Exxon Valdez Oil Spill
Long-Term Herring Research and Monitoring Program Final Report

Surveys and age, sex, and size collection and processing

Exxon Valdez Oil Spill Trustee Council Project 21160111-F
Final Report

Jennifer Morella

Alaska Department of Fish and Game
401 Railroad Avenue
Cordova, Alaska

With contributions from Stormy Haught

June 2023

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Study History:

This study was a continuation of *Exxon Valdez* Oil Spill Trustee Council project 16120111-T. Prior to becoming a Trustee Council project the surveys were supported by Alaska Department of Fish and Game, but because there was no commercial fishery the surveys were slated to end due to budget reductions. Spring aerial survey data have been collected by the Alaska Department of Fish and Game since 1972 (Funk 1994). Herring age, sex, and size data are available since 1973 (Sandone 1988); however, collections of both data sets have been more extensive since the early 1980s.

Aerial surveys were used to document spring herring biomass and were the primary management tool prior to the development of the first age structured assessment model in 1988 (Brady 1987, Funk and Sandone 1990). Biomass is estimated as school surface area converted to biomass from a few paired observations of aerial observers and vessel harvests (Brady 1987, Fried 1983, Funk and Sandone 1990). Surface area and biomass conversion methods are as described in Brady (1987) and Lebida and Whitmore (1985). Prior to 1988, the aerial survey program's primary objectives were to collect biomass data for an annual index, document the distribution and linear extent of milt, document herring temporal movements, and document the distribution of the commercial fleet (Brady 1987). Additionally, the locations of large aggregations of Stellar sea lions and other marine mammals were often noted on paper maps.

Age and biomass data from this project as well as the modeling and stock assessment project (21120111-C) are evaluated annually by Alaska Department of Fish and Game fisheries managers relative to regulatory thresholds in The Prince William Sound Herring Management Plan (5 AAC 27.365). Summary results and discussion are published annually in Prince William Sound Area Finfish Management Reports and in annual and synthesis reports to the *Exxon Valdez* Oil Spill Trustee Council. Annual Prince William Sound herring summaries are also included in the National Oceanic and Atmospheric Administration Gulf of Alaska Ecosystem Status Report. Shapefiles of aerial survey observations and age, sex, and size tabular data are uploaded to the Alaska Ocean Observing System data portal annually and age and size compositions are disseminated to acoustic biomass, disease, and modeling Herring Research and Monitoring projects. An analysis of historical shifts in Prince William Sound herring spawn timing and distribution using aerial survey and age, sex and size data was published by McGowan et al. in 2021.

Abstract:

This monitoring project conducted spring aerial surveys to document Pacific herring milt distribution and biomass as well as the distribution and abundance of sea lions, other marine mammals, and birds associated with herring schools or spawn from 2017 through 2021. Additionally, this project collected, and processed age, sex, and size samples of herring collected by spawning surveys and compiled annual age compositions. Aerial survey and age, sex, and size data have been collected since the early 1970s and are an essential part of the age-structured models used by the Alaska Department of Fish and Game to estimate the historical and future biomass for fisheries management.

Key words:

Aerial surveys, *Clupea pallasii*, mile-days of milt, Pacific herring, Prince William Sound, scales

Project Data:

Data and information products developed during the reporting period include: 2017-2021 individual aerial survey maps (distributed to Herring Research and Monitoring participants, other herring researchers, and a variety of stakeholders within 24hrs of survey), 2008-2021 aerial herring biomass observations shapefiles, 1973-2021 aerial herring spawn observations shapefiles, 1997-2021 herring aerial survey routes shapefiles, 2008-2021 aerial survey marine bird observations shapefiles, 2008-2021 aerial survey marine mammal observations shapefiles, 2008-2021 aerial survey sea lion observations shapefiles, and 1973-2021 age, sex, and size data.

https://gulf-of-alaska.portal.aoos.org/#metadata/35fd35d8-f6f1-4762-9cf0-8e2e970755c4/project

The data custodian is Carol Janzen, Director of Operations and Development, Alaska Ocean Observing System, 1007 W. 3rd Ave. #100, Anchorage, AK 99501, 907-644-6703. janzen@aoos.org.

Data are archived by Axiom Data Science, a Tetra Tech Company, 1016 W. 6th Ave., Anchorage, AK 99501.

Citation:

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

EXECUTIVE SUMMARY

This project helped meet the overall program goal of improving predictive models of herring stocks through observations and research. There were no proposed hypotheses to be tested directly from this project; however, this project continued long-term monitoring programs to 1) conduct aerial surveys to collect data associated with spring Pacific herring (*Clupea pallasii*) spawning events, 2) collect and process age, sex, and size (ASL) samples from prespawn and spawning aggregations of Pacific herring, and 3) provide vessel support for spring disease sampling, and collection and processing of ASL samples for target strength assessment.

Spring aerial survey data have been collected since 1972. ASL data are available since 1973; however, collections of both data sets have been more consistent since the early 1980s. Aerial surveys were used to document spring herring biomass and were the primary management tool prior to the development of the first statistical catch-at-age model or age structured assessment (ASA) model in 1988. Prior to 1988, the aerial survey program's primary objectives were to collect biomass data for an annual index, document the distribution and linear extent of milt, document herring temporal movements, and document the distribution of commercial fishing boats, fishing tender boats, and processor boats.

In 1987, J. A. Brady of the Alaska Department of Fish and Game (ADF&G) described how herring arrive on the spawning grounds over time and may be available to document on multiple aerial surveys. Therefore, the biomass over several days of surveys cannot be summed to estimate the total or peak biomass. Consequently, peak biomass was calculated as the largest biomass observed in all areas on a single survey. Brady also detailed how the variable bathymetry of herring spawning areas in Prince William Sound (PWS) has a large influence on the observer's ability to see herring schools. Herring may spawn in shallow bays (e.g., Rocky Bay, Montague Island), shallow beaches (e.g., Hells Hole beach), or deep bays (e.g., Fairmont Bay on the North Shore). The influence of bathymetry on observer efficiency suggests an aerial biomass index will probably not be comparable across years. Although peak biomass values may be a useful relative abundance, issues with biomass observations caused ADF&G to investigate the use of an index of spawn from observations of milt. The advantages of milt observations compared to school biomass observations include a lower likelihood of double- or multiple-counting because herring schools likely spawn a single time (e.g., a single day), but a herring school may be observed for several days prior to, or after spawning. Milt is also relatively easy to observe from the air across a range of survey environmental conditions and observation efficiency of milt is generally not influenced by ocean bathymetry; however it is likely one factor that will influence the biomass of spawning fish for each linear mile of milt observed. Further

research by Willette collected paired spawn deposition survey estimates from dive surveys and aerial survey estimates of miles of milt; the short tons (dive survey) per mile of milt (aerial survey) were much larger on Montague Island beaches when compared to short tons per mile of milt in northern or northeastern PWS beaches. Montague Island shoreline typically has large shallow, subtidal areas with complex kelp structure while the northern and northwestern beaches tend to have a steeper gradient to deep waters and less complex kelp structure.

Two indices considered for spawn documented from aerial surveys were 1) discrete miles of milt over the season and 2) the sum of miles of milt for all survey days (mile-days of milt). Discrete miles of milt do not account for multiple spawning events in the same area, so are unlikely to be a good index of total abundance in areas with multiple days of spawning on the same beach. Mile-days of milt probably provide a better index to abundance because they account for multiple spawning days on the same beach but may be biased if the number of surveys varies significantly across years. In 2008, ADF&G began using a tablet computer and a geographic information system (GIS) application to collect aerial survey data. Because digital maps are scalable and allow much more data to be added to a small area (contrast with the 25 paper maps used prior to 2008), and because of interest in herring predators distribution and abundance, additional effort was employed in documenting numbers and locations of predators such as Stellar sea lions, humpback whales, killer whales, Dall's porpoises, and bird aggregations (mostly gulls) associated with herring schools or spawn.

Age, sex, and size data from Pacific herring have been collected from commercial fisheries and fishery-independent research projects since the early 1970s. ADF&G currently has an archive containing approximately 210,000 scales paired with size and sex data. Processing methods are similar to those published by Baker et al. (1991); however, electronic fish measuring boards have been used since 1989 to enter sample summary data and individual fish data (standard length in mm, whole body weight in grams, and sex) at the time of processing. Gonad weights have been collected from prespawning fish (both sexes) in most years since 1994.

Scales are used to estimate age for PWS collections rather than otoliths because they are much easier to collect and prepare for examination. Additionally, research published by Chilton and Stocker (1987) reported that Chi-square tests of age compositions from paired otoliths and scales collected off the British Columbia coast could not refute the null hypothesis that they were from the same population. Interpretation of age from otoliths indicated that there were older fish than interpreted from scales; however, few fish older than age-10 are found in PWS, so fish interpreted at age-9 and older are combined into an age category 9+. No age validation or tests of paired age structures have been completed for PWS herring.

This project conducted aerial surveys to collect data related to spring herring spawning events, provided vessel support for disease sample collections; and captured and processed herring to generate age, sex, and size summaries and mean target strength for acoustic biomass estimates. Aerial survey, acoustics estimates, and ASL data sets are essential parts of age structured model ADF&G uses to estimate the historical biomass and project pre-fishery run biomass a year ahead for management. Additionally, the mile-days of milt and ASL data are part of the Bayesian formulation of the ASA model.

This project documented mile-days of milt and age composition of the spawning population of Pacific herring in PWS from 2017 through 2021. The 2018 mile-days of milt estimate is the lowest documented estimate since the surveys began in 1972. Mile-days of milt have consistently increased since this historic low, primarily driven by the large recruitment of age-3 fish to the spawning population in 2019. This cohort has composed a large proportion of the spawning population since.

INTRODUCTION

Pacific herring (*Clupea pallasii*) are a critical link in pelagic and nearshore food chains between primary production and higher trophic levels and are an important food resource for a number of piscivorous predators (Livingston 1995). Additionally, Pacific herring have provided valuable commercial fisheries throughout Alaska's history and subsistence fisheries that pre-date recorded history (Woodby et. al. 2005). Beginning in 1993, the Prince William Sound (PWS) herring population experienced a sharp decline (Pearson et. al. 1999). Various hypotheses regarding the cause of the decline have been examined including the *Exxon Valdez* oil spill in 1989, the disease pathogens hemorrhagic viral septicemia virus (HVSV) and *Ichthyophonus hoferi*, and density dependent factors influencing overall condition (Hulson et. al. 2008, Marty et. al. 2010, Pearson et. al. 1999, Pearson et. al. 2011, Thorne and Thomas 2008).

Commercial herring fisheries in PWS closed following the decline until 1997 when they were re-opened but closed again in 1998 due to concerns over declining biomass (Pearson et. al. 2011). Hay et. al. (2001) found that collapsed herring stocks on average take about 10 years to recover; however, the PWS population has not recovered to pre-1993 levels (Woodby et. al. 2005). Several hypotheses to explain the lack of recovery are being explored, including increased predation by marine mammals, increased susceptibility to disease from lingering oil toxicity, and interspecific competition and predation by juvenile pink salmon (*Oncorhynchus gorbuscha*) from large hatchery releases. The lack of recovery is still poorly understood (Marty et. al. 2010, Pearson et. al. 2011). Monitoring the PWS herring population plays an important role in understanding the lack of recovery and enhancing recovery efforts for this resource.

Pacific herring begin sexual maturation at the end of summer and progress through winter, reaching full sexual maturity in the early spring months. As they reach maturity, herring migrate from overwintering areas and form aggregations in or near spawning habitat in shallow coastal waters, typically large bays and inlets (Hay 1985). Herring spawn primarily in the subtidal zone from about 0-4m in depth, although deeper spawning events do occur, and select for habitats with aquatic vegetation present for egg deposition (Gerke 2002). Herring spawning activity is typically conspicuous; milt concentration turns water cloudy white, and the herring school attracts high concentrations of herring predators such as gulls, sea lions, and other marine mammals (Hay and Kronlund 1987). These factors make herring spawning season an ideal time to collect data regarding overall herring biomass, spawning habitat utilization, and herring predator populations in PWS.

This five-year monitoring project was a continuation of aerial survey and age, sex, and size data that have been collected since 1972 and 1973, respectively. Data was collected to meet the overall program goal of improving predictive models of herring stocks through observations and research. Furthermore, the results of both the aerial surveys and age/size structure are critical to the management of herring commercial fisheries in PWS. The estimates aerial biomass as well as acoustic biomass and age structured assessment (ASA) model outputs are central in evaluating the population in relation to regulatory thresholds set in the PWS Herring Management Plan (5 AAC 27.365).

OBJECTIVES

Data were collected to meet the overall program goal of improving predictive models of herring stocks through observations and research. These surveys provided necessary biomass and population structure data to evaluate herring stocks in relation to regulatory thresholds and provide critical inputs to modeling, disease, and acoustic biomass projects. These data added to data collected since 1972 (aerial surveys) and 1973 (age, sex, and size data) and are critical to both PWS herring fisheries management and ongoing research efforts. Details of this project are also described in Shepherd and Haught (2019).

Objectives of this project were:

1) Conduct spring aerial surveys to collect data on survey routes, location and linear extent of herring milt, classification of herring milt, herring school biomass; distribution and abundance of sea lions, other marine mammals and bird aggregations associated with herring or herring spawn; and other relevant environmental or anthropogenic observations.

2) Collect, process, summarize, and distribute age, sex, and size data from herring collected during acoustics surveys, spawning grounds surveys, *Herring Disease Program* surveys, or other relevant collections.

3) Provide a vessel (*R/V Solstice*) as a research platform for an adult acoustics survey, disease sampling, and collection of pre-spawn and spawning Pacific herring samples. Mean length from pre-spawn samples will be used to estimate Pacific herring target strength for the acoustics work.

METHODS

Procedural and Scientific Methods

Aerial Surveys

Aerial surveys generally began in mid- to late March. First survey date was earlier if there were reports of herring aggregations, spawn, or large predator aggregations. The first survey typically covered the eastern side of PWS because the spawn timing is generally earlier on the east side (Port Gravina and Port Fidalgo). The first survey was occasionally expanded based on boat or pilot reports from other areas. Surveys continued once or twice a week until herring schools or spawn were detected by a survey flight or reported by other pilots or boats. Once spawning began, surveys were conducted daily in the area where spawn was detected if weather conditions were appropriate. Surveys were expanded to other portions of the PWS area (North shore, Naked Island, Montague Island, and Kayak Island) in April or based on pilot or boat reports. Survey interval, duration, and area were adjusted in-season to allow available funding to last until approximately early to mid-May.

Surveys were conducted in a float equipped, fixed-wing aircraft flying at an elevation of ~1,200 feet. Primary and secondary observers were used for each flight. The primary observer sat in the back seat and used a tablet computer to enter survey metadata in a spreadsheet and georeferenced survey data in an ESRI ArcPad application connected to a Bluetooth GPS (Bochenek 2010). The primary observer also attached a camera to the inside of the back window facing out to collect either video or a still image every 1 or 2 seconds.

The secondary observer sat in the front passenger seat and reported observations to the primary observer, collected observations on paper maps as a hardcopy duplicate in case of digital failure, deployed a handheld global positioning system (GPS) as a backup to the Bluetooth GPS, and took georeferenced photos of spawning events, large biomass aggregations, and large herring predator groups with a GPS-enabled digital single lens reflex (DSLR) camera and fast lens (F2.8).

Herring spawn activity was located visually through discoloration of water in coastal regions caused by the presence of herring milt (Fig. 1). The linear extent of miles of milt was estimated visually utilizing landmarks, coastal features, and detailed GIS shapefiles. Milt observations were digitized directly into ESRI ArcPad on the survey tablet using a stylus. Spawn activity was assigned a qualitative descriptor based on density and extent of discoloration: active light, active medium, active heavy, dissipating, and drift (Table 1). These categories were recorded in the database associated with the digitized shapefile. Precise estimations of miles of milt were calculated using ArcGIS measurement tools after the survey data was reviewed and compared with digital photographs and video from the survey.

Biomass of individual herring schools was estimated using a surface area to short tons (st) conversion (Lebida and Whitmore 1985, Brady 1987). A sighting tube with a known focal length was used to calibrate observer estimation of surface area on a few herring schools at the beginning of each survey. Gridlines within the sighting tube provide a visual reference for known ground distances at a given elevation (Fig. 2). Herring school sizes were then estimated based on the surface area proximity to gridlines within the tube and were generally split into three classifications with corresponding biomass conversions: Small, medium, and large (Table 2). Very large and/or irregularly shaped schools were visually separated into small size class sections and the total number of these sections enumerated for the school. Size classes were used as guidelines for estimating biomass of schools that fell in between the general classifications.

Figure 1. Discoloration of water due to presence of milt from herring spawning activity.

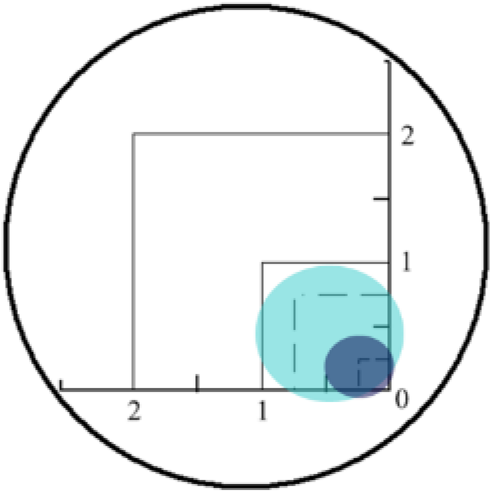


Figure 2. Gridlines within sighting tube used for calibrating estimation of herring school surface area. The shaded circles represent herring schools.

Table 1. Herring spawning activity classifications by presence and extent of milt.

