TRENDS IN THE PACIFIC HERRING (*CLUPEA PALLASII*) METAPOPULATION IN THE CALIFORNIA CURRENT ECOSYSTEM

SARAH ANN THOMPSON
Farallon Institute
101 H St. Ste. Q
Petaluma, CA 94952
and
Climate Impacts Group
University of Washington
Box 355674
Seattle, WA 98195
sathompson@faralloninstitute.org

WILLIAM J. SYDEMAN,
JULIE A. THAYER
Farallon Institute
101 H St. Ste. Q
Petaluma, CA 94952

ANNA WEINSTEIN,
KATHERINE L. KRIEGER
Audubon California
220 Montgomery St., Ste. 1000
San Francisco, CA 94104

DOUG HAY
Pacific Biological Station
Fisheries and Oceans Canada
3190 Hammond Bay Rd.
Nanaimo, BC
V9T 6N7 Canada

ABSTRACT

Pacific herring are important to fisheries and trophic interactions in the California Current Ecosystem (CCE). In this paper we test the hypothesis that herring biomass across the ecosystem has declined over the past three decades. Overall, herring spawning stock biomass has decreased since the mid to late 1980s, though some populations at the local to regional scale appear stable or have even increased. For regional populations in the northern CCE studied over a much longer time period (six decades), cyclic patterns of abundance are evident, suggesting that the shorter-term trend may be part of a longer-term, Pacific Decadal Oscillation (PDO)-scale cycle. In the southern part of the herring range (California and Oregon), population fluctuations are increasing, which may be related to increasing climate variability there (Sydeman et al. 2013; Black et al. 2014). Large-scale trophic mechanisms to local distribution shifts are implicated in metapopulation fluctuations. Future abundance assessments for herring in the CCE should address how climate and fisheries may synergistically impact populations.

INTRODUCTION

Pacific herring (*Clupea pallasii*) occur from Baja California, Mexico, north to the Beaufort Sea and the Arctic Ocean, and west to Japan. Pacific herring have been extremely important to humans; archeological evidence suggests human exploitation of herring at least 8,000 years ago (Thornton et al. 2010), they were the most utilized fish species by communities of the northwest coast during the last several thousand years (McKechnie et al. 2014), and fisheries for this species persist today. All life stages of herring also support key trophic relationships for North Pacific piscivorous fish, seabirds, and mammals (Womble and Sigler 2006; Rice et al. 2010; Schweigert et al. 2010; Koehn et al. 2016); a recent meta-analysis showed that herring ranks fourth in importance to all predators in the California Current Ecosystem and second in importance for seabirds (Szoboszlai et al. 2015), thus there is potential for competition between human fisheries and marine consumers for this resource.

In the California Current Ecosystem (CCE) off the west coast of North America, some other forage fish species, notably sardine (*Sardinops sagax*) and northern anchovy (*Engraulis mordax*), are currently at very low abundance (e.g., Hill et al. 2016; MacCall et al. 2016). An assessment of herring population trends for this ecosystem has yet to be implemented. Centers of herring spawning biomass are found in localized, sheltered inlets, bays, and estuaries, and population centers may shift. In British Columbia, for example, spawning location changes in any given year, but generally occurs on less than 2% of coastline (Hay et al. 2009). Industrial-scale commercial fishing of CCE herring began in the late 19th century with substantial harvest for many decades (McKechnie et al. 2014). Peak harvest in British Columbia and Washington occurred around 1930, and populations in these regions collapsed by the late 1960s (Outram and Humphreys 1974; Boxberger 2000; McKechnie et al. 2014). Today, fisheries supply markets for sac roe ("kazunoko," exported for sale in Japan) and whole fish that are used for bait in other fisheries (e.g., salmon) (DFO 2015). Most current herring fisheries occur in spawning locations during the spawning season. In British Columbia, two large management areas—Prince Rupert District and Strait of Georgia—support the majority of commercial landings which typically extract up to ~20,000 metric tons (MT) per year (DFO 2015). In Washington, commercial landings take place in Puget Sound and recently ranged from 222–462 MT (Stick et al. 2014). Commercial landings in Oregon have recently ranged from 0–250 MT, with the majority of landings taking place in Yaquina Bay (Leal 2008; T. Buell, pers. comm.). In California, recent commercial landings have ranged from 0–3,000 MT (CDFW 2014).

Starting in the 1950s, annual or periodic stock assessments have been conducted to inform management

TABLE 1
From south to north in the CCE, descriptive characteristics for each region and Washington primary sites. Shown are approximate latitude for the region/site, time period covered by the data, mean ± standard deviation (S.D.) and sample size (N years) for spawning stock biomass (given in tonnes), and the management authority for the region. CA: California; OR: Oregon; WA: Washington; BC: British Columbia; CDFW: California Department of Fish and Wildlife; ODFW: Oregon Department of Fish and Wildlife; WDFW: Washington Department of Fish and Wildlife; FOC: Fisheries and Oceans Canada.

Regions	Approx. Latitude °N	Time Period	Biomass Mean ± S.D. (N years)	Management Authority
San Francisco Bay, CA	37.8	1979–2012	52079 ± 28610 (33)	CDFW
Yaquina Bay, OR	44.6	1979–2011	487 ± 501 (31)	ODFW
South Puget Sound, WA	47.2	2000–2013	2802 ± 1454 (14)	WDFW
Hood Canal, WA	47.7	1976–2013	3317 ± 1077 (22)	WDFW
Olympic, WA	48.1	1980–2011	814 ± 956 (17)	WDFW
Whidbey, WA	48.3	1996–2013	2394 ± 1029 (18)	WDFW
Anacortes, WA	48.6	1996–2013	932 ± 458 (16)	WDFW
Whatcom, WA	48.8	1975–2013	5009 ± 3058 (35)	WDFW
Strait of Georgia, BC	49.1	1951–2012	93756 ± 39274 (62)	FOC
WC Vancouver Island, BC	49.4	1951–2012	41100 ± 24290 (62)	FOC
Central Coast, BC	51.9	1951–2012	34142 ± 17156 (62)	FOC
Haida Gwaii, BC	53.1	1951–2012	25125 ± 19129 (62)	FOC
Prince Rupert District, BC	54.4	1951–2012	28353 ± 16398 (62)	FOC
WA Primary Sites				
Quartermaster Harbor, S. Puget Sound	47.4	1976–2013	990 ± 536 (38)	WDFW
Port Gamble, Hood Canal	47.9	1976–2013	1702 ± 766 (38)	WDFW
Discovery Bay, Olympic	48.0	1976–2013	880 ± 938 (38)	WDFW
Port Susan, Whidbey	48.1	1982–2013	654 ± 533 (32)	WDFW
Fidalgo Bay, Anacortes	48.5	1980–2013	615 ± 417 (31)	WDFW
Cherry Point, Whatcom	48.8	1973–2013	4809 ± 3926 (41)	WDFW

decisions, including harvest quotas, but these data have yet to be synthesized across the entire ecosystem and many time series vary in duration; most stocks, however, have been assessed annually since the early 1980s. Herring stocks are discrete enough to be assessed individually and managed on small-scale stock-by-stock basis (Miller and Schmidtke 1956; Hay and McCarter 1999; Stick et al. 2014), although overlap in some stocks suggests the need for regional management. Spawning stock biomass is calculated primarily by assessing the area occupied and amount of egg deposition yearly in relation to the abundance of adult fish (Hay 1985; Stick and Lindquist 2009; Stick et al. 2014). In this study, we tested the hypothesis that herring biomass in the CCE has declined in a monotonic fashion over the past three decades. To address this hypothesis, we assessed trends in summed herring biomass at sites and regions in British Columbia, Washington, Oregon, and California. This study is significant as to date there has been no synthesis of available herring biomass data across the entire CCE, and given the central role of herring in trophic interactions, particularly for species in the northern CCE, updating and understanding trends in herring abundance can contribute to an ecosystem approach to herring fisheries management.

METHODS

Data Preparation

We obtained spawning biomass data spanning 14–62 years. Information for each site is given in Table 1, and field survey methods are described in the supplementary material. We included information on northern British Columbia populations in this analysis (i.e., as part of the CCE) as in some years the bifurcation of the North Pacific Current, which may be taken as the northern boundary of the CCE, may shift as far north as Haida Gwaii (formerly known as the Queen Charlotte Islands) (Sydeman et al. 2011). All time series were based on existing and ongoing annual surveys. The uncertainty of annual abundance estimates is generally unknown due to the methods used, so weighting analyses by precision was not possible.

Herring spawning biomass data in California were provided by the California Department of Fish and Wildlife. We excluded Humboldt Bay and Tomales Bay from our analysis due to limitation of the time series (<10 years). The time series for San Francisco Bay included 33 years of data. In Oregon, data from Yaquina Bay were provided by Oregon Department of Fish and Wildlife and covered 31 years.
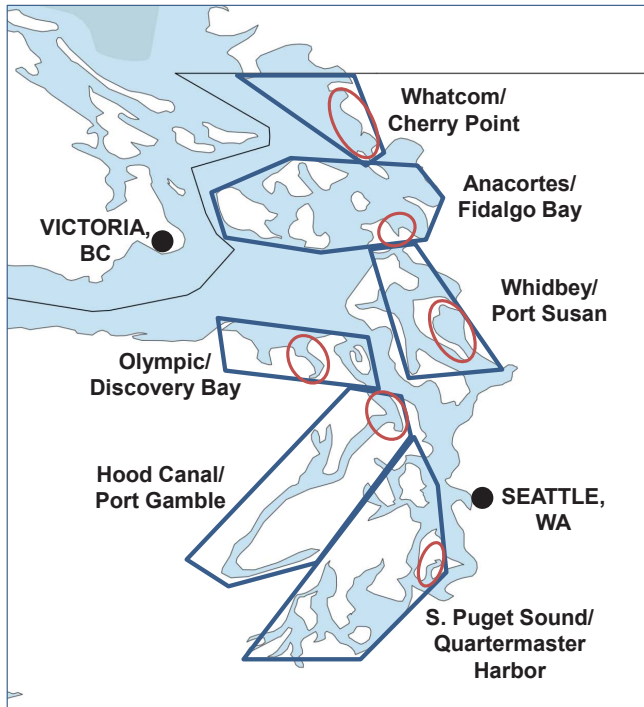
Figure 1. Map of herring spawning regions in Washington State (blue). Also shown are the primary sites examined for each region (red). Labels indicate region/site.

