CP, Anderson JH, Kemp IM, Kendall NW and others (2017) Salish Sea Chinook salmon exhibit weaker coherence in early marine survival trends than coastal populations. *Fish Oceanogr* 26:625–637
- Samhuri JF, Levin PS, James CA, Kershner J, Williams G (2011) Using existing scientific capacity to set targets for ecosystem-based management: a Puget Sound case study. *Mar Policy* 35:508–518
- Samhuri JF, Stier AC, Hennessey SM, Novak M, Halpern BS, Levin PS (2017) Rapid and direct recoveries of pred-

- ators and prey through synchronized ecosystem management. *Nat Ecol Evol* 1:0068
- Sandell T, Lindquist A, Dionne P, Lowry D (2019) 2016 Washington State herring stock status report. Fish Program Technical Report No. FPT 19-07. Washington Department of Fish and Wildlife, Olympia, WA
- ✦ Schindler DE, Leavitt PR, Johnson SP, Brock CS (2006) A 500-year context for the recent surge in sockeye salmon (*Oncorhynchus nerka*) abundance in the Alagnak River, Alaska. *Can J Fish Aquat Sci* 63:1439–1444
- Schmitt CS, Quinnell S, Rickey M, Stanley M (1991) Groundfish statistics from commercial fisheries in Puget Sound, 1970–1988. Washington Department of Fish and Wildlife, Olympia, WA
- ✦ Shelton AO, Satterthwaite WH, Beakes MP, Munch SB, Sogard SM, Mangel M (2013) Separating intrinsic and environmental contributions to growth and their population consequences. *Am Nat* 181:799–814
- ✦ Siple MC, Shelton AO, Francis TB, Lowry D, Lindquist AP, Essington TE (2018) Contributions of adult mortality to declines of Puget Sound Pacific herring. *ICES J Mar Sci* 75:319–329
- ✦ Siple MC, Essington TE, Barnett LAK, Scheuerell MD (2020) Limited evidence for sardine and anchovy asynchrony: re-examining an old story. *Proc R Soc B* 287: 20192781
- ✦ Sobocinski KL, Greene CM, Schmidt MW (2018) Using a qualitative model to explore the impacts of ecosystem and anthropogenic drivers upon declining marine survival in Pacific salmon. *Environ Conserv* 45:278–290
- ✦ Spencer PD, Collie JS (1997) Patterns of population variability in marine fish stocks. *Fish Oceanogr* 6:188–204
- Stan Development Team (2017) Stan. <https://mc-stan.org/>
- Stick KC, Lindquist A, Lowry D (2014) Washington State herring stock status report. Fish Program Technical Report FPA 14-09. Washington Department of Fish and Wildlife, Olympia, WA
- ✦ Sugihara G, May R, Ye H, Hsieh CH, Deyle E, Fogarty M, Munch S (2012) Detecting causality in complex ecosystems. *Science* 338:496–500
- ✦ Swetnam TW, Allen CD, Betancourt JL (1999) Applied historical ecology: using the past to manage for the future. *Ecol Appl* 9:1189–1206
- ✦ Tallis H, Levin PS, Ruckelshaus M, Lester SE, McLeod KL, Fluharty DL, Halpern BS (2010) The many faces of ecosystem-based management: making the process work today in real places. *Mar Policy* 34:340–348
- ✦ Thorson JT, Shelton AO, Ward EJ, Skaug HJ (2015) Geostatistical delta-generalized linear mixed models improve precision for estimated abundance indices for West Coast groundfishes. *ICES J Mar Sci* 72:1297–1310
- ✦ Van Houtan KS, Kittinger JN (2014) Historical commercial exploitation and the current status of Hawaiian green turtles. *Biol Conserv* 170:20–27
- ✦ Vehtari A, Gelman A, Gabry J (2017) Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Stat Comput* 27:1413–1432
- ✦ Ward EJ, Levin PS, Lance MM, Jeffries SJ, Acevedo-Gutiérrez A (2012) Integrating diet and movement data to identify hot spots of predation risk and areas of conservation concern for endangered species. *Conserv Lett* 5:37–47
- Washington PM (1977) Recreationally important marine fishes of Puget Sound. National Marine Fisheries Service, Seattle, WA
- Washington Department of Fish and Wildlife (2008) Priority habitat and species list. Washington Department of Fish and Wildlife, Olympia, WA
- ✦ West JE, O'Neill SM, Ylitalo GM (2008) Spatial extent, magnitude, and patterns of persistent organochlorine pollutants in Pacific herring (*Clupea pallasii*) populations in the Puget Sound (USA) and Strait of Georgia (Canada). *Sci Total Environ* 394:369–378
- ✦ Williams GD, Levin PS, Palsson WA (2010) Rockfish in Puget Sound: an ecological history of exploitation. *Mar Policy* 34:1010–1020
- ✦ Ye H, Beamish RJ, Glaser SM, Grant SCH and others (2015) Equation-free mechanistic ecosystem forecasting using empirical dynamic modeling. *Proc Natl Acad Sci USA* 112:E1569–E1576
- ✦ Yodzis P (2000) Diffuse effects in food webs. *Ecology* 81: 261–266
- ✦ Zimmerman MS, Irvine JR, O'Neill M, Anderson JH and others (2015) Spatial and temporal patterns in smolt survival of wild and hatchery coho salmon in the Salish Sea. *Mar Coast Fish* 7:116–134

Editorial responsibility: Franz Mueter,
Juneau, Alaska, USA

Reviewed by: J. Baum and 2 anonymous referees

Submitted: August 5, 2020

Accepted: October 21, 2020

Proofs received from author(s): December 5, 2020