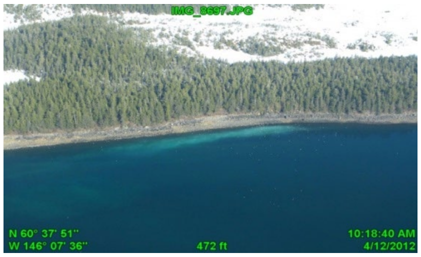
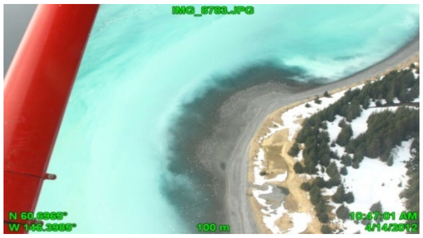
CLASS	Description	Example photo
Active Light	Fish actively spawning, but little milt in the water and very light coloring. Usually some marine mammals (sea lions, harbor seals, or harbor porpoises) or sea birds associated with the spawn.	
Active Medium	Fish actively spawning and moderate amounts of milt in the water and much lighter coloring. Almost always some marine mammals (sea lions, harbor seals, or harbor porpoises) or larger groups of sea birds associated with the spawn.	
Active Heavy	Fish actively spawning, and large amounts of milt in the water. The color is usually bright white to blue green. Almost always larger groups of marine mammals (sea lions, harbor seals, or harbor porpoises) or sea birds associated with the spawn.	
Dissipating	Milt that is likely from the previous day. Very dispersed with few marine mammals. May still be many sea birds on the beach eating eggs. Generally not included in our summary of mile-days of spawn unless we did not document the active spawn previously.	
Drift	Areas of milt that have drifted with the current offshore or away from the areas of active spawn. For example, tides or currents regularly cause milt to drift offshore for up to a mile or more off points. Drift is not summed with active spawn for calculating the total extent of spawn.	

Table 2. Herring school size class and corresponding surface area, diameter, and biomass (short tons, st).

Size Class	Surface Area	Diameter	Biomass
Small	1962 ft^2 (181 m^2)	50 ft (15.2 m)	10 st
Medium	7850 ft^2 (725 m^2)	100 ft (30.4 m)	40 st
Large	31400 ft^2 (2902 m^2)	200 ft (60.8m)	160 st

Surface area of herring schools for the remainder of the survey were estimated visually without the sighting tube after calibration and required the use of polarized lens eyewear (Fig. 3). Herring school observations and size estimation were entered as point data in the tablet's ArcPad application, georeferenced via GPS or placed with the stylus based on landmarks and map features.

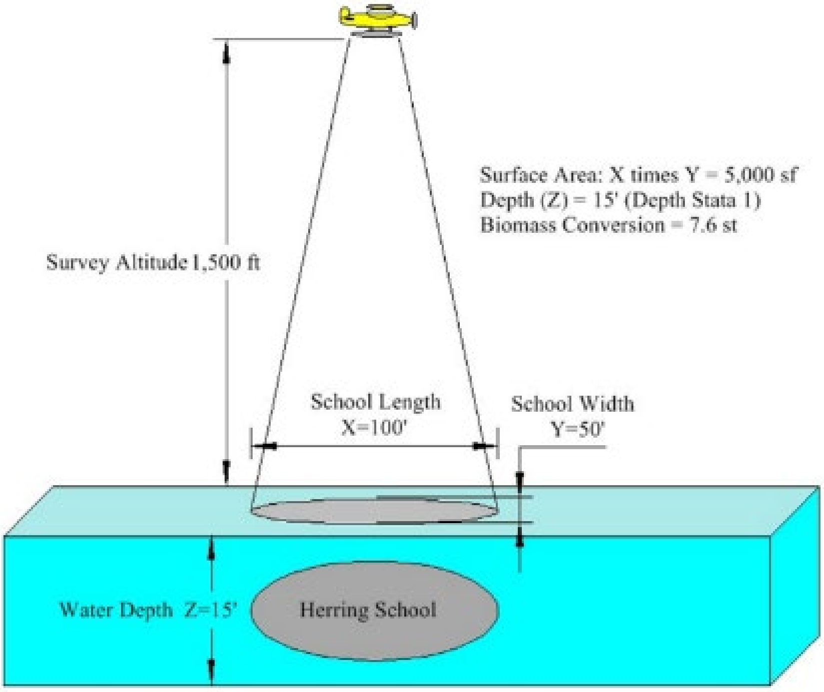


Figure 3. Aerial estimation of herring school surface area for conversion to short tons biomass (Lebida and Whitmore 1985).

Marine mammal sightings were recorded in the tablet ArcPad application as point data, and bird aggregations as line data, using GPS and landmarks. Marine mammals and bird aggregations were identified at the species or type level (e.g., Stellar sea lion, gulls), and abundance was directly counted for small groups (~<30 individuals) or estimated for larger groups (~>30 individuals).

After each survey all electronic data were transferred to the local Cordova Alaska Department of Fish and Game (ADF&G) network. ArcPad data were downloaded from the tablet for processing with ESRI ArcMap. DSLR photos were transferred for editing with Adobe Lightroom. The handheld GPS data were downloaded with DNRGPS software. Videos or images were downloaded from the video camera using either GoPro Quik or Garmin VIRB software. Observations on paper maps were examined for complete survey information and stored for use in post-season processing.

At the end of the survey season, milt locations, classification, and lengths were adjusted by comparing data collected on the GIS application to the digital photography and video imagery. Estimates of large marine mammal aggregations (~>30 individuals) were adjusted by counting individuals from survey photographs. After adjustments were complete, the individual survey GIS data were combined into shapefiles for the year and then added to the historical GIS shapefiles. These historical shapefiles allow comparison across all years for milt observations (1973–2021), survey routes (1997–2021), sea lion location and abundance (currently 2008–2021), other marine mammals (currently 2008–2021), and birds (currently 2008–2021).

Age, Sex, Size Sampling

Age, sex, and size (ASL) processing methods are outlined in Baker et al. (1991) with only a few changes. Samples were stratified by area, time, and gear. Sample sizes (n=450) were set to estimate the age composition of each sample to within ±5% of the true proportion 90% of the time (Thompson 1992) assuming no more than 10% of the scales were unreadable. Herring were collected in the field and frozen in large 6 mm plastic bags with labels inside the bag that document the date, time, location, gear, samplers, and the number of bags. Other information including the coordinates of the sample location were collected and added to a sample log. Often more than 450 fish were collected, so an equal number of fish were randomly selected from each bag for processing to meet the sample goal. From the fish selected for processing, 10 fish at a time were placed on a tray and their length was measured to the nearest mm using calipers (standard length, tip of snout to hypural plate (Fig. 4)), and whole weight to the nearest gram was collected from an electronic balance. Sex was determined from examination of the gonads (1=male, 2=female, 3= unknown), and gonad condition was estimated from examination of the gonad (scale of 1-undeveloped to 8-recovering from spawning). Weights were collected with an electronic balance that was checked with calibration weights (and recalibrated if necessary) prior to each sampling event.

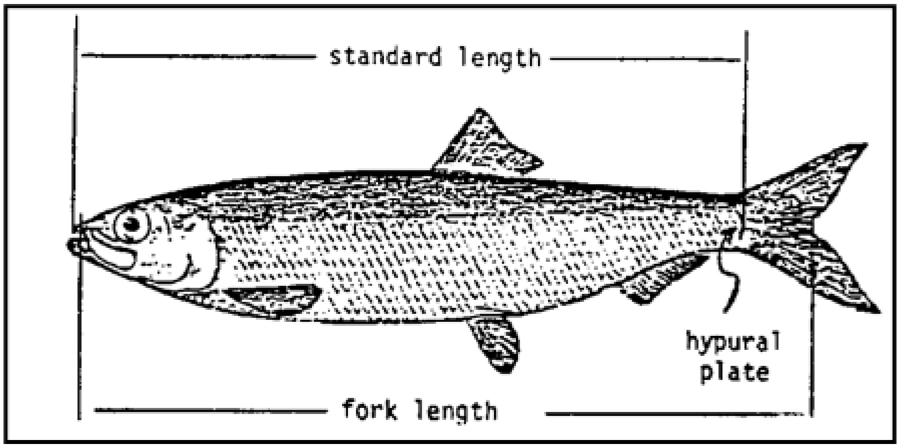


Figure 4. Standard length (tip of snout to end of hypural plate) and fork length measurements (tip of snout to fork of tail).

A scale was then collected from the left side of the fish from a preferred area when possible (Fig. 5). The preferred area is above the lateral line and 3–4 rows of scales back from the operculum. This area generally has symmetrical growth patterns and distinct annuli. Scales were cleaned and placed on a pre-labeled glass microscope slide after dipping in a solution of 1:10 mucilage glue to water. A single scale from each of 10 fish was placed as two rows of 5 scales on each slide (Fig. 6). Scales were viewed on a microfiche to ensure they were readable for age (not regenerated) then covered with a second slide and taped together at the label end of the slide. All slides were stored in a labeled box or cabinet tray until examining for age.

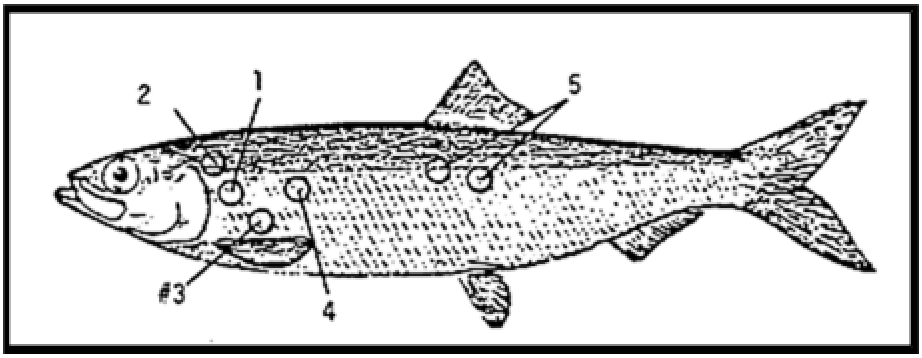


Figure 5. Preferred areas for collecting scales for age from Pacific herring. Numbers are in order of preference (#1 is most preferred). Scales collected from left side of fish when possible.

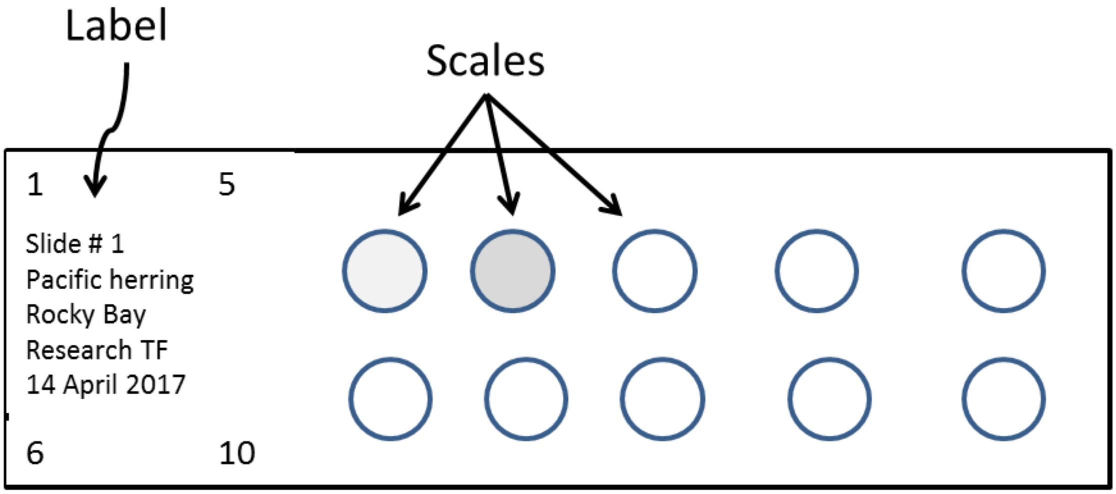


Figure 6. Example cartoon herring scale slide with scales 1 through 5 (top left to right) and scales 6 to 10 (bottom left to right).

Once a sample was complete, data were entered into a spreadsheet. The scales were examined for age interpretation on a microfiche by two or three readers. Ages were interpreted independently and then the readers discussed any differences before agreeing on an age by consensus. The crew leader spot checked all samples to reduce the chance of divergence of age estimates by different readers over time (reader drift) in age interpretation. Ages were keyed into the spreadsheet once age interpretation from scales was completed. ASL composition summaries that included sample size, percentage by age class and sex, and mean and standard deviation of weight and length by age class and sex, were generated. Historical data (1973–present) were stored and summarized in spreadsheet form and in the ADF&G PWS herring relational database.

Data Analysis and Statistical Methods

For ASL data, age composition was estimated in each sampling event by gear type for time and area strata with sample sizes sufficient to simultaneously estimate all age proportions to within ± 5% at the 90% level of precision. Mean standard length and whole body weight was estimated for each sampling event by gear type for time and area strata with sample sizes such that the relative error is ±5% at the 95% level of precision. Mean gonad weight of prespawning fish was estimated for time and area strata with sample sizes such that the relative error was ±5% at the 95% level of precision. Sex composition was estimated in each sampling event by gear type for time and area strata with sample sizes sufficient to estimate proportions to within ±5% at the 95% level of precision. For input into the ASA model, ASL data from each herring district is weighted by the mile-days of milt in each district to estimate the total population age, size, and sex data.

Description of Study Area

The study area included all PWS and Copper River/Bering River coastal areas between Cape Suckling to the east and Cape Puget to the west. The bounding coordinates are 61.300 N, -144.00 W and 59.750 N, -148.760 W.

RESULTS

2017

We conducted 59 hours of aerial surveys during 22 flights between March 22 and May 6, 2017 (Fig. 7). PWS herring schools observed in 2017 were less aggregated and smaller than observed in prior years. Spawn was documented in eastern PWS near Knowles Head and Red Head (April 13–17); on the north shore of Hawkins Island near Canoe Passage (April 15–21); and near Kayak and Wingham Island (April 14) (Fig. 11). Total PWS mile-days of milt were estimated at 9.50 mile-days, all of which was in the Southeast Area. No spawn was documented in other areas of PWS.

A total of 3,595 herring were collected with purse seine, cast net and variable mesh gillnet from Rocky Bay, Hell's Hole, Red Head, Canoe Pass, and South Humphries hole. The overall observed spawning age composition was 51.7% age-3, 21.6% age-4, 16.6% age-5, and 3.8% age-6 and 5.6% age-7 or older fish (Fig. 8).

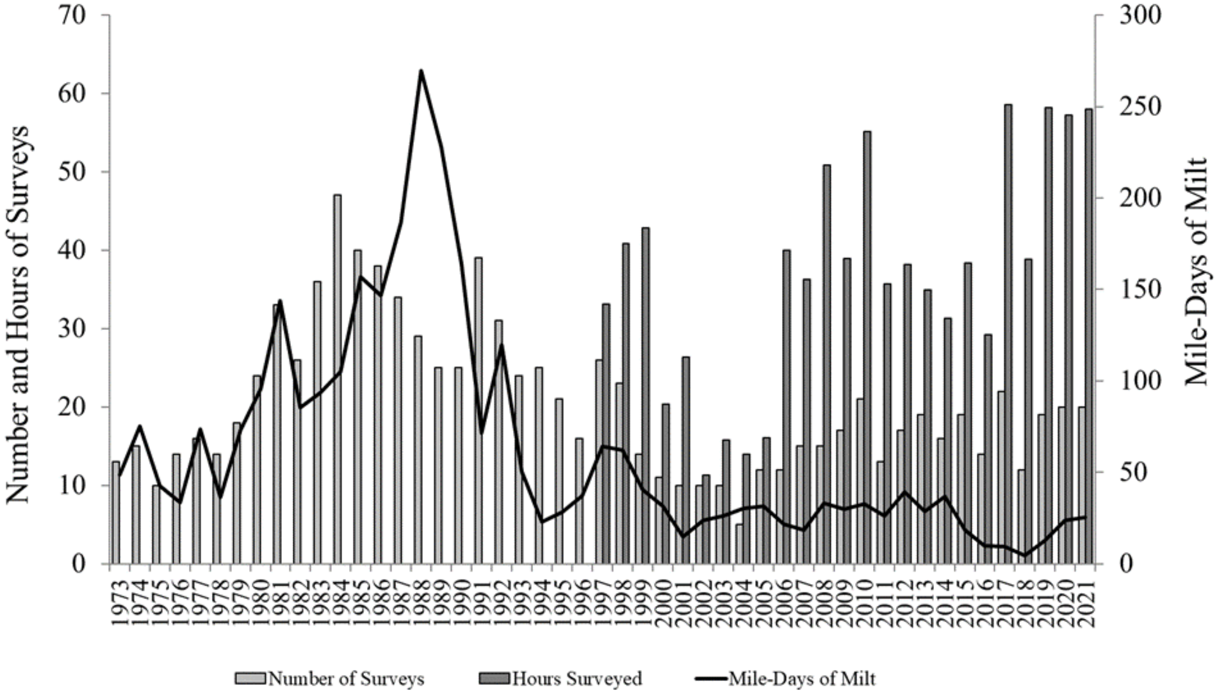


Figure 7. Prince William Sound herring aerial survey effort and mile-days of milt.

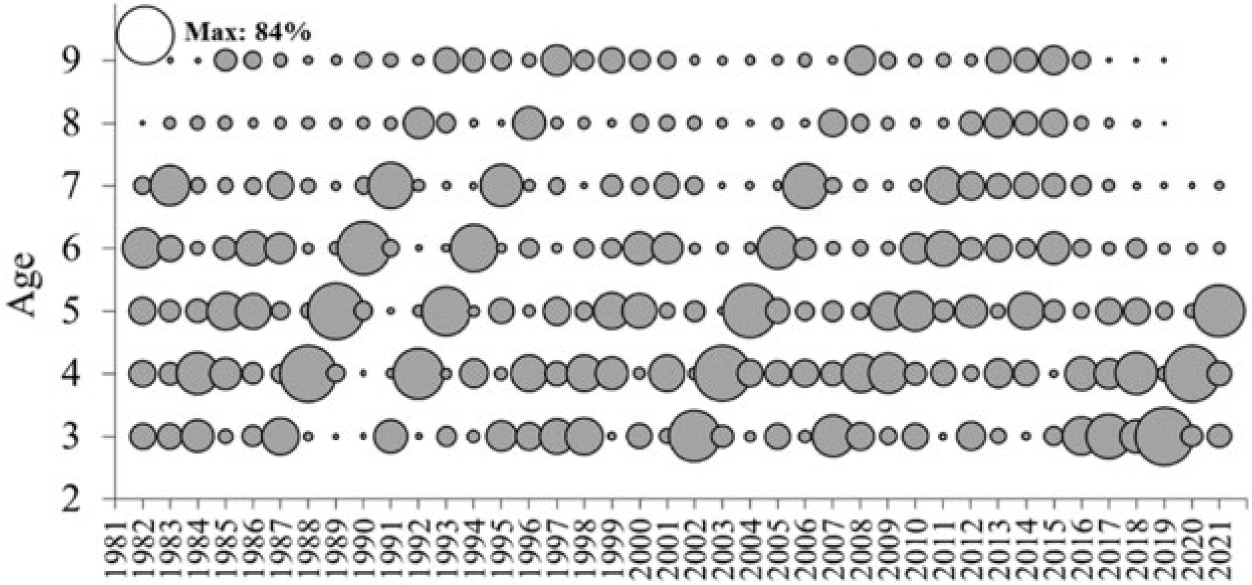


Figure 8. Spring Prince William Sound herring age composition by year, 1982-2021.