Data for herring spawning biomass in the Puget Sound area were provided by Washington Department of Fish and Wildlife. Due to well-known interactions among spawning populations in Puget Sound, we summarized these data by grouping them into six regions, and summing the biomass for years in which all sites in each region were surveyed. Regions were delineated based on local geographic and oceanographic characteristics (fig. 1). The southernmost region was South Puget Sound, encompassing sites in the central and south basins, south of Whidbey Island. Two sites in this region were excluded from the study for having very short time series compared to the other sites (n = 2 and 6 years). The Hood Canal region contained data from three sites. The Whidbey region contained data from sites on the eastern side of Whidbey and Camano Islands. The Olympic region encompassed sites on the northeast portion of the Olympic Peninsula on the Strait of Juan de Fuca. Sites in the San Juan Islands and Samish and Padilla Bays were included in the Anacortes region. Our northernmost region was Whatcom, encompassing herring spawning sites along Cherry Point and in Semiahmoo Bay. In addition to having regional sums, we also retained data from one primary spawning site in each region that, with one exception, had no gaps in its time series (Fidalgo Bay in the Anacortes region was missing three consecutive years of data). We used the longer time series available

from primary sites to verify regional patterns of change. The primary sites by region were: Quartermaster Harbor in South Puget Sound, Port Gamble in Hood Canal, Discovery Bay in Olympic, Port Susan in Whidbey, Fidalgo Bay in Anacortes, and Cherry Point in Whatcom. The longest time series in Washington was for Cherry Point (41 years), and the shortest time series was for the summed region South Puget Sound (14 years; table 1). In order to understand change in Washington overall, we also summed the data for the years 1980–2013 from the six primary sites. There were a few years for two sites that were without data. To have a complete time series for 1980–2013, we used the value from 1982 as a proxy for 1980 and 1981 at Point Susan. Fidalgo Bay was missing data for 1988–90, and for those years we used the average value for the adjacent six years (average of 1985–87 and 1991–93).

We used herring spawning biomass data for five regions in British Columbia for the years 1951–2012 (62 years). The British Columbia regions (fig. 2) were delineated by Fisheries and Oceans Canada, who provided the data for this study. The Strait of Georgia region covered spawning areas on the east side of Vancouver Island and the mainland coast along the strait. The West Coast (WC) Vancouver Island region encompassed spawning areas along the west coast of Vancouver Island. The Central Coast region covered spawning sites along the central mainland coast, while the Prince Rupert District encompassed sites on the northern mainland coast. The Haida Gwaii region covered spawning areas around the islands that comprise Haida Gwaii.

Trends in Biomass
All data were ln-transformed prior to analysis. We used linear and quadratic regression to assess monotonic trends over time for each region, as well as the Washington primary sites, for 1980–2013. Additionally, we analyzed the British Columbia regions with linear and quadratic regression by their full time series (n = 62 years). To compare and select the best model (linear or curvilinear/quadratic), we used the Akaike Information Criterion (AIC); the lowest score indicates the best model (Akaike 1974). From the linear regression results we calculated the annual rate of population growth/decline (λ) by back-transforming regression coefficients. Following the regressions, we synthesized herring biomass across the ecosystem and examined commonalities in trends using Principal Component Analysis (PCA; Jolliffe 2002) (the Washington summed time series was not included to avoid replication of the primary sites). We also calculated the coefficient of variation (CV) in biomass by decade for each region. When there were fewer than six years of data available in a decade, those years were included in the next
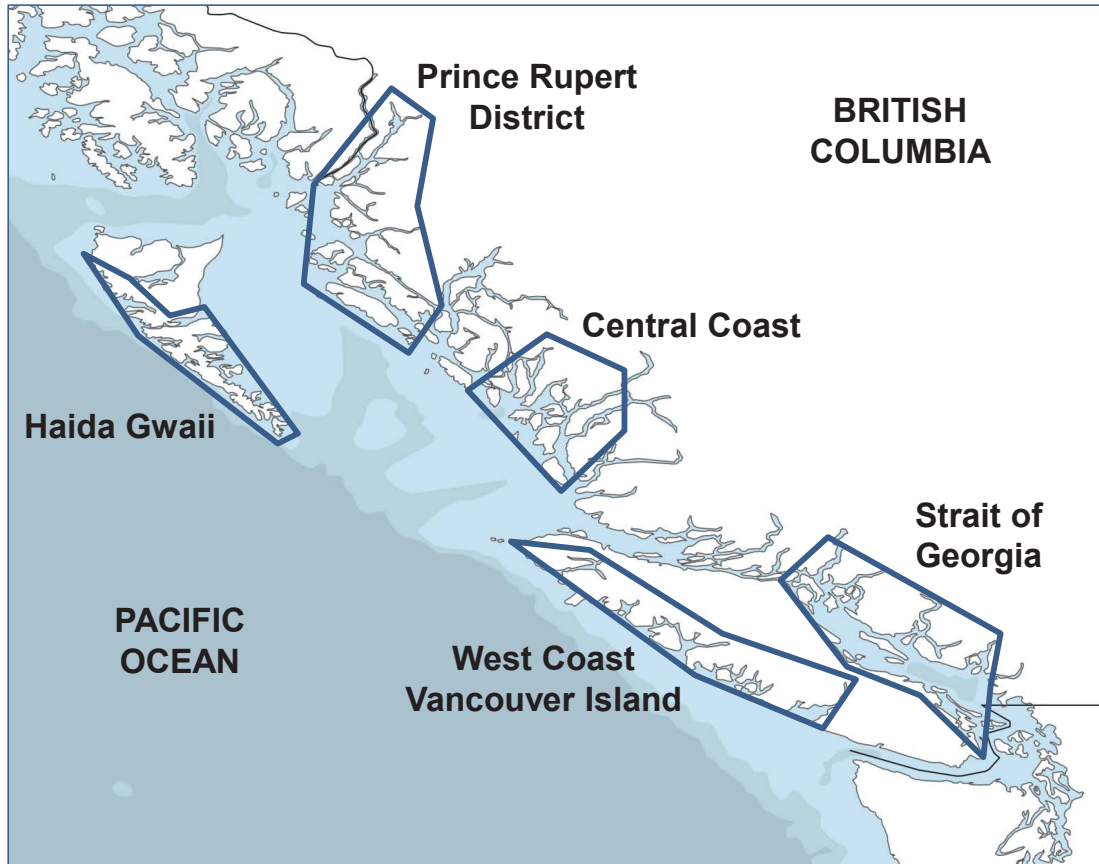
Figure 2.   Map of herring spawning regions in British Columbia.

complete decade. To assess whether there was change in the variability in biomass, we used Spearman rank correlations to look for trends in the decadal–scale CV.

RESULTS

Trends in Biomass, 1980–2013

In most regions, herring spawning biomass declined since 1980 (table 2, fig. 3). Among the regions with statistically significant declines, $\lambda = -1\%$ to -12% per year (table 2). All Washington primary sites also had trends of decreasing spawning biomass, and for those sites λ ranged from -5% to -15% per year (table 2, fig. 4). Many of the regions and sites showed curvilinear declines, but most were monotonic within this time period (table 2, figs. 3–4). In all of these cases, the quadratic regression was supported with a lower AIC by a margin >2, with the exception of Port Susan (table 2). For Port Susan as well as several other sites and regions, the difference in the AIC between the linear and quadratic models was <2, which indicates that the second-best model cannot be excluded from consideration (Burnham and Anderson 2002). In these cases, we selected the linear model after considering

the strength of the other statistics (e.g., R^2 values; tables 2, 4, figs. 3–4). All regions in British Columbia had significant quadratic change in biomass over time, and interestingly, the curve for Haida Gwaii differed from the others since biomass there increased slightly since 2000 (fig. 3). When we summed all Washington data as a region, it also showed a curvilinear decline in biomass (table 2, fig. 3). Hood Canal had non-significant results for both regression models (table 2).

PCA of the 1980 to 2013 biomass data across sites and regions revealed one dominant mode (PC1) that explained about 45% of the variability in herring biomass in the CCE (table 3); with the exceptions of San Francisco Bay and the Strait of Georgia, all sites and regions loaded on PC1 similarly strongly. PC2 explained about 14% of the variability and had an eigenvalue <2, indicating this is not a dominant mode of variability. PC1 demonstrated an overall decline in herring biomass across the ecosystem from 1980 to 2013, in support of our hypothesis, and suggesting that the decline was more substantial from ~1990 to 2013 than from 1980 to 1990 (fig. 5). PC2 reflects the pattern of variability in the Strait of Georgia (table 3, figs. 3, 6) and also shows a decline later in the time period, 2000–13.