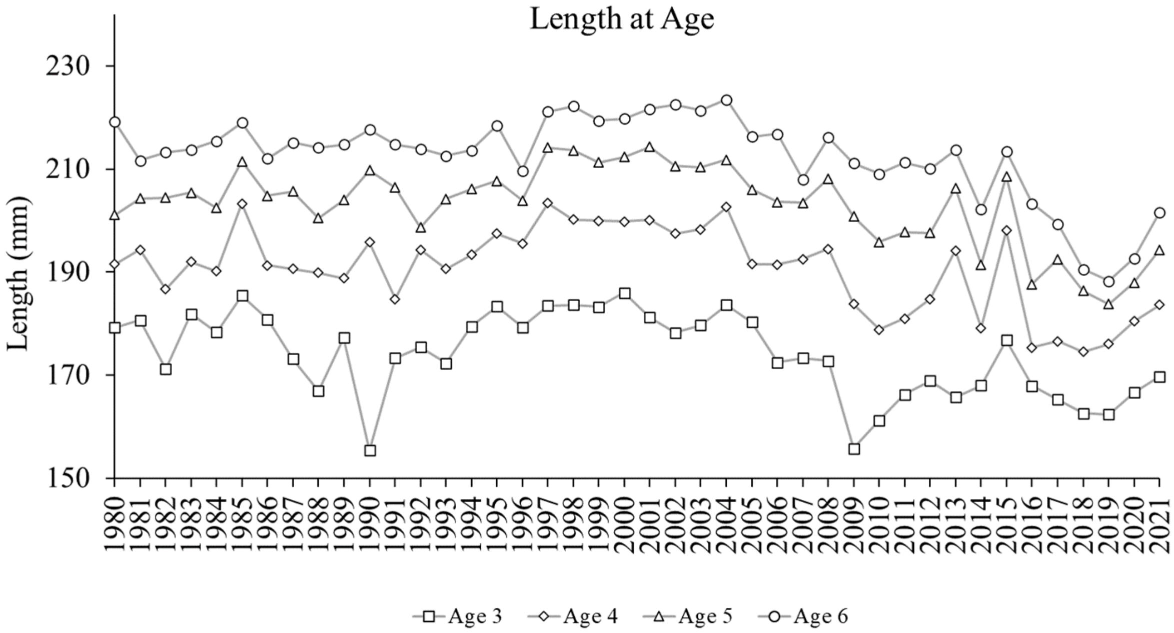


Figure 9. Spring Prince William Sound herring length at age, 1980-2021.

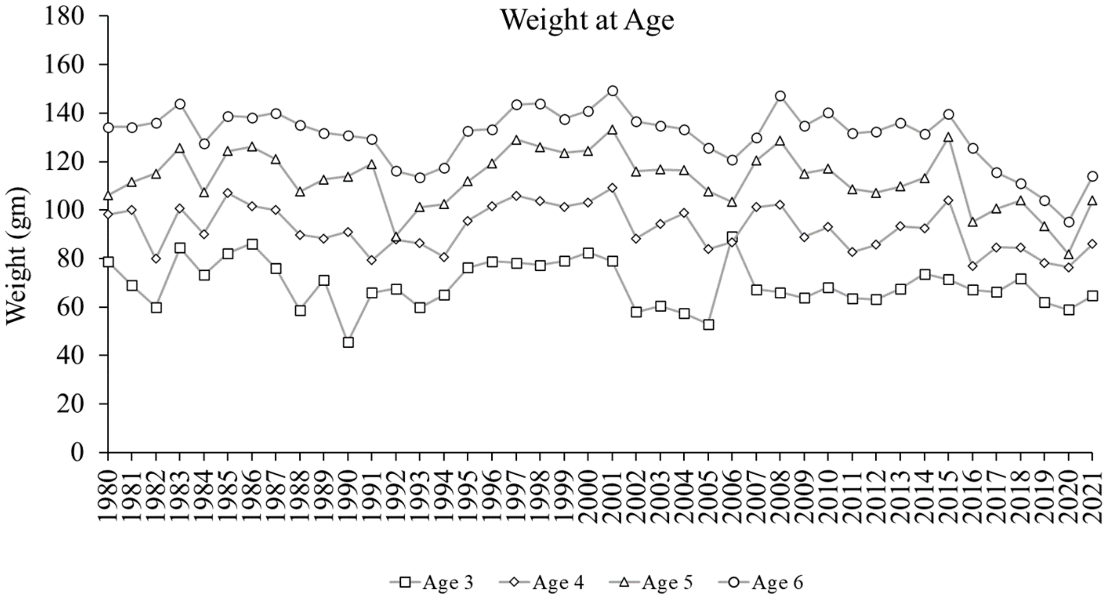


Figure 10. Spring Prince William Sound herring weight at age, 1980-2021.

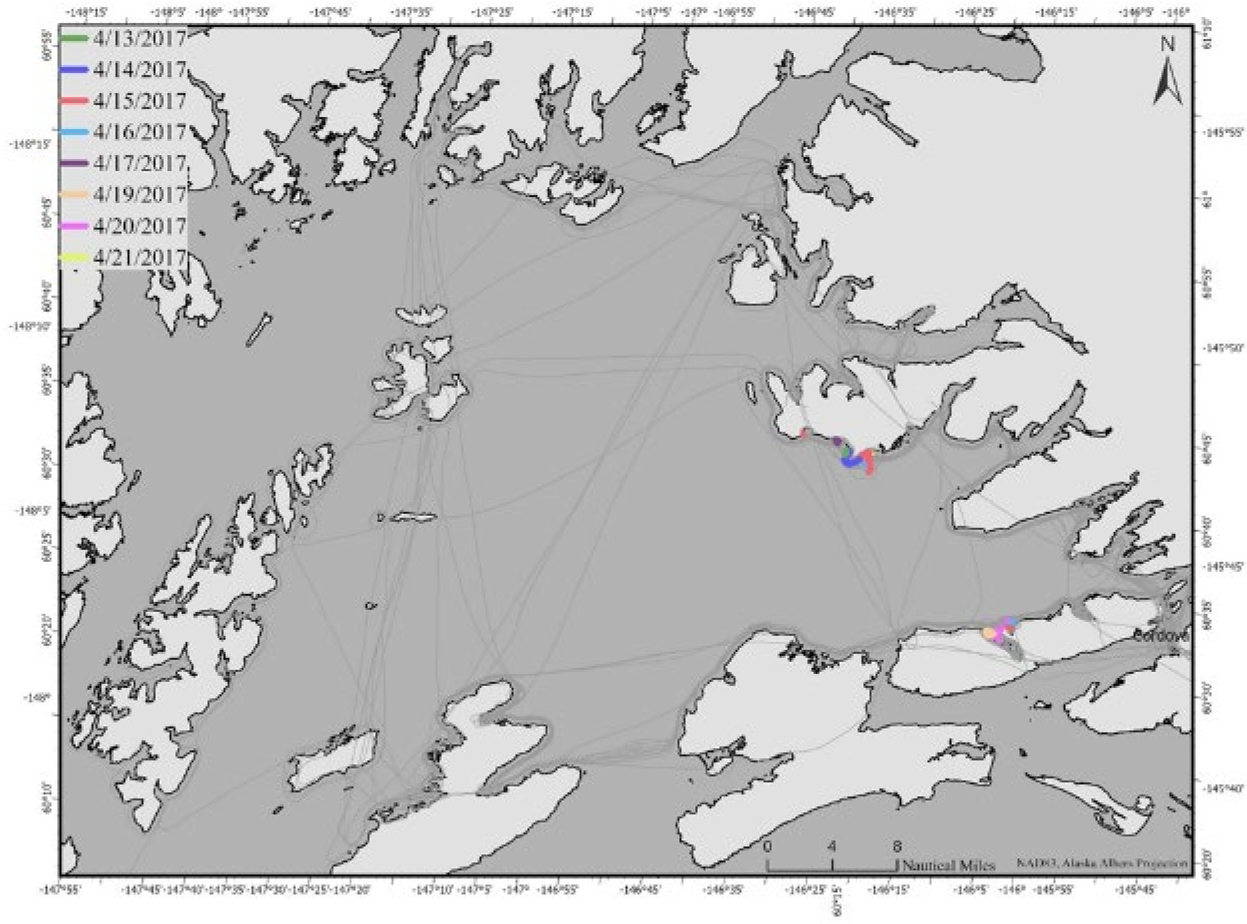


Figure 11. 2017 timing and distribution of Prince William Sound herring spawn. Gray lines are aerial survey routes.

2018

We conducted 39 hours of aerial surveys during 12 flights between March 24 and April 19, 2018 (Fig. 7). PWS herring schools observed in 2018 were less aggregated and smaller than observed in recent years. Spawn was documented in eastern PWS near Red Head (April 7–8); on the north shore of Hawkins Island near Canoe Passage (April 16–17); and near Kayak and Wingham Island (April 13) (Fig. 12). Total PWS mile-days of milt were estimated at 4.52 mile-days, all of which was in the Southeast Area. No spawn was documented in other areas of the sound.

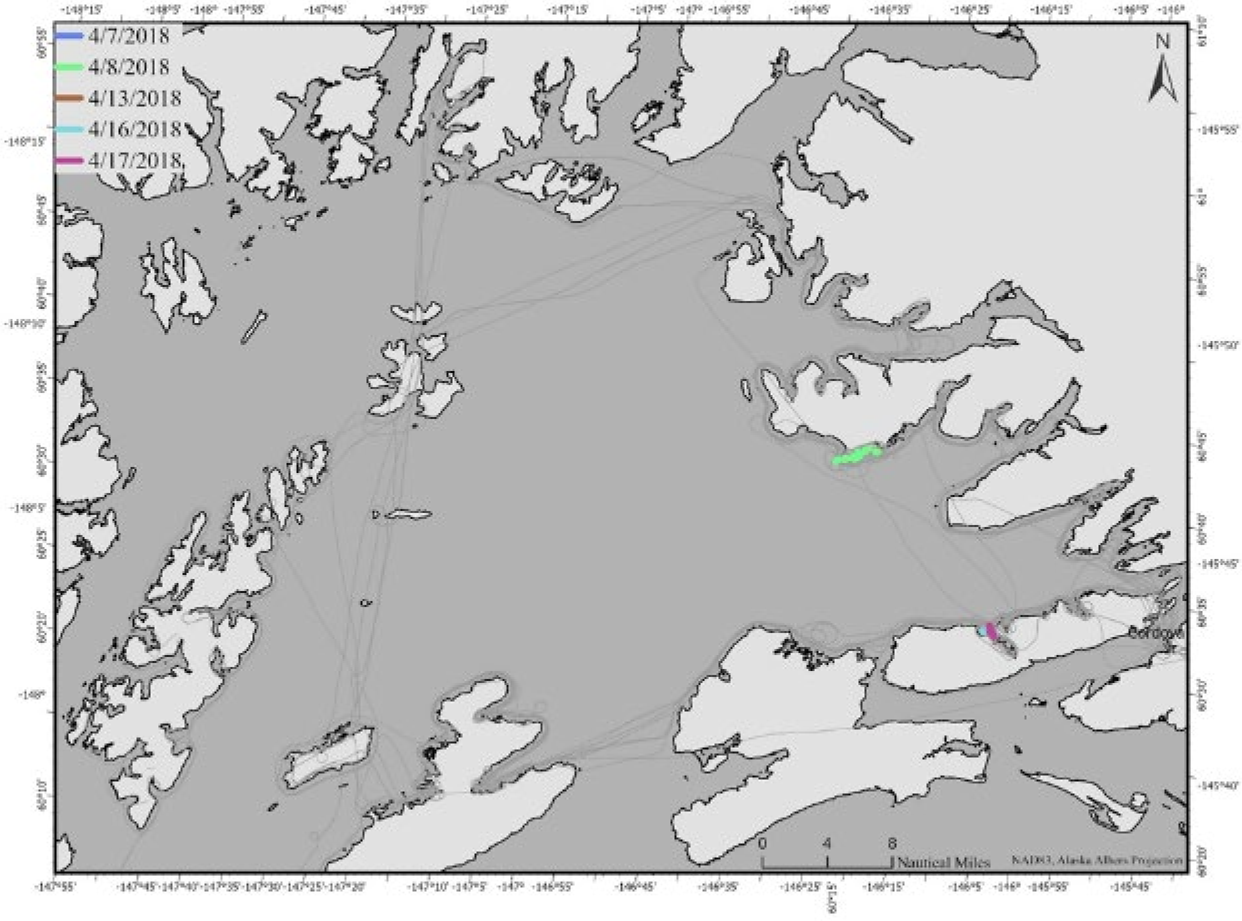


Figure 12. 2018 timing and distribution of Prince William Sound herring spawn. Gray lines are aerial survey routes?

We collected a total of 1,678 herring with purse seine and cast net from Rocky Bay, Hell's Hole, Red Head, Canoe Pass, and Cedar Bay. The overall observed spawning age composition was 27.6% age-3, 44.2% age-4, 16.9% age-5, and 8.8% age-6 and 2.5% age-7 or older fish (Fig. 8).

2019

We conducted 58 hours of spring aerial surveys during 19 flights from March 19 to May 3, 2019 (Fig. 7). Herring schools observed in 2019 were more widespread and numerous than in recent years. Spawn was documented on the north shore of Hawkins Island near Canoe Passage (March 26); between Hells Hole and Knowles Bay (April 1–May 3); on the southeast shore of Green Island (April 5); in Port Fidalgo (April 16–May 3); in Rocky Bay (May 3); and near Kayak and Wingham Island (March 31–April 16) (Fig. 13). Total PWS mile-days of milt were estimated at 12.7 mile-days.

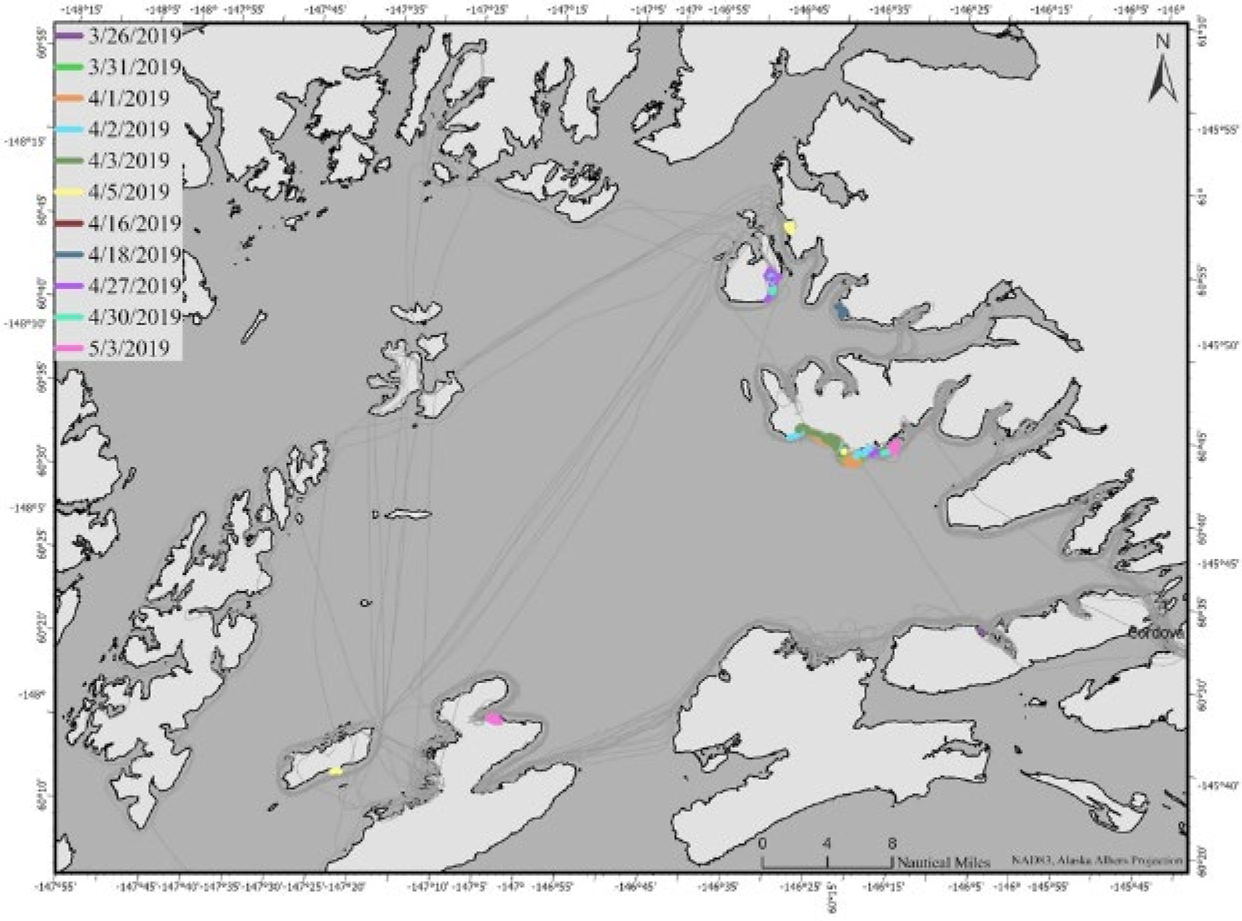


Figure 13. 2019 timing and distribution of Prince William Sound herring spawn. Gray lines are aerial survey routes.

We collected a total of 2,250 herring with purse seine and cast net from Double Bay, Canoe Pass, Whiskey Cove, and Rocky Bay. The overall observed spawning age composition was 84.4% age-3, 4.9% age-4, 7.1% age-5, and 2.7% age-6 and 0.9% age-7 or older fish (Fig. 8). PWS herring, as well as other stocks statewide, saw a large recruitment of age-3 fish in 2019.