TABLE 2
Results of linear and quadratic regression on herring spawning stock biomass by region and Washington primary sites for 1980–2013. Also given is the AIC statistic and the calculated percent change in biomass per year (λ; linear models only). Bold figures show significant p-values (p < 0.1). Shaded lines show the best selected models. In most cases this was the model with the lowest AIC, but we chose the linear model with a higher AIC for Port Susan (see Results for further details).

| Regions	Model	N	F	p>F	R^2	Term	% change per year	t	p>|t|	AIC
San Francisco Bay, CA	linear	32	3.38	**0.076**	0.101	year	−2.25	−1.84	**0.076**	67.22
	quadratic	32	1.94	0.161	0.118	year		−1.16	0.254	68.61
						year^2		0.74	0.463	
Yaquina Bay, OR	linear	30	8.39	**0.007**	0.231	year	−6.54	−2.9	**0.007**	98.56
	quadratic	30	4.39	**0.022**	0.246	year		0.03	0.973	99.97
						year^2		−0.73	0.469	
South Puget Sound, WA	linear	14	22.97	**<0.001**	0.657	year	−12.01	−4.79	**<0.001**	16.11
	quadratic	14	17.8	**<0.001**	0.764	year		1.87	**0.088**	12.87
						year^2		−2.23	**0.047**	
Hood Canal, WA	linear	20	1.28	0.274	0.066	year	1.21	1.13	0.274	10.53
	quadratic	20	1.02	0.381	0.108	year		1.03	0.317	11.62
						year^2		−0.89	0.388	
Olympic, WA	linear	17	24.23	**<0.001**	0.618	year	−10.67	−4.92	**<0.001**	36.6
	quadratic	17	13.25	**<0.001**	0.654	year		−0.37	0.719	36.88
						year^2		−1.22	0.242	
Whidbey, WA	linear	18	0.35	0.563	0.021	year	−1.21	−0.59	0.563	24.52
	quadratic	18	5.26	**0.019**	0.412	year		3.08	**0.008**	17.35
						year^2		−3.16	**0.007**	
Anacortes, WA	linear	16	18.47	**<0.001**	0.569	year	−7.04	−4.3	**0.001**	12.82
	quadratic	16	9.68	**0.003**	0.598	year		−1.38	0.19	13.69
						year^2		0.97	0.348	
Whatcom, WA	linear	32	48.66	**<0.001**	0.738	year	−4.96	−9.2	**<0.001**	15.03
	quadratic	32	41.68	**<0.001**	0.742	year		−2.74	**0.01**	16.59
						year^2		0.63	0.534	
Washington	linear	34	219.83	**<0.001**	0.873	year	−5.99	−14.83	**<0.001**	0.9
	quadratic	34	159.71	**<0.001**	0.912	year		2.02	0.052	−9.42
						year^2		−3.68	**0.001**	
Strait of Georgia, BC	linear	33	0.48	0.494	0.015	year	0.37	0.69	0.494	14.22
	quadratic	33	8.48	**0.001**	0.361	year		4.12	**<0.001**	1.93
						year^2		−4.03	**<0.001**	
WC Vancouver Island, BC	linear	33	53.02	**<0.001**	0.631	year	−6.44	−7.28	**<0.001**	49.89
	quadratic	33	58.58	**<0.001**	0.796	year		2.44	**0.021**	32.31
						year^2		−4.93	**<0.001**	
Central Coast, BC	linear	33	55.58	**<0.001**	0.642	year	−4.46	−7.46	**<0.001**	23.36
	quadratic	33	47.72	**<0.001**	0.761	year		1.57	0.127	12.04
						year^2		−3.86	**0.001**	
Haida Gwaii, BC	linear	33	103.54	**<0.001**	0.77	year	−6.2	−10.18	**<0.001**	25.21
	quadratic	33	87.04	**<0.001**	0.853	year		−7.04	**<0.001**	12.38
						year^2		4.13	**<0.001**	
Prince Rupert District, BC	linear	33	7.02	**0.013**	0.185	year	−1.16	−2.65	**0.013**	1.67
	quadratic	33	7.12	**0.003**	0.322	year		1.7	0.1	−2.41
						year^2		−2.46	**0.02**	
WA Primary Sites										
Quartermaster Harbor, S. Puget Sound	linear	34	26.06	**<0.001**	0.449	year	−5.08	−5.1	**<0.001**	61.92
	quadratic	34	20.84	**<0.001**	0.574	year		1.53	0.136	55.21
						year^2		−3.01	**0.005**	
Port Gamble, Hood Canal	linear	34	31.36	**<0.001**	0.495	year	−4.62	−5.6	**<0.001**	49.04
	quadratic	34	29.73	**<0.001**	0.657	year		2.09	**0.045**	37.85
						year^2		−3.83	**0.001**	
Discovery Bay, Olympic	linear	34	39.27	**<0.001**	0.551	year	−15.06	−6.27	**<0.001**	125.56
	quadratic	34	19.24	**<0.001**	0.554	year		−1.07	0.291	127.34
						year^2		−0.44	0.662	
Port Susan, Whidbey	linear	32	23.73	**<0.001**	0.442	year	−6.76	−4.87	**<0.001**	74.41
	quadratic	32	13.56	**<0.001**	0.483	year		0.41	0.686	73.93
						year^2		−1.53	0.137	
Fidalgo Bay, Anacortes	linear	31	12.42	**0.001**	0.3	year	−5.52	−3.52	**0.001**	83
	quadratic	31	45.65	**<0.001**	0.765	year		5.73	**<0.001**	51.12
						year^2		−7.45	**<0.001**	
Cherry Point, Whatcom	linear	34	103.62	**<0.001**	0.764	year	−6.23	−10.18	**<0.001**	29.2
	quadratic	34	51.78	**<0.001**	0.77	year		−3.3	0.002	30.38
						year^2		0.87	0.393	
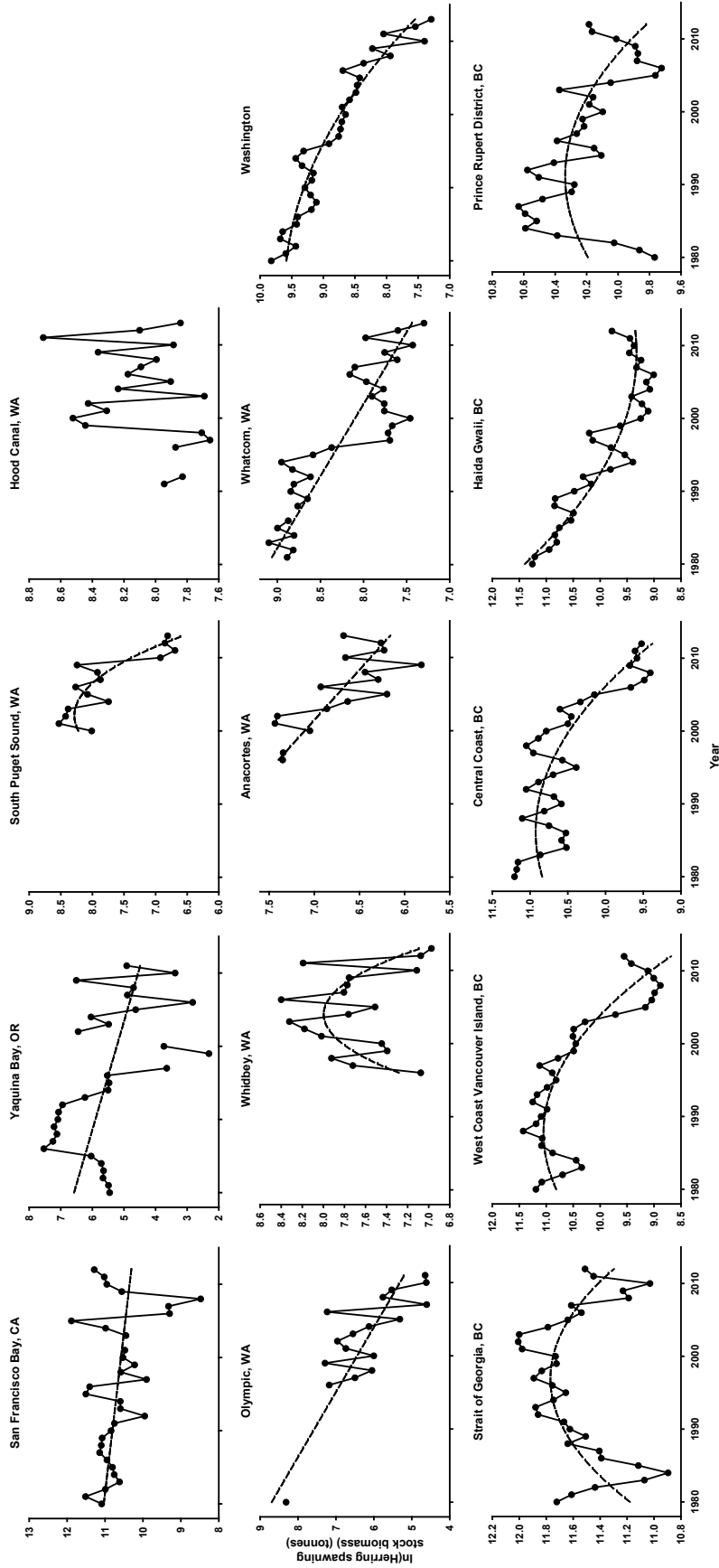
Figure 3.   Trends in herring spawning stock biomass by region for the period 1980–2013. Trend lines (dashed) are shown corresponding to the best regression model (linear or quadratic), determined by lowest AIC (see table 2). Hood Canal has no regression line since neither model was significant.
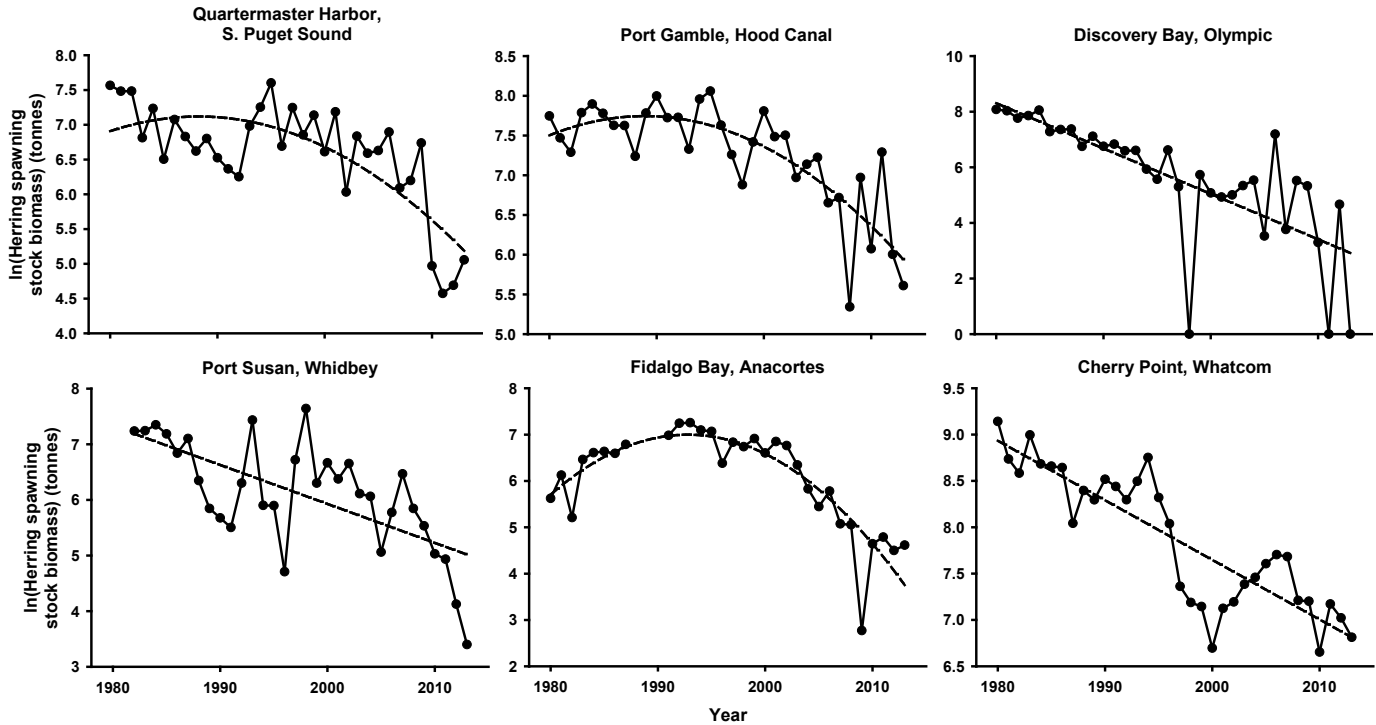
Figure 4. Trends in herring spawning stock biomass for Washington primary sites for the period 1980–2013. Trend lines (dashed) are shown corresponding to the best regression model (linear or quadratic), determined by lowest AIC (see table 2).

Figure 5. Scores for the first (solid line) and second (dashed line) principal components for 1980-2013. See Table 4 for site/region loadings.

TABLE 3
Results of principal component analysis (PCA) for regions and Washington primary sites for 1980–2013. (A) eigenvalues and proportion variance explained, (B) site/region loadings on PC1, PC2, and PC3. Loadings > |0.2| are shaded.
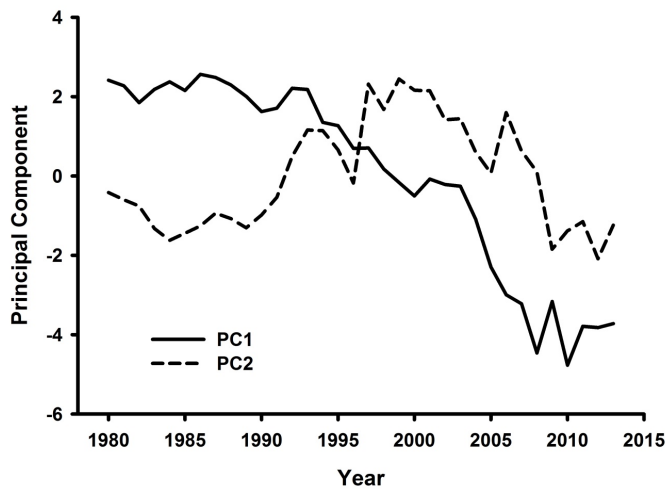
(A)

Component	Eigenvalue	Proportion	Cumulative
1	5.8466	0.4497	0.4497
2	1.8460	0.1420	0.5917
3	1.6107	0.1239	0.7156

(B)

	Eigenvectors		
Site	1	2	3
San Francisco Bay, CA	0.1366	−0.2970	0.3856
Yaquina Bay, OR	0.2142	−0.3582	0.2557
Quartermaster Harbor, WA	0.2855	0.2619	−0.3391
Port Gamble, WA	0.3332	0.0703	0.0282
Discovery Bay, WA	0.2771	−0.1044	−0.4039
Port Susan, WA	0.2544	0.2152	−0.3290
Fidalgo Bay, WA	0.2961	0.3761	0.1053
Cherry Point, WA	0.3293	−0.2315	−0.2250
Strait of Georgia, BC	0.0592	0.5279	0.4001
WC Vancouver Island, BC	0.3682	0.0456	0.2594
Central Coast, BC	0.3520	0.1452	0.1444
Haida Gwaii, BC	0.2924	−0.3698	−0.0701
Prince Rupert District, BC	0.2382	−0.1382	0.2895

TABLE 4
**Results of linear and quadratic regression on herring spawning stock biomass for full time series of British Columbia regions.
Also given is the AIC statistic and the calculated percent change in biomass per year (λ; linear models only).
Bold figures show significant p-values (p < 0.1). Shaded lines show the best selected models.**

| Regions	Model	N	F	p>F	R^2	Term	% change per year	t	p>|t|	AIC
Strait of Georgia, BC	linear	62	13.82	**<0.001**	0.187	year	1.29	3.72	**<0.001**	88.03
	quadratic	62	7.04	**0.002**	0.193	year		0.3	0.766	89.62
						year^2		0.63	0.53	
WC Vancouver Island, BC	linear	62	1.16	0.286	0.019	year	−0.57	−1.08	0.286	141.09
	quadratic	62	22.01	**<0.001**	0.427	year		5.94	**<0.001**	109.72
						year^2		−6.49	**<0.001**	
Central Coast, BC	linear	62	0.56	0.459	0.009	year	0.31	0.75	0.459	109.8
	quadratic	62	5.88	**0.005**	0.166	year		3.43	**0.001**	101.1
						year^2		−3.33	**0.001**	
Haida Gwaii, BC	linear	62	0.04	0.844	0.001	year	−0.11	−0.2	0.844	152.51
	quadratic	62	5.75	**0.005**	0.163	year		3.23	**0.002**	143.52
						year^2		−3.38	**0.001**	
Prince Rupert District, BC	linear	62	0.14	0.707	0.002	year	−0.14	−0.38	0.707	101.46
	quadratic	62	0.56	0.586	0.018	year		−1.03	0.307	102.48
						year^2		0.97	0.337	
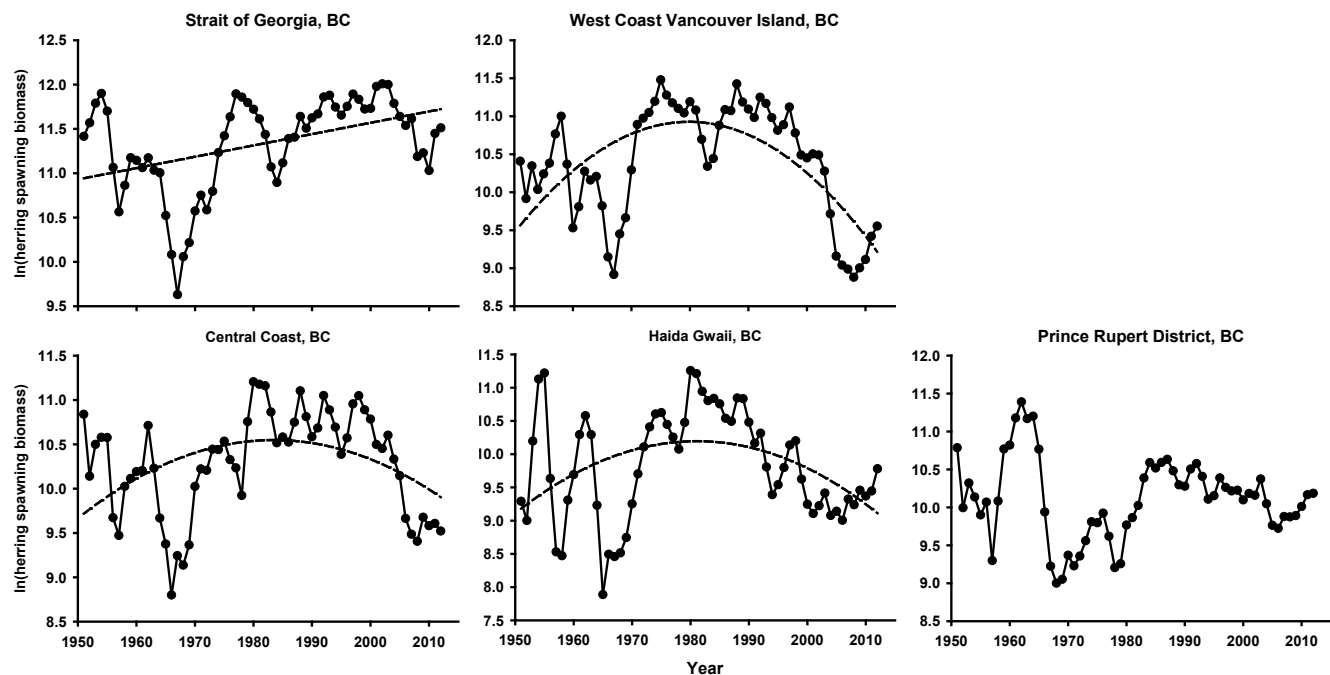
Figure 6. Trends in herring spawning stock biomass (tonnes) by region for the full time periods in the British Columbia regions. Trend lines (dashed) are shown corresponding to the best regression model (linear or quadratic), determined by lowest AIC (see table 4). Graphs show best timeline and biomass scale for each data set; note differing scales on each axis.

Trends in Biomass, 1950 to Present, British Columbia

One region, the Strait of Georgia, had an increase in herring spawning biomass since 1951 (λ = 1.29%/ year; table 4, fig. 6). No linear decreases were found, and instead spawning biomass for the West Coast Vancouver Island, Central Coast, and Haida Gwaii demonstrated cyclical (quadratic) patterns of change over time (table 4, fig. 6). Lastly, Prince Rupert District had insignificant trends in both the linear and quadratic models (table 4).