2020

We conducted 57 hours of spring aerial surveys during 20 flights from March 19 to May 10, 2020 (Fig. 7). Observations of PWS herring schools observed in 2020 were more increasingly widespread and numerous. Spawn was documented at Red Head (April 2–4), Hells Hole, and Knowles Bay (April 9–24), Canoe Pass (April 23–26), Double Bay (April 24–27), Zaikof Bay (April 23–27), Rocky Bay and Stockdale Harbor (April 28–29), and near Kayak Island (April 10) (Fig. 14). Total PWS mile-days of milt were estimated at 23.7 mile-days.

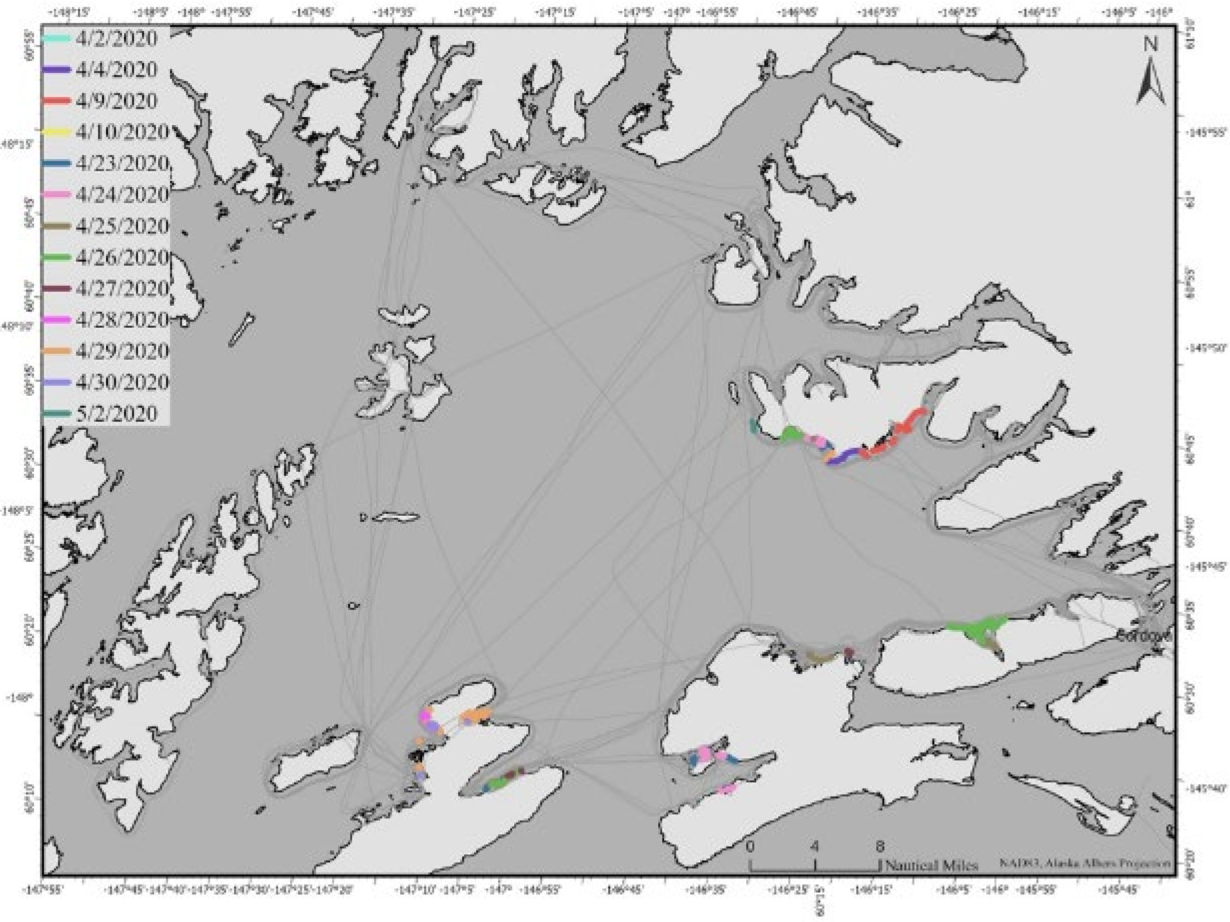


Figure 14. 2020 timing and distribution of Prince William Sound herring spawn. Gray lines are aerial survey routes.

Herring sampling surveys were not conducted from the *R/V Solstice* in 2020 due to the COVID-19 pandemic. Instead, community members and ADF&G staff opportunistically collected a total of 1,355 herring samples with cast net near Hells Hole and Red Head, Double Bay, and Canoe Pass. Overall spawning age composition was 11% age-3, 79% age-4, 4% age-5, 3% age-6, 2.6% age-7 or older fish (Fig. 8).

2021

We conducted 58 hours of spring aerial surveys during 20 flights from March 28 to April 29, 2021 (Fig. 7). PWS herring schools observed in 2020 and 2021 were more widespread and numerous than in recent years. Spawn was documented at Red Head (March 28), Hells Hole and Knowles Bay (April 1–7), Tatitlek (April 21–29), Boulder Bay (April 18–19), near Bligh Island

(April 18–22), Port Etches (April 21–22), Hawkins cutoff (April 18), Canoe Pass (April 19), Zaikof Bay (April 19–20), Stockdale Harbor (April 20–21), Graveyard Point (April 20–21), and near Kayak Island (April 16-17) (Fig. 15). Total PWS mile-days of milt were estimated at 25.6 mile-days.

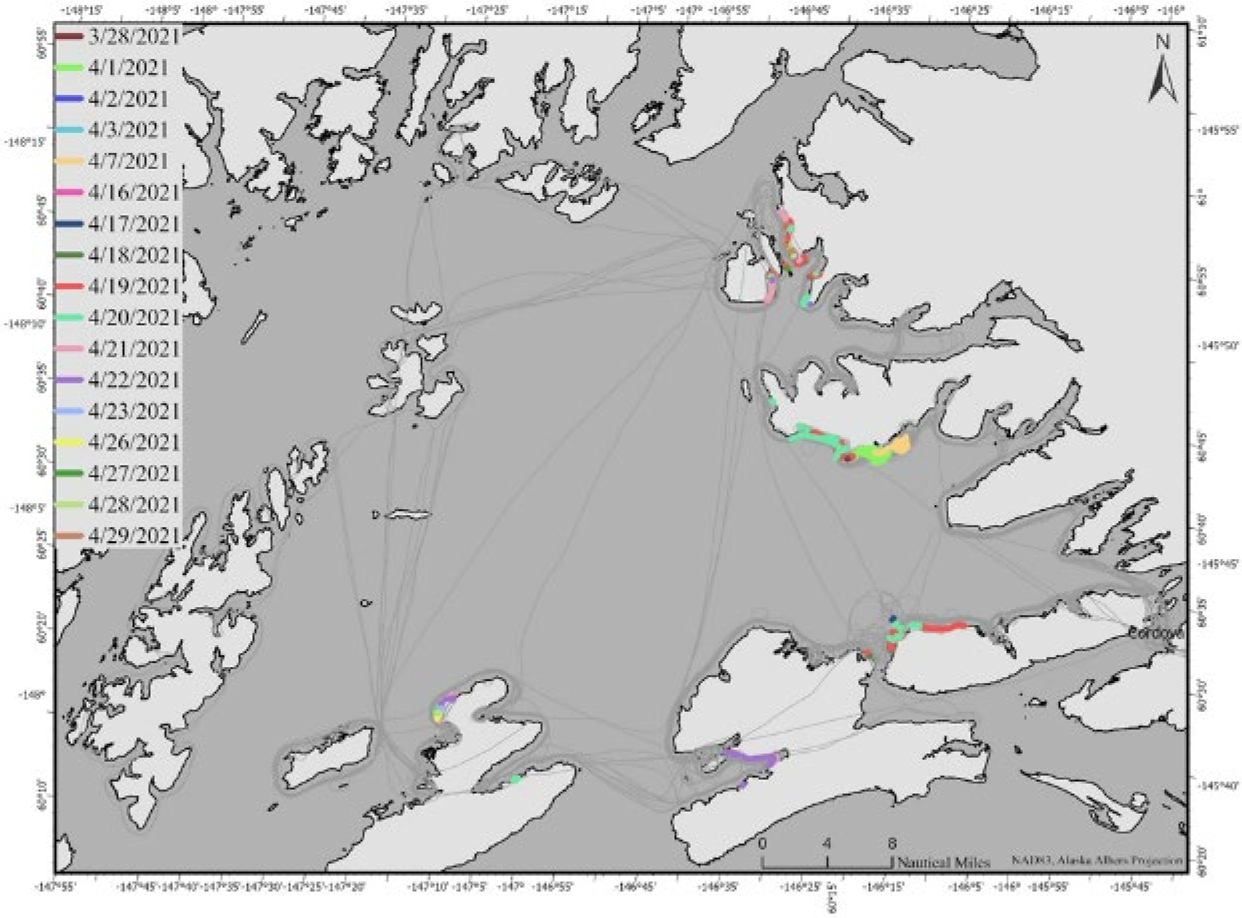


Figure 15. 2021 timing and distribution of Prince William Sound herring spawn. Gray lines are aerial survey routes.

Sampling was conducted aboard the *R/V Solstice* and by private vessels contracted by the Prince William Sound Science Center (PWSSC). A total of 4,120 herring were collected from 8 locations: Bligh Island, Canoe Pass, Double Bay, Graveyard Point, Hell's Hole, Kayak Island, Port Etches, and Zaikof Bay. 2021 was the first year an ASL sample has been collected from Port Etches. Overall spawning age composition of PWS samples collected were 14% age-3, 14% age-4, 67% age-5, 3% age-6, 2% age-7, and <1% age-8 or older fish (Fig. 8).

DISCUSSION

There were no hypotheses to be tested from this monitoring project. We continued long-term monitoring efforts of aerial surveys to collect data associated with spring Pacific herring spawning events and collected and processed ASL samples from pre-spawn and spawning aggregations of Pacific herring. These objectives were completed with methodology consistent with the historical time series. The lowest level of documented spawn as well as the most contracted area of spawn since surveys began in 1972 occurred in 2018. Since 2019 we have observed an increase in mile-days of milt, spawning biomass and spawning area. This is driven by the large recruitment event of age-3 fish to the spawning population in 2019 which was observed in other herring stocks statewide. Length at age declined in most age classes between 2017 and 2019, reaching the lowest values observed since 2009/2010. Length at age increased in 2020-2021. Weight at age declined in all age classes between 2017 and 2020 reaching the lowest values observed since 2005/2006. Weight at age increased in 2021. We have continued to document a male sex bias in cast net sampling from performing concurrent ASL collections with varying gear types, including variable mesh gillnet, purse seine and cast net.

This project successfully met the objective of providing a vessel, the *R/V Solstice*, as a research platform and providing data to other Herring Research and Monitoring (HRM) projects. We coordinated and collaborated with all HRM projects. We provided daily aerial survey results and boat-based observations to field programs and ADF&G management and research staff. We provided ADF&G personnel, equipment, and facilities for disease sampling (project 21120111-E), and reproductive maturity sampling (project 19170111-D). We aged ~300 herring, collected gonad samples, and provided transport logistics for the disease project annually (project 21120111-E). We provided herring ASL results to the adult acoustics survey (project 21120111-G) and tagging and tracking project (211720111-B) and provided aerial survey and ASL results to the modeling and stock assessment project (project 21120111-C) for the duration of this project. ASL and aerial survey data were provided for spawn phenology analysis published in Dias et al. (2022). During the COVID-19 pandemic, we performed disease sample collection and field processing for the U. S. Geological Survey Marrowstone Lab in collaboration with the PWSSC in 2020 and 2021.

The results of both the aerial surveys and age/size structure have been critical to the management of herring commercial fisheries in PWS. The estimates of aerial biomass as well as acoustic biomass and age structured assessment model outputs were central in evaluating the population in relation to regulatory thresholds set in the PWS Herring Management Plan (5 AAC 27.365).

CONCLUSIONS

This project documented mile-days of milt and age composition of the spawning population of Pacific herring in Prince William Sound from 2017 through 2021. The 2018 mile-days of milt estimate is the lowest documented estimate since the surveys began in 1972. Mile-days of milt have consistently increased since this historic low, primarily driven by the large recruitment of age-3 fish to the spawning population in 2019. This cohort has composed a large proportion of the spawning population since.

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This project is part of the HRM program. These findings and conclusions presented by the author(s) are their own and do not necessarily reflect the views or position of the *Exxon Valdez* Oil Spill Trustee Council.

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APPENDIX A MULTI-DECADAL SHIFTS IN THE DISTRIBUTION AND TIMING OF PACIFIC HERRING (*CLUPEA PALLASII*) SPAWNING IN PRINCE WILLIAM SOUND (MCGOWAN ET AL. 2021)

Canadian Science Publishing

ARTICLE

Multi-decadal shifts in the distribution and timing of Pacific herring (*Clupea pallasii*) spawning in Prince William Sound, Alaska

David W. McGowan, Trevor A. Branch, Stormy Haught, and Mark D. Scheuerell

Abstract: The location and timing of spawning play a critical role in pelagic fish survival during early life stages and can affect subsequent recruitment. Spawning patterns of Pacific herring (*Clupea pallasii*) were examined in Prince William Sound (1973–2019) where the population has failed to recover since its collapse in 1993. Abrupt shifts in spawn distribution preceded the rapid increase in population size in the 1980s and later its collapse by one and two years, respectively. Following the population collapse, spawning contracted away from historical regions towards southeastern areas of the Sound, and the proportion of occupied spawning areas declined from 65% to <9%. Spatial differences in spawn timing variation were also apparent, as the median spawn date shifted earlier by 26 days in eastern and 15 days in western areas of Prince William Sound between 1980 and 2006, and then shifted later by 25 (eastern) and 19 (western) days over a 7-year period. Effects of contracted spawning areas and timing shifts on first-year survival and recruitment are uncertain and require future investigation.

Résumé : Le lieu et le moment du frai jouent un rôle critique dans la survie des poissons pélagiques durant les premières étapes de la vie et peuvent avoir une incidence sur le recrutement subséquent. Nous avons examiné les motifs de frai du hareng du Pacifique (*Clupea pallasii*) dans le golfe du Prince William (1973–2019), où la population ne s'est pas encore rétablie dans la foulée de son effondrement en 1993. Des changements abrupts de la répartition du frai ont précédé, d'un et de deux ans respectivement, l'augmentation rapide de la population dans les années 1980 et son effondrement plus tard. Après l'effondrement de la population, l'aire de répartition du frai s'est contractée dans les secteurs historiques de frai pour se déplacer vers des secteurs du sud-est du golfe, et la proportion des lieux de frai occupés est passée de 65 % à <9 %. Des différences spatiales de la variation du moment du frai ressortent également, la date médiane du frai étant de 26 jours plus hâtive dans les secteurs est et de 15 jours plus hâtive dans les secteurs ouest du golfe en 2006 qu'en 1980, pour ensuite être repoussée de 25 jours (à l'est) et de 19 jours (à l'ouest) sur une période de 7 ans. Les effets de la contraction de la répartition du frai et des changements du moment du frai sur la survie et le recrutement durant la première année ne sont pas bien établis et nécessitent plus d'études. [Traduit par la Rédaction]

Introduction

The location and time of spawning plays a critical role in the survival of pelagic fish during early life stages that subsequently affects recruitment. For herring (*Clupea* spp.), spatial differences among spawning sites can influence embryo mortality rates (Rooper et al. 1999; Shelton et al. 2014; Keeling et al. 2017) and the transport and retention of larvae in nursery areas (Sinclair and Tremblay 1984; Cowan and Shaw 2002). Temporal shifts in spawning can affect the duration of egg and larval stages (Houde 2016), predation risk, and the availability of prey to larvae during the critical early feeding period (Cushing 1990).

A typical Pacific herring (*Clupea pallasii*, hereafter herring) population will collectively spawn batches of eggs over a period of days to months across numerous sites (Hay 1985), a strategy which is adapted to increase opportunities for herring offspring to survive early life stages. Although individual herring spawn once per season, staggered spawning across the entire population in space and time has the effect of hedging against uncertainty in the timing and location of optimal conditions for egg and larval survival (Lambert 1990). Spatial and temporal diversity in spawning among metapopulations also buffers the larger population from abundance fluctuations (i.e., the portfolio effect; Schindler et al. 2010) — herring spawning that is broadly distributed in space and time increases population resilience to perturbations in their environment (Hay 1985; Lambert 1987; Siple and Francis 2016). Accordingly, changes in the number or spatial diversity of spawning locations, and temporal shifts in the onset or duration of spawning may impact long-term productivity of herring populations (Ruzzante et al. 2006; Dragesund et al. 2008).

Spatial patterns of herring spawning are determined by population size and processes that affect fidelity to spawning areas and dispersal to new locations (Ware and Schweigert 2001; Flostrand et al. 2009). The persistence of spawning at known locations over a number of years indicates conservation of migration patterns across generations, while variations from established migration patterns indicates straying or diffusion that results in the

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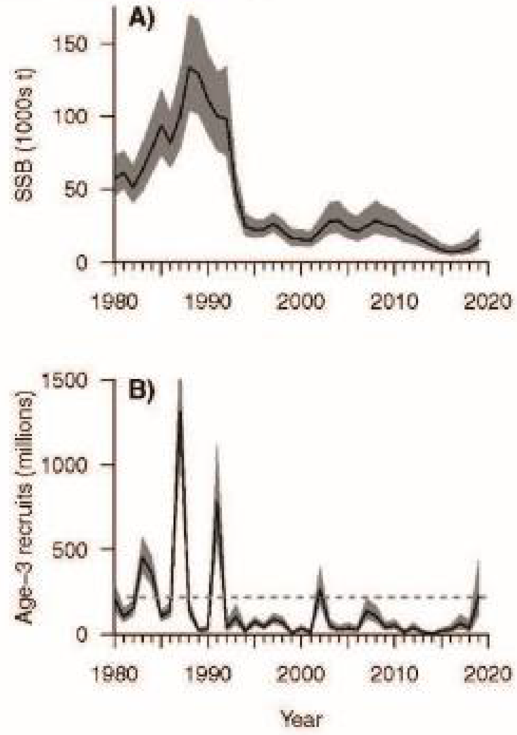
colonization of new areas or reoccupation of previously active locations (Petitgas et al. 2006). Young herring are hypothesized to learn migration patterns by schooling with older, repeat spawners in the year before they first spawn and follow them to spawning areas, thereby increasing the likelihood of cross generation fidelity to the general spawning area in successive years (McQuinn 1997; Corten 2002; MacCall et al. 2019). If this hypothesis is true, variations in migration patterns would occur if the social learning process is disrupted due to naïve fish not mixing with older fish, stock collapse, or a predominance of naïve fish following a strong recruitment (Huse et al. 2002, 2010; Corten 2002). Unguided young herring may also be more likely to stray from migration patterns due to increased sensitivity to environmental conditions (Macdonald et al. 2018), thus expanding or shifting population distribution. Large perturbations in the environment may also affect adult migration patterns (Petitgas et al. 2006). Knowledge of spawning areas may be lost when a metapopulation experiences high mortality due to natural processes (e.g., disease outbreak, localized predation) or anthropogenic effects (fisheries, oil exposure), thereby affecting the diversity and number of spawning sites and potentially altering reproductive success.

In the Northeast Pacific, interannual variations in herring spawn timing have been primarily attributed to population demographics and temperature (Hay 1985; Ware and Tanasichuk 1989). Gonad maturation rate is determined by fish weight and daily temperature (Ware and Tanasichuk 1989), resulting in earlier spawning by larger fish and during warmer years. In populations comprising multiple age cohorts, spawning may be staggered in discrete waves with older fish spawning earlier than younger fish (Hay 1985; Ware and Tanasichuk 1989). If population age structure is dominated by one cohort or truncated by fishing (e.g., Barnett et al. 2017), spawning duration is likely to be shortened. State-dependent life-history modeling also suggests that variations in food availability to adult fish may result in spawn timing shifts to optimize self-fitness (Ljungström et al. 2019).

We examined changes in spawning patterns in a once-thriving herring population in Prince William Sound, Alaska. Herring are a key forage species in this ecosystem, and they have supported commercial fisheries for more than a century (Muradian et al. 2017). The population collapsed abruptly in 1993 (Quinn et al. 2001; Deriso et al. 2008; Hulson et al. 2008; Muradian et al. 2017) and has yet to recover to pre-collapse biomass levels due to a lack of strong year classes that recruit and carry through the adult population (Fig. 1A). There is uncertainty as to the causes of the initial population collapse and subsequent lack of recovery, with hypotheses including poor nutrition (Pearson et al. 1999, 2012), infectious disease (Rice and Carls 2007; Hulson et al. 2008), and the combined effects of the 1989 *Exxon Valdez* oil spill and overexploitation by the fishery (Thorne and Thomas 2008). Continued low population size and poor recruitment have been attributed to repeating disease cycles from multiple pathogens (Rice and Carls 2007), shifts in environmental conditions in the Gulf of Alaska (Pearson et al. 2012; Ward et al. 2017), humpback whale (*Megaptera novaeangliae*) predation (Pearson et al. 2012), competition with hatchery-released pink salmon (*Oncorhynchus gorbuscha*) (Deriso et al. 2008; Pearson et al. 2012), and cardiac abnormalities resulting from trace exposure to lingering oil (Incardona et al. 2015). Since the collapse, no recruitment events have come close to the magnitude of the 1980, 1981, 1984, and 1988 birth years (Muradian et al. 2017), and there have only been two cohorts of moderate size (1999, 2016 birth years) in the past 30 years (Fig. 1B; J. Trochta, University of Washington, personal communication, 23 December 2019), creating uncertainty as to which conditions are required for recovery.

Fig. 1. Prince William Sound herring stock assessment model estimates for (A) median spawning stock biomass (SSB) and (B) number of age-3 recruits from 1980 to 2019 (J. Trochta, University of Washington, personal communication, 23 December 2019). Shaded area indicates 95% confidence interval. Cohort sizes greater than 220 million age-3 recruits (dashed line) are considered strong recruitment events (EVOSTC 2010).



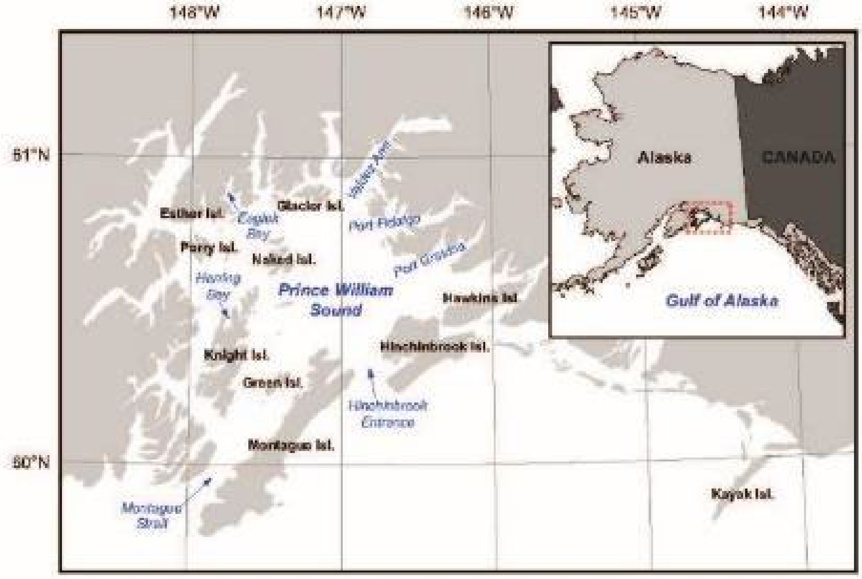
The match–mismatch hypothesis (Cushing 1990) and portfolio effect (Schindler et al. 2010) highlight the critical influence that spawn timing and location, and diversity of spawning areas, have on herring reproductive success. We used a 47-year time series of spawning distributions in Prince William Sound from aerial survey data to examine (1) decadal and interannual shifts in the distribution of spawn locations; (2) interannual shifts in spawn timing; and (3) the spatial structure of spawning areas based on spawn timing trends. Recruitment dynamics and spatial patterns of population age structure, commercial harvest, and impacted coastline from the *Exxon Valdez* oil spill were also examined to assess whether shifts in spawning distributions coincided with spatial changes in recruitment and local exploitation, and the oil spill.

Materials and methods

Data collection

Active herring spawning was observed during aerial surveys conducted by the Alaska Department of Fish and Game (ADF&G) in the Prince William Sound management area between 1973 and 2019. The ADF&G aerial survey is a non-random survey that attempts to account for all spawning within the Sound. Weather, time, and funding constraints preclude implementation of a randomized or complete survey design; therefore, flight plans are based on the most recent information of where herring schools and spawning aggregations are most likely to be located from numerous sources

Fig. 2. Prince William Sound management area. Red box within the inset map of Northeast Pacific outlines the study area. Bathymetric (blue) and geographic (black) features mentioned in text are labeled. Maps created using ArcGIS 10.71 with data from the Alaska Department of Natural Resources (ADNR 2018) and Esri (Esri 2020). [Colour online.]



that include fish and marine mammal distributions from the prior day, reports from boats on the Sound, and observations from non-survey flight traffic.

Active herring spawn is measured as the total length of milt clouds along the coastline per day (mile-days of milt; 1 mile = 1.609 km) following Shepherd and Haught (2019). Mile-days of milt is a key index of relative abundance in the stock assessment for Prince William Sound herring (Muradian et al. 2017). Aerial surveys are flown between late-March and mid-May (refer to online Supplementary Table S1[1]). At the start of each spawning season, scheduled surveys are flown once or twice per week, and then flown more frequently (up to twice a day) when spawning or pre-spawning aggregations are observed. Surveys end when there is no observed spawning or anecdotal reports of spawning in the Sound. Surveys are flown along the coastline at approximately 460 m (1500 ft.) altitude for up to 5 hours, covering about 800 km (~500 mi) per survey.

Survey coverage has changed over the study period. Prior to 1981, coverage was primarily in the northern and eastern Sound from Glacier Island and lower Valdez Arm to Port Gravina, and the southern Sound along the northern coasts of Hawkins and Hinchinbrook islands and Northeast Montague Island (Fig. 2, Supplementary Fig. S1[1]). In the 1980s, surveys were expanded to the northern Sound west of Glacier Island to Esther Island, and in the western Sound to include Knight, Naked, and Perry islands. In 2007, additional surveys were flown infrequently over Kayak Island.

Prior to 2008, most surveys were conducted by a pilot and one observer who photographed and recorded spawn observations on paper maps (Brady 1987). Since 2008, an additional observer has been added and spawn observations are digitally recorded inflight as polylines using Esri ArcPad (Esri Inc., Redlands, California) with a Bluetooth GPS for georeferencing (Shepherd and Haught 2019). Post-processing of digital data uses photographs and video to refine the mile-days of milt data in ArcGIS (Esri Inc., Redlands, California). Observations originally recorded on paper maps were digitized as polylines in ArcGIS. Survey effort was converted to polygons from historical logbooks (1973 to 1999) or polylines for the later georeferenced flight paths (1997 to 2019). Processed spawn and survey effort data (1973 to 2018) are publicly available through the Alaska Ocean Observing System (https://portal.aoos.org, Bochenek 2010; Haught and Moffitt 2018), and were combined for this study with survey data from 2019.

Spatial analysis

Survey coverage and spawning data were partitioned into 10 km × 10 km grid cells (Fig. 3). ArcGIS polylines and polygons that occurred in two or more grid cells were split into segments at the borders of each cell. Polyline segments for mile-days of milt were assigned values equivalent to the length of the segment within the grid cell. Grid cells were assigned binary values for survey coverage (0 = no coverage, 1 = coverage) based on coverage polygon or polyline segments. Consistent with prior analyses of spawn patterns in Prince William Sound, grid cells were grouped into regions (Fig. 3) based on ADF&G herring districts within the Prince William Sound management area (e.g., Russell et al. 2017): Montague Island, Naked Island, North Shore, Northeast Shore, Southeast Shore, and Kayak Island.

Spatial patterns of herring spawning were characterized at decadal and interannual scales across Prince William Sound and by region from 1973 to 2019. To examine decadal spatial patterns, mile-days of milt (MDM) were summed within each grid cell by decade, and plotted by decade as quantiles of all years combined in 10% increments. To examine interannual spatial patterns, MDM values were summed within each grid cell by year from 1973 to 2019. Quantiles for annual MDM values were calculated in 20% increments for all years combined and plotted as heat maps

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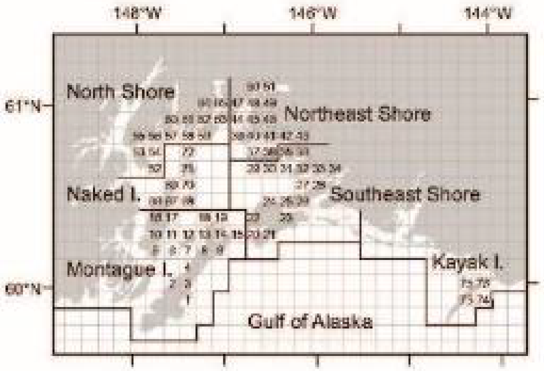
[1] Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2021-0047.

Fig. 3. Boundaries for Prince William Sound regions and the Gulf of Alaska adapted from appendix G4 in Russell et al. (2017). Numbered 10 km × 10 km grid cells indicate areas within each region where herring spawning was observed between 1973 and 2019. Map created using ArcGIS 10.7.1 with data from the Alaska Department of Natural Resources (ADNR 2018).



by year and grid cell. Grid cells with positive survey coverage values for each year were identified in the heat map to indicate interannual changes in the survey domain. To show interannual spatial variations in cumulative spawn, MDM values were summed across grid cells within each region by year.

To quantify interannual changes in how evenly distributed spawning was across Prince William Sound, we used an index of spatial dispersion (Payne et al. 2005) adapted from Pielou (1966) species evenness index, based in turn on Shannon's species diversity index (Shannon and Weaver 1949):

$$(1) \qquad D_t = \frac{-\sum_{j=1}^{s} p_{j,t} \ln(p_{j,t})}{\ln(s)}$$

where $p_{j,t}$ is the proportion of total spawn (MDM) in each grid cell j in year t, and s is the total number of grid cells in which active spawning was observed within Prince William Sound in any year between 1980 and 2019. Observations from the 1970s and Kayak Island were not included in the dispersion index calculation due to gaps in survey coverage. Index values D_t range from 0 (all spawning in one grid cell) to 1 (evenly distributed across all grid cells). Although not all grid cells were surveyed each year, under this approach we assume that all grid cells were either directly sampled by the survey or indirectly via other methods (e.g., anecdotal reports from other aircraft or vessels) each year. It is not known what proportion of total spawn remains unobserved each year, but the dispersion index is assumed to be sufficiently robust to quantify relative changes in evenness given the high proportion of sites (>50%) that are sampled each year (Payne et al. 2005).

To assess if shifts in spawning distributions coincided with spatial changes in population age structure and recruitment patterns, age composition data were summarized within each region and compared to spawning spatial patterns. Herring age data have been collected from catches and surveys since the 1970s (Shepherd and Haught 2019), and are used in the stock assessment (Muradian et al. 2017). Age composition data were summarized for herring two years and older by region from 1980 to 2019 using commercial catch and survey samples collected by purse seine or cast net. Data were pooled for North Shore and Naked Island due to low sample sizes. We compared age compositions among the regions by year to determine if there were spatial differences in recruitment patterns of the seven largest cohorts with >220 million age-3 recruits (Fig. 1B; EVOSTC 2010; Muradian et al. 2017). We assessed whether regional differences in age structure coincided with changes in spawning distributions.

Commercial catch data were also summarized by region to assess whether local exploitation rates greater than 20% preceded sharp declines in spawning. This threshold was based on the maximum management target rate of 20% harvest for spawning biomass throughout Prince William Sound (Prince William Sound Herring Management Plan, 5 AAC 27.365(b)). Fish ticket records (ADF&G 2019a, 2019b) for the purse seine and gillnet sac-roe fisheries and the spawn-on-kelp pound fishery were summarized within each region from 1980 to 1999, the last year in which commercial fishing occurred. Landings from the sac-roe fisheries were reported in total whole fish weight (t). The pound fishery, in which herring were impounded to produce spawn-on-kelp, reported only the spawn-on-kelp product weight (t). To generate pound-fishery landings data equivalent to the sac-roe fisheries, we used a conversion factor developed by ADF&G to estimate the weight of utilized herring biomass, that assumes 12.5 t of herring would produce 1 t of spawn product (Morstad et al. 1992). For all fisheries, catch data were pooled for North Shore and Naked Island due to uncertainty in the location of some reported catches. The location of fishing associated with each fish ticket i was cross-referenced with sample locations from the age database and ADF&G annual management area reports to verify that commercial catches were accurately tallied within each region.

The exploitation rate (ER) of the commercial fishery in year t within each region n was calculated as

$$(2) \qquad \mathrm{ER}_{n,t} = \frac{\sum_{i=1}^{f} h_{i,n,t}}{\frac{\mathrm{MDM}_{n,t}}{\mathrm{MDM}_t} \times \mathrm{SSB}_t}$$

(i.e., the sum of commercial landings from the three fisheries h divided by estimated spawning stock biomass (SSB) from the stock assessment). SSB was allocated to regions by assuming that MDM in each region is proportional to SSB in each region (see Fig. 3). A Pearson's χ^2 test for independence was used to determine if the probability of changes in spawning of ±50% from the prior year (ΔMDM) was similar under different levels of local exploitation. For each year and region, observations were categorized based on the change in total spawn from the prior year ($\Delta\mathrm{MDM} < -50\%$, $-50\% \le \Delta\mathrm{MDM} \le -50\%$, $\Delta\mathrm{MDM} > 50\%$) and whether the local exploitation rate from the prior year was either high ($\mathrm{ER} > 0.2$), low ($0 < \mathrm{ER} \le 0.2$), or there was no fishing ($\mathrm{ER} = 0$). A separate 3 × 3 contingency table grouped observations based on exploitation in the prior two years: high ($\mathrm{ER} > 0.2$) in both years; no fishing ($\mathrm{ER} = 0$) in both years; or all other observations where exploitation was either high in only one year or low ($0 < \mathrm{ER} \le 0.2$) in one or both years. P values were estimated using Monte Carlo simulations with 10 000 replicates.

Spawning patterns were also examined relative to the distribution of shoreline impacted by the *Exxon Valdez* oil spill. Spawn distributions were summarized into four periods: the decade prior to the spill (1980–1988); the year of the spill (1989); the three-year period following the spill that preceded the collapse of the herring population (1990–1992); and the post-collapse period (1993–2019). Shoreline oiling data are from surveys conducted in the summer and fall 1989 and spring 1990 that assessed coastline as being "very lightly" to "heavily" impacted by the spill and cleanup (ADNR 1996a, 1996b).

Temporal analysis

Interannual variation in spawn timing was examined across Prince William Sound and by region from 1980 to 2019, excluding

Table 1. Number of days of survey coverage (mean days·year^{-1}, $\bar{x}$, and standard deviation, SD) summarized by decade and region within Prince William Sound.

	All regions		Montague Island		Southeast Shore		Northeast Shore		North Shore		Naked Island		Kayak Island	
Decade	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
1970s	13.6	2.4	3.6	1.8	3.3	3.6	11.9	3.4	3.7	2.8	—	—	—	—
1980s	30.2	6.2	19.3	5.0	19.8	5.9	26.4	6.5	20.6	6.3	15.8	9.9	0.1	0.3
1990s	20.9	5.3	17.8	5.3	15.7	4.7	17.1	6.0	13.3	8.6	12.5	8.3	—	—
2000s	11.7	3.1	8.6	2.3	11.1	2.5	9.7	2.2	5.5	1.6	6.4	2.5	0.7	1.2
2010s	16.8	3.3	8.6	4.1	16.3	3.2	14.6	3.3	4.0	2.1	5.3	3.4	1.7	1.2

Note: A dash (—) indicates no survey coverage.

Table 2. Total spawn (mean mile-days of milt·year^{-1}, $\bar{x}$, and standard deviation, SD) summarized by decade and region within the Prince William Sound management area (note, the Kayak Island region is not shown due to inconsistent sampling).