Trends in Variance

Five of the Washington regions had time series that were too short in order to be included in this analysis. All other regions, and the Washington primary sites, had at least three decades of data. In the south, San Francisco Bay and Yaquina Bay showed significantly increasing variance in biomass through time (table 5). In Washington, the overall numbers as well as three primary sites had significant increases in variance while the Whatcom region and the three other primary sites had nonsignificant change in variance. In contrast, to

TABLE 5
**Spearman rank correlation on changes in variance
in herring biomass over time. Only one region in
Washington, Whatcom, had a time series long enough
for this analysis. Shown are the sample size (N),
Spearman Rho, and the associated p-value.**

Regions	N	Rho	P-value
San Francisco Bay, CA	3	1.00	0.000
Yaquina Bay, OR	3	1.00	0.000
Whatcom, WA	3	−0.50	0.667
Washington	3	1.00	0.000
Strait of Georgia, BC	6	−0.03	0.957
WC Vancouver Island, BC	6	−0.60	0.208
Central Coast, BC	6	−0.26	0.623
Haida Gwaii, BC	6	−0.83	0.042
Prince Rupert District, BC	6	−0.83	0.042
WA Primary Sites			
Quartermaster Harbor, S. Puget Sound	3	1.00	0.000
Port Gamble, Hood Canal	3	1.00	0.000
Discovery Bay, Olympic	3	0.50	0.667
Port Susan, Whidbey	3	1.00	0.000
Fidalgo Bay, Anacortes	3	0.50	0.667
Cherry Point, Whatcom	4	0.80	0.200

the north, the Prince Rupert District and Haida Gwaii showed significantly decreasing variance.

DISCUSSION

Population Trends

Using a comprehensive data set for herring spawning stock biomass at sites and regions from California, Oregon, Washington, and British Columbia, we tested the hypothesis that herring biomass in the CCE has declined over the past three decades. To test this hypothesis, we used geographic classifications previously established by others conducting syntheses of herring population statistics in British Columbia (e.g., Hay et al. 2009), along with new site groupings in Puget Sound. For this period, we evaluated herring spawning stock biomass data for monotonic linear and curvilinear trends and changes in variance over time. The results from our study support our hypothesis of overall ecosystem-scale decline from the mid to late 1980s to the present (fig. 5), but even within this period, a few spawning populations showed no change or increased.

At two locations, Hood Canal and Strait of Georgia (using the full time series), herring biomass had an increasing trend. In both cases it is plausible that these increases reflect distributional shifts in local populations. The Strait of Georgia region is very close to Cherry Point, Washington, and while Strait of Georgia herring biomass has been increasing, biomass at Cherry Point has had a strong decline in the same time period. Similarly, though the Hood Canal region shows increasing

biomass, most sites near it have been decreasing (including Port Gamble, the primary site that we identified in that region in terms of time series completeness). The increasing herring biomass there is probably a product of emigration from other areas, not intrinsic growth of the Hood Canal population (Siple and Francis 2016).

Perhaps more significantly, when we examined the full time series (n = 62 years) from British Columbia, cyclic population fluctuations were evident, suggesting that that the decline since ~1990 may reflect only the declining period of a low-frequency cycle. Cyclically fluctuating herring populations in other regions of the CCE may also occur; we found some curvilinear population trends at several sites in Washington. Though these other populations may also cycle, at present we do not have long enough time series at the other sites to conclusively describe this pattern. Cyclical patterns of herring abundance and other population characteristics such as growth have been related to climate indicators such as the Pacific Decadal Oscillation (Siple and Francis 2016), as well as specific ocean conditions such as sea surface temperature and salinity (Rose et al. 2008; Ito et al. 2015).

Independent of the longest modes of variability, biomass declined significantly across the ecosystem since the mid to late 1980s including in all five British Columbia coastal regions, except the Strait of Georgia (though see above note about Cherry Point). This interpretation of general decline is complicated by regional variation; abundance in the most recent years in San Francisco Bay, Yaquina Bay, Hood Canal, and Haida Gwaii (in addition to Prince Rupert District) was not exceptionally high nor low, though South Puget Sound, Olympic, Whidbey, and Whatcom all experienced very low biomass. Relatedly, in the last several years, herring biomass was at historically low values at all six of the Washington primary sites that we examined (Siple and Francis 2016) and we found a strong declining trend for Washington as a whole region since 1980. Continued monitoring and evaluation of herring population trends will provide a better understanding of the details of these individual population trends, relative to the entire CCE metapopulation.

Changes in Variance

For the longest time series available in our data set, we also examined changes in the variance in herring biomass by calculating the coefficients of variation by decade. Though the sample size is admittedly very low (n = 5 decades), some interesting patterns of population variability are evident. Most notably, the southernmost sites in the CCE, San Francisco Bay and Yaquina Bay, showed increasing variability in biomass, as did the Washington region when summed. The northernmost regions, Haida Gwaii and Prince Rupert District,

showed decreasing variability through time, and spawning populations in the center of the herring range in the CCE, as we defined it, showed no change in variance. Such changes in population variance could be attributed to a variety of factors. For one, it is predicted that climate change may increase variability in both physical and biological properties of marine ecosystems (IPCC 2013); these changes may be most apparent in the southern portions of species' ranges (Poloczanska et al. 2013; Pinsky et al. 2013). San Francisco Bay is near the southern end of herring range in the Northeast Pacific (Miller and Lea 1972), and variance in a variety of ecosystem properties in this region appears to be increasing (Sydeman et al. 2013; Black et al. 2014). A corresponding decrease in variability in the northern portion of species' ranges, such as we observed here, is also plausible relative to climate change, but has not been predicted by theory. Alternatively, the decreasing variability in the Prince Rupert District and Haida Gwaii may relate to the fact that these regions are located in an oceanographic transition zone between the CCE and Gulf of Alaska. Differences in population variability between the southern population of San Francisco Bay, and to a lesser extent Yaquina Bay, and northern British Columbia may also be related to the inverse production regime hypothesis (Hare et al. 1999), which indicates that ecosystem productivity in the CCE and Gulf of Alaska covary out of phase (i.e., are negatively correlated). However, Teo et al. (2009) showed similar variability in salmonid survival rates between the CCE and the Gulf of Alaska in similar periods, so this hypothesis is equivocal. Furthermore, the age structure of the northern populations do not show the same age structure changes as those to the south, but size at age has been decreasing (Therriault et al. 2009; Hay et al. 2012), and there is some evidence that recruitment is becoming more variable (Therriault et al. 2009). Understanding the variability of herring populations throughout the CCE will take more dedicated effort to examine age structure and size at age in relation to environmental conditions and other impacts.

Herring and the Forage Fish Community

The CCE is not a wasp-waist system (sensu Cury et al. 2000) in that many species make up the mid trophic levels responsible for energy transfer from primary producers to secondary and tertiary consumers (Miller et al. 2010). Along with northern anchovy, Pacific sardine, juvenile (age-0) rockfish and hake, smelts of various species, and mesozooplankton, notably euphausiid crustaceans, herring is one of the primary forage species (Brodeur et al. 2014; Szoboszlai et al. 2015). Lately, the CCE forage community has received considerable attention (Kaplan et al. 2013), mainly due to the decline of sardine, which constitutes an important fishery resource. A persistent decline in

sardine abundance from about 2005 to 2015 (Zwolinski and Demer 2012; Zwolinksi et al. 2014) resulted in closure of that fishery across the CCE in 2016; as of the writing of this paper, the fishery is still closed, with estimated biomass in the entire ecosystem approximately 100,000 MT (Hill et al. 2016). The northern anchovy population has also shown a major decline in the heart of its range off south-central California (Koslow and Davison 2015; Sydeman et al. 2015a), with a current estimated biomass of <100,000 MT (MacCall et al. 2016; Thayer et al. in press). The precipitous decline of the central subpopulation of anchovy began in 2007–08 after a substantial spike in abundance in 2005–06, and there is little evidence of recovery by 2015–16 (Thayer et al. in press). Patterns of change in age-0 forage fish (juvenile rockfish and hake) are less clear. Juvenile rockfish catch per unit effort (CPUE) in the central CCE declined from the late 1980s to late 1990s before rebounding in the early 2000s, then declining to its lowest levels in 2005–07 before increasing again in recent years (Leising et al. 2015). Based on stock assessment models, the production of juvenile hake declined through the 1980s and 1990s, but has also recently rebounded (Grandin et al. 2016). Trends in euphausiid abundance have been variable, with some species showing low-frequency decreases (*Nyctiphanes simplex*, Di Lorenzo and Ohman 2013), while others are increasing (*Thysanoessa spinifera*, Sydeman et al. 2015a), or are stable (*Euphausia pacifica*, Brinton and Townsend 2003; Lavaniegos and Ohman 2007). The structure of the euphausiid community, however, has certainly shifted through time.

We may now add the CCE Pacific herring metapopulation to the list of recently declining forage fish, but with inconsistencies in subpopulation trends and uncertainty in whether patterns of change are unidirectional or part of a low-frequency cycle. Herring are more important to predators in the northern CCE (Szoboszlai et al. 2015), where they are also generally more abundant (this study). Fortunately, in the largest center of herring abundance in British Columbia, trends have not been negative (e.g., Strait of Georgia), though since the 1980s, most populations in British Columbia have also been in decline. The stronghold in the south, the San Francisco Bay population, shows weak evidence of decline, but its numbers have been volatile and this population cannot be considered stable. The pronounced decline in many species of the forage community, including herring, since the mid to late 1980s (fig. 5) may be related to the "biotic regime shift" of 1989–90 (Hare and Mantua 2000), coupled with increasing "marine climate" variability (e.g., Sydeman et al. 2013; Black et al. 2014). It is well known that herring recruitment is influenced by environmental conditions, such as water temperature and upwelling (Zebdi and

Collie 1995). Considering the late 1990s and 2000s, environmental conditions have been notably variable, including a major and rapid shift between extreme El Niño to La Niña conditions from 1998–99 (Chavez et al. 1999), highly delayed upwelling in 2005 (Schwing et al. 2006), record upwelling in 2013 (Leising et al. 2014) followed by an unprecedented marine heat wave ("The Blob") in 2014–15 (Bond et al. 2015; Gentemann et al. 2017), and a severe El Niño in 2015–16 (Jacox et al. 2016). These conditions affected different regions of the CCE differently and produced a variety of ecosystem consequences, and this spatial variability may explain some of the differences observed in this study between populations.

Mechanistically, herring populations in the CCE are likely to be affected trophically through the availability of zooplankton prey, by changes in the abundance and distribution of major herring predators such as hake (Ware and MacFarlane 1995) and whales (Rice et al. 2011), or by water temperature and metabolic factors (Portner et al. 2008; Sydeman et al. 2015b). Indeed, humpback whales are significant predators of herring in the Northeast Pacific and their steadily increasing abundance means that they will have increased predatory influence on populations of herring and other forage fish species (Rice et al. 2011). Overall though, if the cause of declining trends were simply a trophic mechanism, we would expect to see similar trends in all populations that migrate and feed in offshore oceanic areas. What we observed, however, is that the subpopulations with a more lengthy "inshore" residence (Strait of Georgia and Puget Sound) have somewhat different trends than those that spend more time on the continental shelf areas. The different temporal trajectories between the Strait of Georgia and Puget Sound versus the West Coast of Vancouver Island and coastal populations to the south that may have the same summer feeding areas point to non-trophic factors, such as changes in habitat quality, as a parsimonious explanation for these differences in population trends between regions. We hypothesize that herring fisheries are unlikely to have been the cause of decline in most subpopulations. However, it has been suggested that fishing, on top of natural variability, may contribute to population fluctuations by altering the structure of populations (Essington et al. 2015). The coincidental recent decline in the central subpopulation of northern anchovy is thought to be almost exclusively environmentally driven (MacCall et al. 2016; Thayer et al. in press), whereas the decline in sardine has been ascribed to fishing during a period of poor recruitment (Zwolinski and Demer 2012; Hill et al. 2016). On a positive note, while the overall herring population biomass trend is negative, the largest regional populations, San Francisco Bay and those in British Columbia, have shown cyclical patterns, some stability, and even slight increases since 2010. However, this pattern may reverse depending on the response of these populations to the recent ocean warming of 2014–16 (Bond et al. 2015; Jacox et al. 2016).

The northeast Pacific is a complex ecosystem in which herring are a vital part of pelagic food webs and important traditional and commercial fisheries. We do not understand the drivers of changes occurring in the herring metapopulation, nor have the consequences to upper trophic levels in this marine ecosystem been investigated comprehensively. Expansion of current monitoring and new directed research on relationships between herring and the environment and higher level consumers is therefore warranted and essential.

ACKNOWLEDGEMENTS

LITERATURE CITED

Akaike, H. 1974. New look at statistical model identification. IEEE Trans. Auto. Cont. AC19:716–723.

Black, B. A., W. J. Sydeman, D. C. Frank, D. Griffin, D. W. Stahle, M. Garcia-Reyes, R. R. Rykaczewski, and S. J. Bograd. 2014. Six centuries of variability and extremes in a couple marine-terrestrial ecosystem. Science 345:1498–1502.

Bond, N. A., M. F. Cronin, H. Freeland, and N. Mantua. 2015. Causes and impacts of the 2014 warm anomaly in the NE Pacific. Geophys. Res. Lett. 42:3414–3420.

Boxberger, D. L. 2000. To fish in common: The ethnohistory of Lummi Indian salmon fishing. University of Washington Press, Seattle, Washington.

Brinton, E., and A. Townsend. 2003. Decadal variability in abundances of the dominant euphausiid species in southern sectors of the California Current. Deep-Sea Res. Pt. II 50:2449–2472.

Brodeur, R. D., J. C. Buchanan, and R. L. Emmett. 2014. Pelagic and demersal fish predators on juvenile and adult forage fishes in the Northern California Current: spatial and temporal variations. Calif. Coop. Oceanic Fish. Invest. Rep. 55:96–116.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: A practical information-theoretic approach. Springer-Verlag New York, Inc. 488 pp.

CDFW. 2014. Pacific herring commercial fishing regulations. Final Supplemental Environmental Document, SCH No. 98052052. California Department of Fish and Wildlife.

CDFW. 2015. Pacific herring commercial fishing regulations. Draft Supplemental Environmental Document, SCH No. 98052052. California Department of Fish and Wildlife.

Chavez, F. P., P. G. Strutton, G. E. Friederich, R. A. Feely, G. C. Feldman, D. G. Foley, and M. J. McPhaden. 1999. Biological and chemical response of the Equatorial Pacific Ocean to the 1997–98 El Niño. Science 286:2126–2131.

Checkley, D. M., and J. A. Barth. 2009. Patterns and processes in the California Current System. Prog. Oceanogr. 83:49–64.

Cury, P., A. Bakun, R. J. M. Crawford, A. Jarre, R. A. Quinones, L. J. Shannon, and H. M. Verheye. 2000. Small pelagics in upwelling systems: Patterns of interaction and structural changes in "wasp-waist" ecosystems. ICES J. Mar. Sci. 57:603–618.

DFO. 2015. Stock assessment and management advice for British Columbia Pacific herring: 2014 status and 2015 forecast. DFO Canadian Science Advisory Secretariat Science Advisory Report 2014/060.

Di Lorenzo, E., and M. D. Ohman. 2013. A double-integration hypothesis to explain ocean ecosystem response to climate forcing. Proc. Nat. Acad. Sci. 110:2496–2499.

Essington, T. E., P. E. Moriarty, H. E. Froehlich, E. E. Hodgson, L. E. Koehn, K. L. Oken, M. C. Siple, and C. C. Stawitz. 2015. Fishing amplifies forage fish population collapses. Proc. Nat. Acad. Sci. 112:6648–6652.

Gentemann, C. L., M. R. Fewings, and M. Garcia-Reyes. 2017. Satellite sea surface temperatures along the West Coast of the United States during the 2014–16 northeast Pacific marine heat wave. Geophys. Res. Lett. 44:312–319.

Grandin, C. J., A. C. Hicks, A. M. Berger, A. M. Edwards, N. Taylor, I. G. Taylor, and S. Cox. 2016. Status of the Pacific hake (whiting) stock in U.S. and Canadian waters in 2016. Joint Technical Committee of the U.S. and Canada Pacific Hake/Whiting Agreement. National Marine Fisheries Service and Fisheries and Oceans Canada. 165 pp.

Hare, S. R., and N. J. Mantua. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. Prog. Oceanogr. 47:103–145.

Hare, S. R., N. J. Mantua, and R. C. Francis. 1999. Inverse production regimes: Alaska and West Coast Pacific salmon. Fisheries 24:6–14.

Hay, D. E. 1985. Reproductive biology of Pacific herring (*Clupea harengus pallasi*). Can. J. Fish. Aquat. Sci. 42:111–126.

Hay, D. E., and P. B. McCarter. 1999. Distribution and timing of herring spawning in British Columbia. Canadian Stock Assessment Secretariat Research Document 99/14. Fisheries and Oceans Canada, Biological Sciences Branch. 44 pp.

Hay, D. E., P. B. McCarter, K. S. Daniel, and J. F. Schweigert. 2009. Spatial diversity of Pacific herring (*Clupea pallasi*) spawning areas. ICES J. Mar. Sci. 66:1662–1666.

Hay, D., J. Schweigert, J. Boldt, J. Cleary, T. A. Greiner, and K. Hebert. 2012. Decrease in herring size-at-age: a climate change connection? *In:* State of the physical, biological, and selected fishery resources of Pacific Canadian marine ecosystems in 2011. J. R. Irvine and W. R. Crawford, eds. DFO Canadian Science Advisory Secretariat Research Document 2012/072. pp. 142.

Hill, K. T., P. R. Crone, E. Dorval, and B. J. Macewicz. 2016. Assessment of the Pacific sardine resource in 2016 for U.S.A. management in 2016–17. NOAA Tech. Memo. NOAA-TM-NMFS-SWFSC-562. NOAA NMFS Southwest Fisheries Science Center.

IPCC. 2013. Climate change 2013: The physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Stocker, T. F., et al. (Eds.) Cambridge University Press. Cambridge, U.K., and New York, N.Y., USA.

Ito, S., K. A. Rose, B. A. Megrey, J. Schweigert, D. Hay, F. E. Werner, and M. N. Aita. 2015. Geographic variation in Pacific herring growth in response to regime shifts in the North Pacific Ocean. Prog. Oceanogr. 138:331–347.

Jacox, M. G., E. L. Hazen, K. D. Zaba, D. L. Rudnick, C. A. Edwards, A. M. Moore, and S. J. Bograd. 2016. Impacts of the 2015–16 El Niño on the California Current System: Early assessment and comparison to past events. Geophys. Res. Lett. 43:7072–7080.

Jolliffe, I. T. 2002. Principal Component Analysis. Springer-Verlag New York, Inc., New York.

Kaplan, I. C., C. J. Brown, E. A. Fulton, I. A. Gray, J. C. Field, and A. D. M. Smith. 2013. Impacts of depleting forage species in the California Current. Env. Cons. 40:380–393.

Koehn, L. E., T. E. Essington, K. N. Marshall, I. C. Kaplan, W. J. Sydeman, A. I. Szoboszlai, and J. A. Thayer. 2016. Developing a high taxonomic resolution food web model to assess the functional role of forage fish in the California Current ecosystem. Ecol. Mod. 335:87–100.

Koslow, J. A., and P. C. Davison. 2015. Productivity and biomass of fishes in the California Current Large Marine Ecosystem: Comparison of fishery-dependent and -independent time series. Env. Dev. 17:23–32.

Lavaniegos, B. E., and M. D. Ohman. 2007. Coherence of long-term variations of zooplankton in two sectors of the California Current System. Prog. Oceanogr. 75:42–69.

Leal, D. R. 2008. A fishermen's agreement and co-op in Yaquina Bay roe herring. FAO Fisheries Technical Paper 504. Food and Agriculture Organization of the United Nations. pp. 415–423.