	All regions		Montague Island		Southeast Shore		Northeast Shore		North Shore		Naked Island	
Decade	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
1970s	68.9	20.7	6.2	7.1	5.5	13.8	56.6	15.0	—	—	—	—
1980s	151.5	62.0	32.6	27.2	8.4	7.5	56.5	29.1	40.4	31.6	12.9	13
1990s	66.1	44.2	32.0	15.2	8.1	6.3	21.6	26.6	3.7	8.7	0.6	1.4
2000s	26.7	7.2	6.9	4.0	11.7	6.1	5.5	3.1	1.2	2.2	0.4	0.7
2010s	42.9	27.1	1.7	2.8	24.5	19.2	10.9	14.2	0.0	0.0	0.0	0.0

Note: A dash (—) indicates spatially limited or no survey coverage. 1 mile = 1.609 km.

observations from the 1970s and Kayak Island due to survey coverage gaps in space and time. MDM values were summed within each region by day of year (DOY) and year. Survey coverage and spawn events were plotted by DOY and year for each region and all regions combined. A time series of spawn timing was calculated for each region based on the day of year when 50% of total MDM for that year had been observed, which corresponds with the peak of spawning activity in most years (Supplementary Fig. S2[1]).

We fit multivariate autoregressive state-space (MARSS) models to time series of spawn timing for each region. The MARSS framework includes separate observation and process models to partition total variance between observation (i.e., sampling) and process (i.e., environmental perturbations) error (Holmes et al. 2012) and to estimate the underlying process that represents true spawn timing from multiple time series while accounting for missing values, autocorrelation among samples, and sampling error associated with aerial surveys. MARSS models can also be used to infer spatial structure of spawning areas to detect regional differences in spawn timing using Akaike's information criterion (AIC) model selection (e.g., Ward et al. 2010; Holmes et al. 2018b; Siple and Francis 2016).

The MARSS process model took one of two different matrix forms:

$$\mathbf{x}_t = \mathbf{B}\mathbf{x}_{t-1} + \mathbf{w}_t,\ \text{where}\ \mathbf{w}_t \sim \text{MVN}(0, \mathbf{Q}) \tag{3a}$$

$$\mathbf{x}_t = \mathbf{x}_{t-1} + \mathbf{u} + \mathbf{w}_t,\ \text{where}\ \mathbf{w}_t \sim \text{MVN}(0, \mathbf{Q}) \tag{3b}$$

Equation 3a is a mean-reverting stationary process, where the $m \times 1$ vector $\mathbf{x}_t$ represents true spawn timing for spawning area m in year t, $\mathbf{B}$ is an $m \times m$ matrix representing the strength of the autoregressive process for each state along the diagonal and zeroes elsewhere, and $\mathbf{w}_t$ is an $m \times 1$ vector of process errors drawn from a multivariate normal distribution (MVN) with mean vector 0 and variance-covariance matrix $\mathbf{Q}$. Equation 3b is a biased (non-stationary) random walk where $\mathbf{u}$ is an $m \times 1$ vector that represents an upward or downward bias in the random walk. We examined three process variance assumptions: (1) not correlated among the trajectories, with equal variances (same q value on the diagonal and zeroes elsewhere); (2) not correlated, with unequal variances (unique q_m values on the diagonal and zeroes elsewhere); or (3) correlated, with equal variances (same q value on the diagonal and the same g value elsewhere).

Our MARSS observation model was

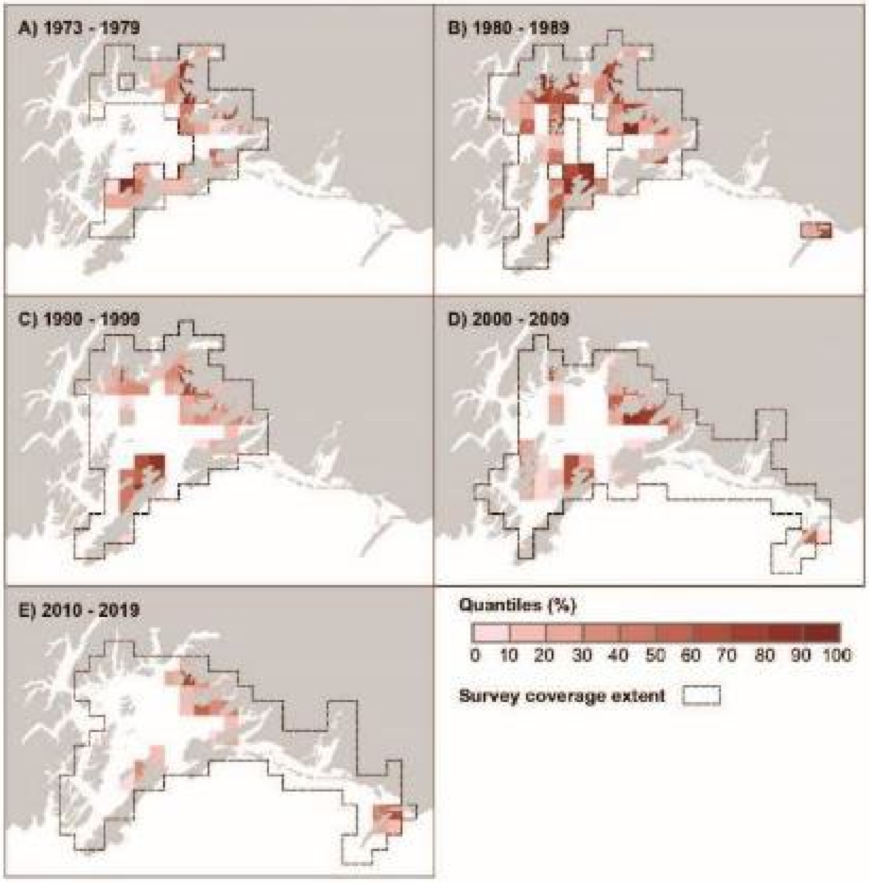
$$\mathbf{y}_t = \mathbf{Z}\mathbf{x}_t + \mathbf{v}_t,\ \text{where}\ \mathbf{v}_t \sim \text{MVN}(0, \mathbf{R}) \tag{4}$$

where $\mathbf{y}_t$ is an $n \times 1$ vector of the observed spawn timing in region n in year t, $\mathbf{Z}$ is an $n \times m$ matrix containing 0s and 1s that maps each time series of observed spawn timing onto an associated true spawn timing $\mathbf{x}_t$ for each spawning area, and $\mathbf{v}_t$ is an $m \times 1$ vector of observation errors for each time series drawn from a multivariate normal distribution with mean vector 0 and variance-covariance matrix $\mathbf{R}$. Because the efficiency of aerial survey sampling may vary among regions, we assumed that sampling errors have unequal observation variances (i.e., unique r_n along the diagonal of $\mathbf{R}$) and are not correlated among time series (i.e., 0s in the off-diagonals of $\mathbf{R}$).

To assess spatial differences in spawn timing, we evaluated data support for 14 spawning area configurations among the five regions. Each model was modified to associate one or more of the observed time series with a corresponding process in $\mathbf{x}_t$. For example, when $m = 1$, data from all regions are treated as observations of a single spawning area; when $m = 5$, each region is modeled independently. For each of the configurations, we fit nine models in which the parameterization of $\mathbf{Q}$ was changed to test the three process error assumptions for three model structures: unbiased random walk (eq. 3a, $\mathbf{B}$ fixed at 1), biased random walk (eq. 3b), and stationary autoregressive process (eq. 3a, $\mathbf{B}$ estimated). Models were fit in R 3.4.3 (R Core Team 2020) using the "MARSS" package version 3.10.10 (Holmes et al. 2018a). Maximum likelihood estimates for parameters were obtained using the expectation-maximization algorithm (Holmes 2013).

We evaluated all 126 models for convergence and used residual scatterplots and autocorrelation function plots to verify that residuals were normally distributed and not autocorrelated in time. We assessed data support for each model using AIC for small sample size (AIC$_c$), with the most parsimonious models having the lowest AIC$_c$ value (Burnham and Anderson 2002).

Fig. 4. Distribution of spawning and extent of survey coverage from 1973 to 2019 by decade. Spawn patterns are represented as quantiles of mile-days of milt summed within each 10 km × 10 km grid cell by decade (plots A–E). Spawn patterns in the 1970s may be biased due to spatial and temporal gaps in coverage. Maps created using ArcGIS 10.7.1 with data from the Alaska Department of Natural Resources (ADNR 2018) and the Alaska Ocean Observing System (Bochenek 2010; Haught and Moffitt 2018). [Colour online.]



Models with $\Delta AIC_c < 2$ were considered statistically similar (Burnham and Anderson 2002).

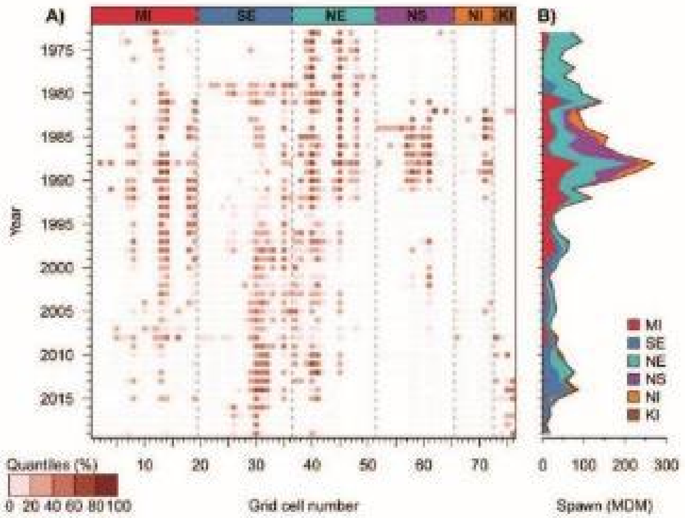
Results

Spatial patterns

The ADF&G aerial survey coverage expanded and contracted over the 47-year study period. In the 1970s, survey coverage was primarily focused in the Northeast Shore region (11.6 days sampled per year versus <4 days·year^{-1} in other regions, Table 1). Coverage expanded across Prince William Sound in the early 1980s (Supplementary Table S1[1]), with flights occurring over all regions within the Sound on more than 50% of the days sampled per year (Table 1), peaking at 30 days·year^{-1} at the peak of population size (Fig. 1). Survey effort declined to 21 days·year^{-1} in the 1990s and 12 days·year^{-1} in the 2000s, reaching a low of 6 days sampled in 2004, and then increased to 17 days·year^{-1} in the 2010s. Survey coverage in the 1990s and 2000s remained above 40% of total days sampled for all regions within the Sound combined, except in 1995, 1996, 1999, and 2000 (Supplementary Table S1[1]). Kayak Island was not surveyed until 2007, except for one flight in 1982, and has since been sampled every year for 1 to 3 days, except in 2010 and 2016.

Pronounced decadal shifts occurred in the distribution of herring spawning within Prince William Sound. Spawning was primarily concentrated in the Northeast Shore and Montague Island regions in the 1970s — although this pattern may be biased due to unbalanced survey coverage — then expanded to all regions as the total cumulative spawn increased in the 1980s, before contracting towards Southeast Shore as spawning declined sharply in 1990s and remained low throughout the 2010s (Table 2; Fig. 4). Prior to the start of the population's rapid increase in biomass in 1983 (Fig. 1), spawning first expanded along North Shore and Naked Island during the early 1980s (Fig. 5), followed by increases in spawning along Montague Island and Northeast Shore a few years later as the population reached its peak size in 1988. Sharp declines in spawning along North Shore and Naked Island in 1990, and Northeast Shore in 1991, preceded the population's collapse in 1993 (Fig. 1). Following the collapse, spawning effectively ceased along North Shore and Naked Island, with only intermittent spawn events in the 1990s and 2000s, while

Fig. 5. Distribution of spawning from 1973 to 2019 by year. Spawn patterns are represented as (A) quantiles of mile-days of milt (MDM; 1 mile = 1.609 km) by 10 km × 10 km grid cell and year (note, quantiles were calculated across all years), and as (B) cumulative spawn within each region (MI = Montague Island; SE = Southeast Shore; NE = Northeast Shore; NS = North Shore; NI = Naked Island; KI = Kayak Island). Grid cell numbers (1–76) correspond to cell locations identified in Fig. 3. Gray dots indicate the extent of survey coverage (i.e., grid cells with no observed spawning). [Colour online.]

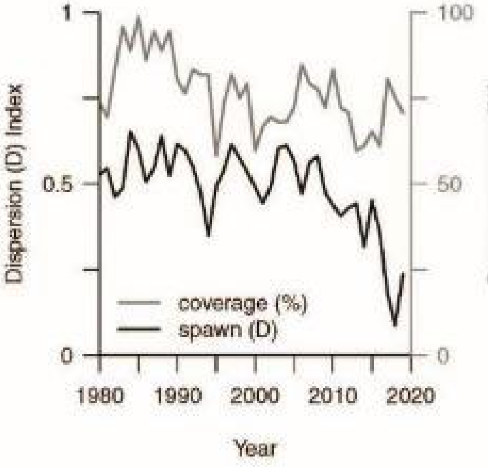


spawning remained low along Northeast Shore through 2010 as spawning within the region contracted southward. Following a brief increase in spawning during 2010–2012, activity along Northeast Shore declined to its lowest levels. Throughout the 1990s, Montague Island usually accounted for at least half of the total spawn, but spawning there steadily declined after 1999 (Fig. 5), and was not observed along Northeast Shore or Montague Island in 2016–2018. In contrast to the other regions within the Sound, spawning along Southeast Shore increased in the mid-1990s (Fig. 5B) and has accounted for the highest annual proportion of total spawn for the past two decades (Table 2).

Initially, herring consistently used at least half of the historical spawning areas throughout Prince William Sound until the 2010s, after which spawning distributions contracted to less than a third of the available areas as spawning biomass continued to decline to its lowest levels. Between 1980 and 2009, the dispersion index averaged 0.54 ± 0.07 (±1 standard deviation, SD), ranging from a peak of 0.65 in 1984 to a low of 0.35 in 1994, and did not differ between periods before and after the population collapse: 0.55 ± 0.06 in 1980–1993 versus 0.54 ± 0.06 in 1995–2009 (Fig. 6). Thus spatial increases in Southeast Shore spawning in the 1990s and 2000s offset declines in other regions (Figs. 4, 5). However, since 2010 dispersion declined sharply to 0.34 ± 0.13 as spawning contracted towards Southeast Shore, reaching an all-time low of 0.09 in 2018 (Fig. 6) that coincided with the most recent decline in spawning biomass (Fig. 1). Survey coverage in the 2010s (70% of all grid cells) was similar to that in 1995–2009 (72%) (Fig. 6). These results suggest that Prince William Sound herring now seldom use the primary spawning areas occupied in the 1980s, and active areas are currently concentrated along the Southeast Shore.

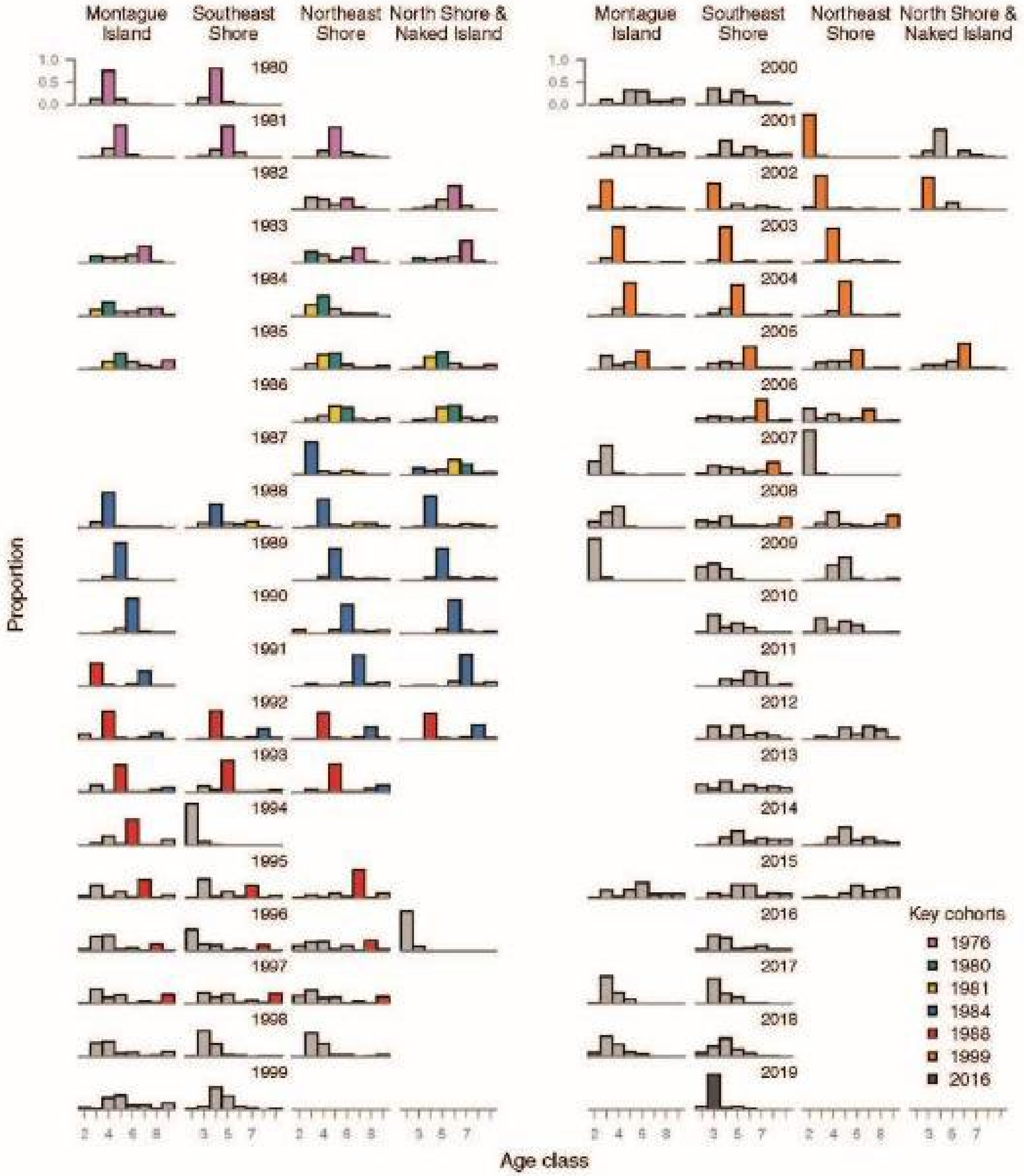
Spatial changes in spawning coincided with the appearance of large year classes. The rapid increase in population size during the 1980s (Fig. 1) was driven by the large 1976, 1980, 1981, and 1984 cohorts (Fig. 7). The total amount of spawn declined rapidly in the early 1990s as these year classes aged out of the population. Prior to their collapse, the 1988 cohort was the last strong year class to recruit to the spawning population.

Fig. 6. Spawning area dispersion index over time. Values of *D* range from 0 (highly aggregated) to 1 (evenly distributed). Survey coverage is represented by the proportion of grid cells sampled each year among the 72 cells in which spawning had occurred since 1980.



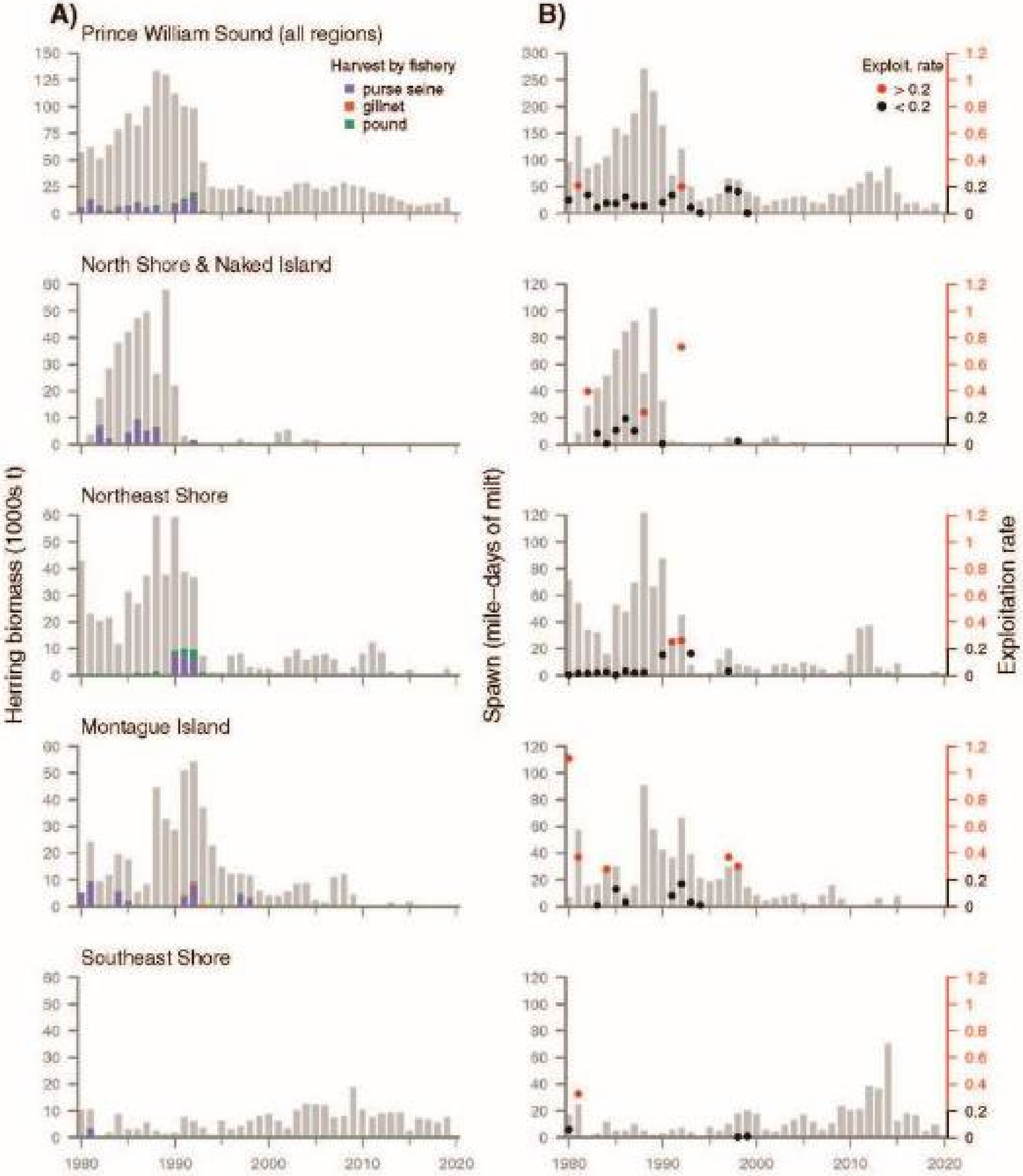
Unlike spatial patterns of spawning, there were minimal spatial differences in the age structure of herring in most years (Fig. 7). The seven largest cohorts typically accounted for a similar proportion of the age composition within each region. During the 40-year study period, regional differences in age structure were only apparent in six years (1987, 1991, 1994, 2001, 2007, and

Fig. 7. Herring age compositions by region and year from 1980 to 2019. Large cohorts (>200 million age-0 recruits) are highlighted in colour by birth year. The absence of a plot indicates no age data were collected from that region and year. [Colour online.]



2008). Among these years, only in 1991 did spatial differences in age structure coincide with notable changes in spawning distributions. Age-3 fish from the 1988 cohort became the dominant year class for spawning aggregations in the Montague Island region in 1991 while the 1984 cohort remained the dominant year class in the North Shore, Naked Island, and Northeast Shore regions. This coincided with sharp declines in spawning from prior years in the northern regions, while total spawn

Fig. 8. Time series of (A) estimated herring spawning stock biomass (t) from 1980 to 2019 within each region (note, the North Shore and Naked Island regions are combined) showing the portion of the biomass estimate that was harvested by purse seine sac-roe, gillnet sac-roe, and pound spawn-on-kelp fisheries from 1980 to 1999. (B) Total survey-observed spawn (mile-days of milt: 1 mile = 1.609 km) and exploitation rate for all fisheries combined within each region (note, data are on separate axes). Harvest levels of less than 500 t are difficult to see in column A, but are included in exploitation rates shown in column B. [Colour online.]



remained relatively stable along Montague Island but proportionally increased from a two-year average of 25% for all regions to 51% (Fig. 8). As the 1988 cohort established itself as the dominant year class across the Sound in the following years (Fig. 7), spawning effectively ceased along North Shore and Naked Island while briefly stabilizing along Northeast Shore before a two-decade period of low spawning activity (Fig. 8). In contrast, spawning along Montague Island fluctuated after the population collapse but remained the most active region through 1998, during which the 1988 cohort remained numerically dominant until 1996. With no strong year classes following the 1988 cohort (Fig. 1), spawning declined to consistently low levels along Montague Island by 2000 while spawning along Southeast Shore increased, largely due to the 1999 cohort.

It is unclear if shifts in spawning distributions followed changes in local exploitation by the fishery. In the 1980s, herring were primarily harvested along North Shore, Naked Island, and Montague Island. Overall exploitation rates for Prince William Sound remained below 0.2 in all years except 1981 (ER = 0.209) and 1992 (ER = 0.201) (Fig. 8), indicating that the intended harvest strategy was followed. While the population was spatially managed as a single stock throughout Prince William Sound, with total allowable catch allocated to multiple fisheries based on gear type and product, harvest was concentrated in only one or two regions each year. Local (region-specific) exploitation rates were greater than 0.2 in 3 of 7 years in North Shore–Naked Island, 2 of 3 years in Northeast Shore, 5 of 8 years in Montague Island, and 1 of 2 years in Southeast Shore (among regions where purse seiners harvested more than 500 t). The probability of changes in spawning was not significantly different under different levels of exploitation in the prior year (χ^2 = 6.81, p value = 0.14; Supplementary Table S2[1]). However, decreases in spawning were more likely to occur following back-to-back years of local exploitation above 0.2 (χ^2 = 12.9, p value = 0.0092; Supplementary Table S3[1]). This result is driven by three instances of back-to-back years with exploitation greater than 0.2 in the Northeast Shore (1991–1992) and Montague Island (1980–1981, 1997–1998) regions that preceded sharp declines in spawning the next year, all of which were followed by extended periods of relatively lower spawning within each region (Fig. 8).

Spawn patterns were not related to the distribution of shoreline impacted by the *Exxon Valdez* oil spill. Immediately following the spill, herring spawned in impacted areas along Naked Island and Montague Island (Supplementary Fig. S3[1]). Prior to the population collapse, sharp declines in spawning primarily occurred in regions that were not oiled (North Shore, Northeast Shore), while spawning fluctuated but remained relatively active near oiled areas along Montague Island throughout most of the 1990s (Figs. 5, 8). The exception was that spawning near oiled areas along Naked Island did decline sharply the year after the spill.

Temporal patterns

There was high interannual and regional variability in herring spawn timing from 1980 to 2019 (Fig. 9). The duration of the spawning season ranged from 4 days (2016) to 59 days (1986), being first observed on dates that spanned from 1 March in 2003 and 26 April in 1982, and last observed on dates ranging from 15 April (2005, 2011) to 21 May (1983, 2007). For all regions combined, the mean date of peak spawning (±1 SD, when 50% of cumulative total spawn was observed) was 17 April (DOY, 107 ± 7.5 days), and was earliest in Southeast Shore (12 April, 101.5 ± 9.1 days), and mostly progressed counter-clockwise from Northeast Shore (16 April, 106.3 ± 8.2 days), to North Shore (21 April, 110.9 ± 10.3 days), Naked Island (24 April, 113.8 ± 8.1 days), and Montague Island (23 April, 113.2 ± 7.7 days).

The two best MARSS models (Z_2 and Z_{13}; Table 3) reveal spatial differences in spawn timing. The Z_2 model suggests separate spawn timing trajectories (i.e., x_t) for the western Shore (Montague Island, Naked Island, and North Shore regions) and the eastern Shore (Southeast Shore, Northeast Shore regions), while the Z_{13} model further subdivided the eastern Shore trajectories by region (Table 3). Both models had correlated process errors with equal variances and estimated a stationary autoregressive process. Diagnostic plots found autocorrelated residuals for all MARSS models in which process errors were independent of other states (with either equal or unique variances) and were therefore rejected. AIC_C values for all random walk models (B fixed at 1) were consistently higher than corresponding models that estimated B (Table 3).

There is greater interannual variation in spawn timing along the western Shore (Z_2:b_{x_1} = 0.25; Z_{13}:b_{x_1} = 0.27) than the eastern Shore (Z_2:b_{x_2} = 0.68; Z_{13}:b_{x_2} = 0.61, b_{x_3} = 0.79) (Table 4). These regional differences in spawn timing trajectories are most apparent between 1980 and 2006 when a shift to earlier spawning occurred at different rates along the eastern and western Shores (Fig. 10). During this 27-year period, spawn timing in the eastern Shore shifted earlier by 26 (Z_2 model) to 30 days (Z_{13} model, Northeast Shore), while spawn timing was more variable in the western Shore and shifted earlier by 15 days in both models. Between 2006 and 2013, both models estimated that spawn timing shifted later by 23–26 days in the eastern Shore and 19 days in the western Shore, returning to the long-term mean spawn time in 2018 (Fig. 10).

The advantage of estimating separate spawn timing states for the eastern and western Shore is apparent when contrasted with the simplest model that estimated one state for all regions (Z_8). The one-state model shows similar shifts in spawn timing in 2006 and 2013, but obscures east-west differences in the rate of change and interannual variability (Fig. 10) and had higher observation variances for all-time series than in the Z_2 and Z_{13} models (Table 4).

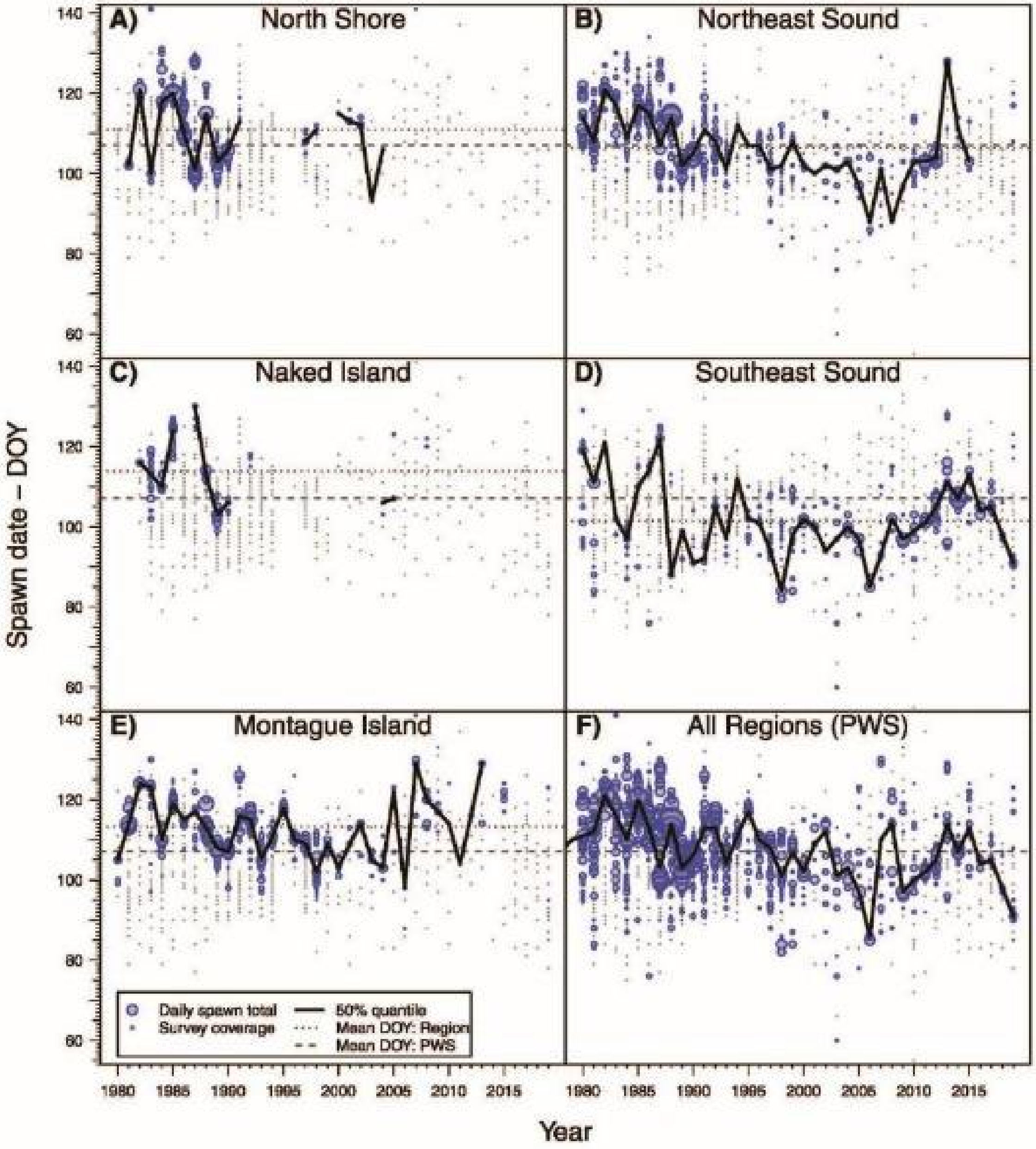
Discussion

Spatial patterns

Herring no longer return to the historical spawning areas in Prince William Sound that were used during a three-decade period when the population reached its peak biomass over the past half century. Between 1973 and 1998, when the population increased from relatively low levels in the 1970s (Funk and Sandone 1990) to peak biomass in the late 1980s before collapsing in the early 1990s (Muradian et al. 2017), nearly all major spawning events occurred along Northeast Shore, North Shore, or Montague Island. After the collapse, contraction of spawning distributions and increased fidelity to general spawning areas would be expected due to relaxation of density-dependent processes as the population declines (Ware et al. 2000); yet spawning did not contract towards regions where spawning was historically high. Instead, spawning shifted towards Southeast Shore, where spawning was low prior to 1998, except briefly in 1979–1981. Despite substantial declines in total spawn, spatial diversity of spawning remained similar 15 years after the collapse compared to the pre-collapse period, as increased activity along Montague Island and later Southeast Shore largely offset decreased spawning in northern regions. This suggests that spatial diversity of spawning areas was not strongly related to spawning biomass at our analysis resolution (100 km^2), consistent with Hay et al.'s (2009) scale-dependent assessment of herring spawning patterns in British Columbia, until the population declined to historic lows (< 10 t) in the 2010s. While decadal patterns of spawning depict this as a gradual change in distributions, abrupt shifts in interannual patterns during the early and late 1990s appear to be largely responsible for the long-term contraction to Southeast Shore.

These and other abrupt shifts in spawning distributions preceded major changes in population size. For example, spawning first expanded into western areas of North Shore and Naked

Fig. 9. Distribution of spawn timing (day-of-year, DOY) from 1980 to 2019 by (A–E) region and (F) for all regions within Prince William Sound (PWS) combined. Daily spawn total is scaled by total mile-days of milt (1 mile = 1.609 km) observed within each region. Each plot shows a time series of the median spawn date, and the mean spawn dates across all years. Survey coverage indicates days in which no spawning was observed within the region during the survey. [Colour online.]



Island the year before the rapid increase in population size began in 1983. Similarly, sharp declines in spawning along North Shore and Northeast Shore occurred two years before the 1993 population collapse and again before more recent abundance declines in the late 1990s and early 2010s along Montague Island. It is possible that these shifts in spawning distributions resulted from increased straying among regions. There is high spatial variability in the rate of fidelity to spawning locations in British Columbia

Table 3. Model performance based on Akaike's information criterion corrected for small sample size (AIC$_c$).