Leising, A. W., I. D. Schroeder, S. J. Bograd, E. Bjorkstedt, J. Field, K. Sakuma, J. Abell, R. R. Robertson, J. Tyburczy, W. T. Peterson, R. D. Brodeur, C. Barcelo, T. D. Auth, E. A. Daly, G. S. Campbell, J. A. Hildebrand, R. M. Suryan, A. J. Gladics, C. A. Horton, M. Kahru, M. Manzano-Sarabia, S. McClatchie, E. D. Weber, W. Watson, J. A. Santora, W. J. Sydeman, S. R. Melin, R. L. DeLong, J. Largier, S. Y. Kim, F. P. Chavez, R. T. Golightly, S. R. Schneider, P. Warzybok, R. Bradley, J. Jahncke, J. Fisher, and J. Peterson. 2014. State of the California Current 2013–14: El Nino looming. Calif. Coop. Oceanic Fish. Invest. Rep. 55:51–87.

Leising, A. W., I. D. Schroeder, S. J. Bograd, J. Abell, R. Durazo, G. Gaxiola-Castro, E. Bjorkstedt, J. Field, K. Sakuma, R. R. Robertson, R. Goericke, W. T. Peterson, R. D. Brodeur, C. Barcelo, T. D. Auth, E. A. Daly, R. M. Suryan, A. J. Gladics, J. M. Porquez, S. McClatchie, E. D. Weber, W. Watson, J. A. Santora, W. J. Sydeman, S. R. Melin, F. P. Chavez, R. T. Golightly, S. R. Schneider, J. Fisher, C. Morgan, R. Bradley, and P. Warzybok. 2015. State of the California Current 2014–15: Impacts of the warm-water "Blob." Calif. Coop. Oceanic Fish. Invest. Rep. 56:31–68.

MacCall, A. D., W. J. Sydeman, P. C. Davison, and J. A. Thayer. 2016. Recent collapse of northern anchovy biomass off California. Fish. Res. 175:87–94.

McKechnie, I., D. Lepofsky, M. L. Moss, V. L. Butler, T. J. Orchard, G. Coupland, F. Foster, M. Caldwell, and K. Lertzman. 2014. Archaeological data provide alternative hypotheses on Pacific herring (*Clupea pallasii*) distribution, abundance, and variability. Proc. Nat. Acad. Sci. 111:E809–E816.

Miller, D. J., and R. N. Lea. 1972. Guide to the Coastal Marine Fishes of California. Fish Bulletin 157, California Department of Fish and Game. 235 pp.

Miller, D. J., and J. Schmidtke. 1956. Report on the distribution and abundance of Pacific herring (*Clupea pallasi*) along the coast of central and southern California. California Fish and Game 42:163–187.

Miller, T. W., R. D. Brodeur, G. Rau, and K. Omori. 2010. Prey dominance shapes trophic structure of the northern California Current pelagic food web: evidence from stable isotopes and diet analysis. Mar. Ecol. Prog. Ser. 420:15–26.

Outram, D. N., and R. D. Humphreys. 1974. The Pacific herring in British Columbia waters. Fisheries and Marine Service, Pacific Biological Station, Nanaimo, B.C., Canada.

Pinsky, M. L., B. Worm, M. J. Fogarty, J. L. Sarmiento, and S. A. Levin. 2013. Marine taxa track local climate velocities. Science 341:1239–1242.

Poloczanska, E. S., C. J. Brown, W. J. Sydeman, W. Kiessling, D. S. Schoeman, P. J. Moore, K. Brander, J. F. Bruno, L. B. Buckley, M. T. Burrows, C. M. Duarte, B. S. Halpern, J. Holding, C. V. Kappel, M. I. O'Connor, J. M. Pandolfi, C. Parmesan, F. Schwing, S. A. Thompson, and A. J. Richardson. Global imprint of climate change on marine life. Nature Clim. Change 3:919–925.

Portner, H. O., and A. P. Farrell. 2008. Physiology and climate change. Science 322:690–692.

Rice, S. D., J. R. Moran, J. M. Straley, K. M. Boswell, and R. A. Heintz. 2010. Significance of whale predation on natural mortality rate of Pacific herring in Prince William Sound. *Exxon Valdez* Oil Spill Restoration Project Final Report. 123 pp.

Rice, S. D., J. R. Moran, J. M. Straley, K. M. Boxwell, and R. A. Heintz. 2011. Significance of whale predation on natural mortality rate of Pacific herring in Prince William Sound. *Exxon Valdez* Oil Spill Restoration Project Final Report (Restoration Project: 100804). National Marine Fisheries Service, Juneau, Alaska. 25 pp.

Rose, K. A., B. A. Megrey, D. Hay, F. Werner, and J. Schweigert. 2008. Climate regime effects on Pacific herring growth using coupled nutrient-phytoplankton-zooplankton and bioenergetics models. Trans. Amer. Fish. Soc 137:278–297.

Schweigert, J. F., J. L. Boldt, L. Flostrand, and J. S. Cleary. 2010. A review of factors limiting recovery of Pacific herring stocks in Canada. ICES J. Mar. Sci. 67:1903–1913.

Schwing, F. B., N. A. Bond, S. J. Bograd, T. Mitchell, M. A. Alexander, and N. Mantua. 2006. Delayed coastal upwelling along the US West Coast in 2005: A historical perspective. Geophys. Res. Lett. 33:L22S01.

Siple, M. C., and T. B. Francis. 2016. Population diversity in Pacific herring of the Puget Sound, USA. Oecologia 180:111–125.

Stick, K. C., and A. Lindquist. 2009. 2008 Washington State herring stock status report. Stock Status Report No. FPA 09–05. Washington Department of Fish and Wildlife, Fish Program, Fish Management Division.

Stick, K. C., A. Lindquist, and D. Lowry. 2014. 2012 Washington State herring stock status report. Fish Program Technical Report No. FPA 14–09. Washington Department of Fish and Wildlife, Fish Program, Fish Management Division.

Sydeman, W. J., S. A. Thompson, J. C. Field, W. T. Peterson, R. Tanasichuk, H. Freeland, S. J. Bograd, and R. R. Rykaczewski. 2011. Does positioning of the North Pacific Current affect downstream ecosystem productivity? Geophys. Res. Lett. 38:L12606.

Sydeman, W. J., J. A. Santora, S. A. Thompson, B. Marinovic, and E. Di Lorenzo. 2013. Increasing variance in North Pacific climate relates to unprecedented ecosystem variability off California. Glob. Change Biol. 19:1662–1675.

Sydeman, W. J., S. A. Thompson, J. A. Santora, J. A. Koslow, R. Goericke, and M. D. Ohman. 2015a. Climate-ecosystem change off southern California: Time-dependent seabird predator-prey numerical responses. Deep-Sea Res. Pt. II 112:158–170.

Sydeman, W. J., E. Poloczanska, T. E. Reed, and S. A. Thompson. 2015b. Climate change and marine vertebrates. Science 350:772–777.

Szoboszlai, A. I., J. A. Thayer, S. A. Wood, W. J. Sydeman, and L. E. Koehn. 2015. Forage species in predator diets: Synthesis of data from the California Current. Ecol. Inform. 29:45–56.

Teo, S. L. H., L. W. Botsford, and A. Hastings. 2009. Spatio-temporal covariability in coho salmon (*Oncorhynchus kisutch*) survival, from California to southeast Alaska. Deep-Sea Res. Pt. II 56:2570–2578.

Thayer, J. A., A. D. MacCall, P. C. Davison, and W. J. Sydeman. California anchovy population remains low, 2012–16. Cal. Coop. Oceanic Fish. Invest. Rep., in press.

Therriault, T. W., D. E. Hay, and J. F. Schweigert. 2009. Biological overview and trends in pelagic forage fish abundance in the Salish Sea (Strait of Georgia, British Columbia). Mar. Ornithol. 37:3–8.

Thornton, T. F., M. L. Moss, V. L. Butler, J. Herbert, and F. Funk. 2010. Local and traditional knowledge and the historical ecology of Pacific herring in Alaska. J. Ecol. Anthropol. 14:81–88.

Ware, D. M., and G. A. McFarlane. 1995. Climate-induced changes in Pacific hake (*Merluccius productus*) abundance and pelagic community interactions in the Vancouver Island upwelling system. Can. Spec. Pub. Fish. Aquat. Sci. 121:509–521.

Womble, J., and M. Sigler. 2006. Seasonal availability of abundant, energy-rich prey influences the abundance and diet of a marine predator, the Steller sea lion *Eumetopias jubatus*. Mar. Ecol. Prog. Ser. 325:281–293.

Zebdi, A., and J. S. Collie. 1995. Effect of climate on herring (*Clupea pallasi*) population dynamics in the Northeast Pacific Ocean. Can. Spec. Pub. Fish. Aquat. Sci. 121:277–290.

Zwolinski, J. P., and D. A. Demer. 2012. A cold oceanographic regime with high exploitation rates in the Northeast Pacific forecasts a collapse of the sardine stock. Proc. Nat. Acad. Sci. 109:4175–4180.

Zwolinski, J. P., D. A. Demer, G. R. Cutter, K. Stierhoff, and B. J. Macewicz. 2014. Building on fisheries acoustics for marine ecosystem surveys. Oceanography 27:68–79.

SUPPLEMENTARY SURVEY METHODS

DETAILS OF FIELD METHODS

A combination of spawning biomass survey methods was used by agencies across the geographic area of interest, and methods varied over the course of the time series for most stocks. The two primary survey methods were spawn deposition surveys, which measure egg deposition, and acoustic/trawl surveys measuring fish abundance (Stick et al. 2014). In British Columbia, surveys initially were shore or vessel based, concentrating on measuring the lengths of spawn deposition along the shore. Beginning in the 1980s, SCUBA surveys were used to estimate the width of spawn deposition (the distance between the highest intertidal and the deepest subtidal occurrence of eggs), and make in situ estimates of the number of egg layers. This approach became routine by the 1990s for the major stocks (Hay and McCarter 1999). In Washington, prior to 1996, the 10–12 larger stocks were assessed by both spawn deposition surveys and acoustic/trawl surveys while the 6–8 smaller stocks were only measured with spawn deposition surveys on a three-year rotation. From 1996 to 2009, one or both of these methods were used. Since 2010, only spawn deposition surveys have been conducted, with the exception of an acoustic/trawl survey of the Cherry Point stock in 2011 (Stick et al. 2014). In Oregon, the number of spawning adults from the previous year was used to estimate spawning biomass (Dauble 2014). In San Francisco Bay, California, spawn deposition surveys were used from 1973 to 1990 and from 2003 to present. From 1991–2002, a combination of spawn deposition and hydroacoustic surveys were used (CDFW 2014).

REFERENCES

California Department of Fish and Wildlife (CDFW). 2014. Pacific herring commercial fishing regulations: Final supplement and environmental document, SCH No. 98052052. State of California Department of Fish and Wildlife.

Dauble, A. 2014. R & E grant application: Pacific herring assessment methodology. Accessed from http://www.dfw.state.or.us/fish/RE/projects/cycle_6_applications/13-100%20app%20w%20attachments%20for%20web.pdf.

Hay, D. E., and P. B. McCarter. 1999. Distribution and timing of herring spawning in British Columbia. Canadian Stock Assessment Secretariat Research Document 99/14. Fisheries and Oceans Canada. Nanaimo, British Columbia. 44 pp.

Stick, K. C., D. Lowry, and A. Lindquist. 2014. 2012 Washington State herring stock status report. Fish Program Technical Report No. FPA 14-09. 97 pp.

SUPPLEMENTARY TABLE 1

Herring spawning stock biomass data (unit: tonnes) for San Francisco Bay, CA, 1979–2012. Data were provided by the California Department of Fish and Wildlife.

Year	San Francisco Bay
1979	53,000
1980	65,400
1981	99,900
1982	59,200
1983	40,800
1984	46,900
1985	49,100
1986	56,800
1987	68,900
1988	66,000
1989	64,500
1990	51,000
1991	46,600
1992	21,000
1993	39,900
1994	40,000
1995	99,100
1996	89,600
1997	20,000
1998	39,500
1999	27,400
2000	37,300
2001	35,400
2002	
2003	34,400
2004	58,900
2005	145,100
2006	10,900
2007	11,200
2008	4,800
2009	38,400
2010	57,100
2011	61,000
2012	79,500

SUPPLEMENTARY TABLE 2

Herring spawning stock biomass data (unit: pounds, unlike all other sites for which biomass was given in tonnes) for Yaquina Bay, OR, 1979-2011. Data were provided by the Oregon Department of Fish and Wildlife, and converted to tonnes for analysis.

Year	Yaquina Bay[1]
1979	610,000
1980	512,000
1981	531,000
1982	631,000
1983	621,000
1984	667,000
1985	920,000
1986	4,120,000
1987	3,090,000
1988★	2,720,000
1989★	2,980,000
1990★	2,640,000
1991★	2,580,000
1992★	2,280,000
1993★	1,120,000
1994★★	537,000
1995★★	521,000
1996★★	550,000
1997★★	82,000
1998	"trace"
1999	20,000
2000	90,000
2001	"trace"
2002[2]	1,386,000
2003	528,080
2004	925,000
2005	223,178
2006	34,941
2007	290,962
2008	239,125
2009	1,473,070
2010	62,506
2011	296,624

★ Values estimated from ODFW unpublished data.
★★ Values estimated, based on the following year's harvest and an assumed 20% harvest rate.
[1] Biomass is determined from observed spawning egg deposition.
[2] ODFW egg deposition survey estimate. BioSonics, Inc. survey of lower Yaquina Bay indicated 766,000 lbs.

SUPPLEMENTARY TABLE 3
**Herring spawning stock biomass data (unit: tonnes) for primary sites in Washington, 1973–2013.
Data were provided by the Washington Department of Fish and Wildlife.**

Year	Quartermaster Harbor	Port Gamble	Port Susan	Discovery Bay	Fidalgo Bay	Cherry Point
1973						14998
1974						13963
1975						10337
1976	1357	1142		697		11844
1977	1413	2525		1488		11097
1978	1860	1984		1305		10973
1979	1941	1790		882		9957
1980	1930	2309		3220	276	9329
1981	1777	1753		3070	456	6219
1982	1778	1463	1391	2356	182	5342
1983	909	2407	1398	2578	640	8063
1984	1386	2685	1555	3144	742	5901
1985	667	2387	1321	1447	761	5760
1986	1181	2050	934	1566	731	5671
1987	924	2046	1216	1593	887	3108
1988	750	1390	570	853		4428
1989	898	2395	345	1225		4003
1990	681	2969	291	855		4998
1991	580	2259	245	925	1079	4624
1992	518	2270	545	727	1399	4009
1993	1075	1521	1693	737	1417	4894
1994	1412	2857	365	375	1207	6324
1995	2001	3158	363	261	1173	4105
1996	805	2058	110	747	590	3095
1997	1402	1419	828	199	929	1574
1998	947	971	2084	0	844	1322
1999	1257	1664	545	307	1005	1266
2000	743	2459	785	159	737	808
2001	1320	1779	587	137	944	1241
2002	416	1812	775	148	865	1330
2003	930	1064	450	207	569	1611
2004	727	1257	429	252	339	1734
2005	756	1372	157	33	231	2010
2006	987	774	321	1325	323	2216
2007	441	826	643	42	159	2169
2008	491	208	345	248	156	1352
2009	843	1064	252	205	15	1341
2010	143	433	152	26	103	774
2011	96	1464	138	0	119	1301
2012	108	404	61	105	89	1120
2013	157	273	29	0	100	908

SUPPLEMENTARY TABLE 4

Herring spawning stock biomass data (unit: tonnes) for regions in Washington, 1975–2013. Data were provided by the Washington Department of Fish and Wildlife. See the Methods section for information about data calculation by region.

Year	S. Puget Sound	Hood Canal	Whidbey	Olympic	Anacortes	Whatcom
1975						11109
1976		1913				12165
1977		3201				11731
1978						
1979						
1980				4075		
1981						7227
1982						6731
1983						8937
1984						6673
1985						8085
1986						7135
1987						
1988						6393
1989						5704
1990						6928
1991		2820				6685
1992		2511				5510
1993						6796
1994						7713
1995						5350
1996		2625	1182	1307	1556	4314
1997		2110	2251	664	1547	2195
1998		2224	2757	423		2241
1999		4644	1625	1461		2134
2000	3012	5025	1712	404	1151	1734
2001	5057	4057	3032	842	1695	2339
2002	4550	4563	3563	1053	1650	2342
2003	4368	2187	4111	699	953	2698
2004	2307	3775	2347	458	757	2363
2005	3217	2707	1824	203	490	2880
2006	3881	3548	4444	1379	1020	3493
2007	2622	3268	2451	100	540	3293
2008	2747	2962	2373	317	625	2014
2009	3795	4284	2333	251	335	2331
2010	1014	2659	1227	101	776	1683
2011	805	6063	3610	104	506	2906
2012	945	3294	1182		524	1999
2013	905	2544	1068		793	1477

SUPPLEMENTARY TABLE 5
Herring spawning stock biomass data (unit: tonnes) for regions in British Columbia, 1951–2012.
Data were provided by Fisheries and Oceans Canada.

Year	Haida Gwaii	Prince Rupert District	Central Coast	Strait of Georgia	WC Vancouver Island
1951	10841	48293	50954	90733	33145
1952	8117	21909	25341	105691	20268
1953	26801	30342	36296	131767	31171
1954	68157	25223	39291	147164	22852
1955	74668	19911	39194	120527	28048
1956	15285	23587	15876	63864	32282
1957	5065	10926	12998	38700	47409
1958	4779	23908	22616	52186	59915
1959	11035	47489	24714	71259	31887
1960	16196	50010	26698	69162	13786
1961	29537	71520	27011	63689	18205
1962	39261	88347	44924	71178	29046
1963	29549	70880	27734	61891	25869
1964	10208	73193	15795	60161	27126
1965	2663	47359	11793	37142	18425
1966	4886	20710	6636	23895	9404
1967	4716	10144	10344	15217	7461
1968	4992	8107	9297	23336	12716
1969	6285	8530	11679	27340	15734
1970	10425	11713	22589	39084	29567
1971	16380	10179	27515	46709	53741
1972	24557	11587	27101	39565	58393
1973	33164	14178	34382	48749	62937
1974	40334	18213	34196	75551	72884
1975	41134	17976	37615	91236	96723
1976	34425	20407	30540	113016	79083
1977	28440	15035	27846	146412	71430
1978	23744	9950	20399	141195	66386
1979	35460	10468	46890	132722	62554
1980	77441	17446	73534	123166	72475
1981	73952	19219	71476	110357	64956
1982	56702	22571	70250	92685	44207
1983	49227	32415	52281	64253	30986
1984	50974	39701	36949	53901	34344
1985	46928	36943	39433	67234	53152
1986	37777	39782	37233	88473	65346
1987	36088	41458	46577	89814	64425
1988	51225	35608	66396	113537	91749
1989	50706	29586	49603	99382	72256
1990	35590	29077	39525	111746	65795
1991	25985	36465	43657	116767	58897
1992	30208	39194	62990	141442	76888
1993	18167	33115	53532	144148	70911
1994	11980	24490	44090	126162	58815
1995	13918	25649	32444	115151	49797
1996	18010	32454	39020	127192	53573
1997	25262	28650	57294	146026	67636
1998	26931	27330	62871	137674	48054
1999	15145	27595	53609	123416	35982
2000	10373	24278	48269	124287	34590
2001	9024	26440	36265	159240	36461
2002	10136	25813	34654	163978	35963
2003	12271	31986	40249	162735	29090
2004	8755	23085	30738	131553	16578
2005	9337	17367	25516	113517	9507
2006	8145	16696	15750	102563	8447
2007	11213	19513	13172	110549	8006
2008	10292	19408	12164	72217	7194
2009	12803	19735	15949	75331	8138
2010	11727	22267	14506	61659	9085
2011	12659	25979	14886	93731	12341
2012	17681	26495	13662	99835	14111