	Spawning area state(s) (x_{1-5})					Q = equal variance and covariance					
						B = 1				B = unique	
	W. PWS			E. PWS		u = zero		u = unique		u = zero	
Num	MI	NS	NI	SE	NE	ΔAIC$_c$	k	ΔAIC$_c$	k	ΔAIC$_c$	k
Z_1	1	1	1	1	1	15.0	7	17.3	8	**11.2**	8
Z_2	1	1	1	2	2	10.6	9	9.1	11	**0.0**	11
Z_3	1	2	1	2	2	16.2	9	14.6	11	8.2	11
Z_4	1	2	2	1	1	18.5	9	17.7	11	11.6	11
Z_5	1	2	2	1	2	19.7	9	24.0	11	17.3	11
Z_6	1	2	1	1	2	19.7	9	22.9	11	15.3	11
Z_7	1	2	2	2	2	18.3	9	17.4	11	10.1	11
Z_8	1	1	1	2	1	19.7	9	20.6	11	9.6	11
Z_9	1	1	1	1	2	17.9	9	20.0	11	9.3	11
Z_{10}	1	2	1	3	2	21.2	10	19.3	13	9.9	13
Z_{11}	1	2	2	1	3	21.6	10	20.3	13	10.0	13
Z_{12}	1	2	2	3	2	22.3	10	21.5	13	—	13
Z_{13}	1	1	1	2	3	16.4	10	14.0	13	**0.9**	13
Z_{14}	1	2	3	4	5	25.4	12	20.5	17	7.0	17

Note: The Z matrix for each spawning area configuration (numbered Z_1 to Z_{14}) indicates corresponding states (x_{1-5}) among the region time series in western or eastern Prince William Sound (W. PWS, E. PWS): MI = Montague Island; NS = North Shore; NI = Naked Island; SE = Southeast Shore; NE = Northeast Shore. Results for three model structures are shown for each Z matrix, including ΔAIC$_c$ values that are relative to the best model (AIC$_c$), and the number of parameters (k). Process errors (Q) were estimated with equal variances that were correlated (equal variance and covariance). The diagonal of the B matrix was set to 1 (i.e., random walk) or estimated for each state (unique). Bias (u) was either set to zero or estimated for each of the random walk models (unique). Bold ΔAIC$_c$ values indicate the three models shown in Fig. 10. A dash (—) indicates a model that did not converge.

Table 4. Parameter estimates (Est) and standard errors (SE) for models in bold in Table 3 identified by their respective Z matrix configuration.

	Model form					
	Z_1		Z_2		Z_{13}	
Coefficient	Est	SE	Est	SE	Est	SE
Observation variance (R)						
r_{MI}	41.72	11.71	28.53	10.12	31.97	10.03
r_{SE}	45.79	12.26	41.55	11.68	38.31	11.9
r_{NE}	36.58	10.49	27.02	8.81	25.51	9.14
r_{NS}	111.36	38.21	79.75	28.42	84.02	29.39
r_{NI}	32.82	16.13	29.55	15.46	30.05	15.14
AR strength (B)						
b_{x_1}	0.59	0.19	0.25	0.24	0.27	0.25
b_{x_2}			0.68	0.12	0.61	0.13
b_{x_3}					0.79	0.09
Process variance–covariance (Q)						
q_{diag}	15.36	7.08	20.88	7.7	18.31	7.38
$c_{offdiag}$			17.99	7.08	17.31	6.5
Estimated state value x_i at time 0						
μ_{x_1}	9.79	9.5	−31.53	42.25	−30.25	40.17
μ_{x_2}			16.59	9.45	28.57	14.13
μ_{x_3}					9.28	7.63

herring within a comparable spatial resolution (statistical areas, ~500–2500 km^2) to regions within Prince William Sound (~700–1900 km^2), and that on average 40% of herring stray to spawn locations in other statistical areas the following year (Hay et al. 2001). Nonetheless, the persistence of spawning within each region in Prince William Sound for periods of a decade or longer, regional differences in spawn timing, and evidence of weak genetic differentiation between herring in the eastern and western Sound (Wildes et al. 2018) suggests that abrupt shifts in spawning within Prince William Sound did not result from random straying.

The occurrence of abrupt shifts in spawning one to two years prior to changes in population size suggests other factors have greater influence on fidelity to general spawning areas in Prince William Sound than spawning biomass. While it is beyond the scope of this study to quantify mechanistic relationships between spawning distributions and explanatory factors, we briefly explore how abrupt shifts in spawning are related to different intrinsic and extrinsic factors to identify potential mechanisms for future studies to investigate. These include: spatial variation in recruitment, effects of social and environmental cues on migration behavior, the 1989 *Exxon Valdez* oil spill, and increased local mortality related to disease, fishing, and predation.

Potential mechanisms for spatial shifts in spawning

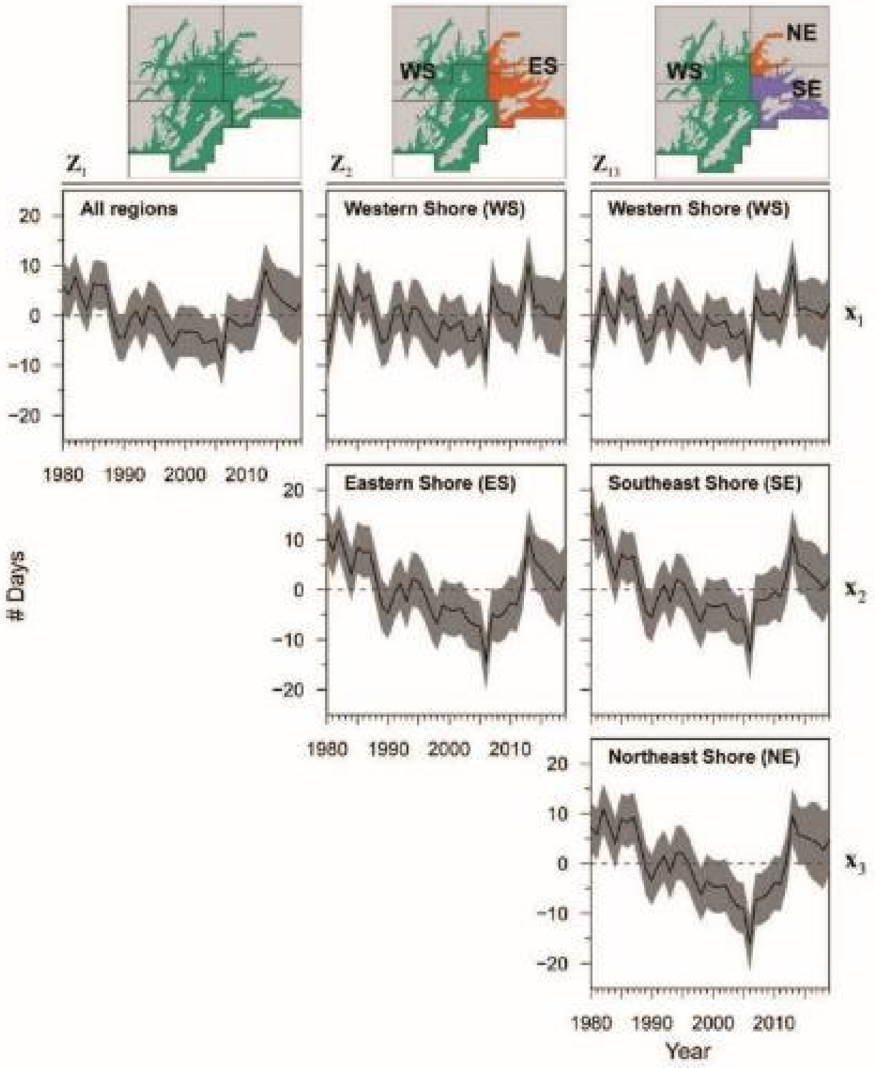
Recruitment

One of the abrupt shifts in spawning distributions coincided with spatial variations in recruitment. In the 1980s, recruits from the three strong cohorts (1980, 1981, and 1984) that were responsible for driving biomass to record highs (Fig. 1) were widely distributed among spawning areas in most regions (Fig. 7), and large spawn events occurred annually in at least three regions (Figs. 5, 8). In contrast, recruits from the last strong cohort (1988) primarily spawned along Montague Island in 1991 as age-3 fish and not in the northern regions where spawning had declined sharply that year or the previous year. Spawning was not observed along North Shore over the next five years, but increased along Montague Island and Northeast Shore where the 1988 cohort became the dominant age class in 1992 as age-4 fish. Regional differences in age structure were not evident during the other major shift in spawning distributions towards Southeast Shore in the late 1990s, nor when recruits from the 1999 and 2016 cohorts first spawned.

Migration behavior

Herring migration behavior is influenced by social and environmental cues (Corten 2002), but the relative importance of

Fig. 10. Estimated time series of spawn timing ($\mathbf{x}_{t}$, solid line) based on MARSS models in bold in Table 3 (shaded area indicates the 95% confidence interval). Time series are centered by their mean for all years (dashed line) to indicate earlier (–) and later (+) median spawn date. Results for each model are shown by column (labels indicate the model's respective **Z** matrix). Rows within columns indicate the different regional groupings with unique spawning area configurations that correspond with shaded areas in map (top row). Maps created using ArcGIS 10.7.1 with data from the Alaska Department of Natural Resources (ADNR 2018). [Colour online.]



such cues is unknown for the Prince William Sound population. Spatial differences in herring recruitment between the 1980s and early 1990s is potentially related to social behavior and availability of older herring with knowledge of migration routes to spawning areas. Herring that spawn for the first time are hypothesized to school with and follow older, experienced fish and spawn in the same locations (McQuinn 1997; Corten 2002; MacCall et al. 2019). Abrupt declines in spawning biomass that coincide with an influx of numerically dominant recruits will reduce spatial overlap between age classes prior to spawning and disrupt the learning process necessary for first-time spawners to return to a general spawning area in successive years (Huse et al. 2002, 2010; Corten 2002). Likewise, the extent of spawning distributions in one year will likely influence spatial variation in recruitment the next year. If first-time spawners are guided by social cues, age composition data would be similar across regions where spawning was active the prior year. In contrast, abrupt shifts in spawning prior to a large influx of recruits that coincides with regional differences in age structure (e.g., 1991) would suggest changes in spawning distributions influenced migration paths of first-time spawners that led to spatial differences in recruitment.

Environmentally driven changes in migration patterns may also have influenced shifts in spawning distributions. A long-term warming trend in Prince William Sound has resulted in spatially complex changes in hydrographic conditions that are most pronounced in the northwest part of the Sound where the effect of glacial meltwater is highest (Campbell 2018). Spawning declines were first evident in northern regions, which have rarely been used by the population since the early 1990s. Changes in hydrographic conditions at spawning locations or along migration paths, including deepening of the seasonal mixed layer, cooling and freshening of surface waters via increased freshwater inputs from melting ice, and warming and increasing salinity of waters at depth (Campbell 2018), could potentially have increased straying to other areas if the population is adapted to select spawning habitat within narrow ranges of temperature and salinity (e.g., Haegele and Schweigert 1985).

Oil spill

It might be expected that herring would avoid spawning near shoreline impacted by the oil spill (Thorne and Thomas 2008). However, as also found by Pearson et al. (2012), sharp declines in spawning after the oil spill occurred primarily in northern regions that were not impacted by oil and cleanup efforts, while immediately after the oil spill, herring spawned within regions directly impacted by the spill and continued to spawn near impacted shoreline along Montague Island (Supplementary Fig. S5[1]). Spawning near oiled areas along Naked Island did decline sharply the year after the spill, but this region contributed relatively little to total spawn prior to the collapse (Fig. 5).

Increased local mortality

Spawning shifts may have also resulted from spatial changes in mortality rates for adult herring linked to disease outbreaks, fishing, and predation. Population-level effects of outbreaks of the protozoan parasite *Ichthyophonus hoferi* and the North American strain of viral hemorrhagic septicemia virus (VHSV) in Prince William Sound have garnered considerable attention since the 1990s, given that high disease-related mortality among adult herring in winter 1992–1993 is hypothesized to be a primary (Rice and Carls 2007; Hulson et al. 2008) or contributing (Deriso et al. 2008; Pearson et al. 2012) factor responsible for the population collapse in 1993, and that recurring outbreaks from multiple pathogens along with poor recruitment are inhibiting population recovery (Rice and Carls 2007; Marty et al. 2010). Despite increasing population-level mortality rates, disease outbreaks have not consistently coincided with declines in total spawn or contracted distributions. Among four disease outbreaks that occurred between 1994 and 2005 (Marty et al. 2010), only the 1998 outbreak coincided with notable shifts in spawning distributions: spawning declined sharply along Northeast Shore in 1998 and Montague Island in 1999, while remaining stable along Southeast Shore until 2001. Increased VHSV prevalence among herring (particularly younger fish) and concentrations of VHSV in water samples were correlated with confinement in closed spawn-on-kelp pounds during the 1998 outbreak (Hershberger et al. 1999), but the study pounds were located in the Southeast region where spawning remained stable for the next several years. It remains unknown if pound fishery operations amplify disease outbreaks among wild herring to effect mortality rates at the region or population level. Localized increases in mortality from disease outbreaks are plausible, particularly if the impacts of a pathogen are age-specific (e.g., Marty et al. 2010). However, we found no evidence of regional differences in age structure during this period (Fig. 7) as would be expected from a local outbreak, and examination of regional differences in disease prevalence was not possible in most years due to data limitations (Rice and Carls 2007).

Changes in predation may also have resulted in increased herring mortality at regional or finer spatial scales, but data were insufficient to examine this relationship. In fall and winter, predation by the increasing humpback whale population is a major source of mortality for overwintering and pre-spawning herring (Pearson et al. 2012; Moran et al. 2018), while adult and juvenile herring are important prey for pinnipeds (Rice et al. 2011), seabirds (Bishop et al. 2015), and groundfish (Gray et al. 2019) in winter. It is unclear how predation on pre-spawning aggregations influenced historical spawning patterns, either by disrupting herring migrations to spawning areas or reduce spawning aggregations, due to data limitations prior to 2008.

In contrast, availability of spatially indexed fishery catch data facilitated assessing whether shifts in spawning were related to local exploitation by fisheries. Annual sound-wide exploitation at the population level was at or below the management target rate of 0.2 in all years, and we found that regional declines in spawning were not related to local exploitation in the prior year (Supplementary Table S2[1]). This is consistent with Hay et al.'s (2008) comprehensive analysis of herring roe fisheries in British Columbia that did not find clear evidence that decreases in spawning frequency or declines in the number of spawning locations were related to fishing. Decreases in spawning within a region were significantly more likely to occur following back-to-back years of local exploitation above 0.2 (Supplementary Table S3[1]), although this is based on only three observations. In British Columbia, high local exploitation contributed to the depletion of herring subpopulations prior to an overall population decline (Okamoto et al. 2020).

Temporal patterns

Trends in spawn timing were also apparent over decadal and interannual scales, along with spatial differences in the magnitude of temporal variation between the eastern and western Sound. During the study period, spawning shifted earlier by 2–4 weeks over two decades, then reverted to later in the season by 3–4 weeks over the next six years, and finally shifted back to earlier dates over the next five years. Spawning patterns for the Sitka Sound herring population in coastal Southeast Alaska (c.f. figure 2 in Hebert 2019) provide context to temporal variation in Prince William Sound spawning. The occurrence of spawn timing shifts in Sitka (1998–1999, 2011–2012, and 2016–2017) do not coincide with major shifts in Prince William Sound (2006–2007, 2013–2014), indicating spawn timing is likely influenced by local factors such as temperature and population demographics (Hay 1985; Ware and Tanasichuk 1989). The magnitude of temporal variation is similar among the populations, suggesting spawn timing may be bounded by processes operating across the Gulf of Alaska that have lagged effects on local conditions near spawning areas.

While the mechanism for the multi-decadal trend towards earlier spawning is unknown, temporal shifts in 2006–2007 and 2013–2014 coincided with transitions between multi-year periods of ocean temperature anomalies in Prince William Sound and the Gulf of Alaska (figure 14 in Campbell 2018). Warm conditions persisted from 2001–2006, cold conditions from 2007–2013, and the Northeast Pacific marine heatwave occurred from 2014–2016 (Bond et al. 2015; Di Lorenzo and Mantua 2016). The coincidence of observed shifts in spawn timing with transitions between warm and cold periods is consistent with expected effects that temperature has on herring gonad maturation rates (Hay 1985; Ware and Tanasichuk 1989).

Demographic changes may also contribute to abrupt shifts in spawn timing trends, similar to how spatial variations in age structure coincided with shifts in spawning distributions in the early 1990s. Age-related differences in spawn timing are well documented from long-term observations for herring populations in British Columbia (Hay 1985) and the Atlantic (Lambert 1987). Similar effects of temperature and demography on spawn timing have been shown for other species, such as walleye pollock (*Gadus chalcogrammus*) in the Gulf of Alaska (Rogers and Dougherty 2019) and capelin (*Mallotus villosus*) in the Northwest Atlantic (Carscadden et al. 1997).

Potential consequences of spawning shifts

Spatial shifts in herring spawning may have contributed to the Prince William Sound population collapse. There is general consensus that high natural mortality in 1992–1993 resulted in the population collapse (Quinn et al. 2001; Deriso et al. 2008; Hulson et al. 2008; Muradian et al. 2017), although an alternate hypothesis suggests a major decline started earlier in 1989 due to the oil spill (Thorne and Thomas 2008). Although the mechanism for the high mortality remains uncertain, poor condition of herring prior to the collapse — likely due to poor nutrition resulting from environmentally driven low prey supply while biomass levels remained high (Pearson et al. 1999, 2012) — may have increased their susceptibility to multiple pathogens that triggered an outbreak (Rice and Carls 2007; Hulson et al. 2008). Rice and Carls (2007) hypothesized that declines in spawning starting in 1990 — due to the sharp decline along the North Shore and Naked Island (Figs. 5, 8) — concentrated spawning aggregations while biomass levels remained high, and that increases in crowding among spawning aggregations while in poor condition may have increased disease transmission (Marty et al. 2003).

The combined effects of low total spawn, reduced diversity of spawning areas, and concentration of spawning along the Southeast Shore may also be inhibiting first-year survival and contributing to the persistence of poor recruitment. Declines in total spawn and spatial diversity of spawning areas have impacted the population's spawning portfolio (i.e., the spatial and temporal diversity of spawning, Schindler et al. 2010), reducing opportunities for offspring to be dispersed to nursery areas that facilitate high first-year survival (Norcross and Brown 2001; Pineda et al. 2007; Rice and Carls 2007). The impacts of a reduced spawning portfolio may be amplified by the contraction of spawning to the Southeast Shore region rather than to other historical spawning areas. Herring larvae spawned along the Southeast Shore are more frequently retained in local nursery areas compared to larvae spawned in other regions that are widely dispersed to all areas of the Sound (Norcross and Brown 2001; Pegau 2013). Limiting larval dispersal to a fraction of available nursery areas reduces the likelihood that offspring are retained in nursery habitat whose suitability may vary from year-to-year. Prey quality and survival rates of juvenile herring during their first winter are also relatively lower in the Southeast Shore region compared to the other regions (Norcross and Brown 2001; Gorman et al. 2018).

Reproductive timing also plays an important role in determining recruitment success by influencing the coincidence of larvae with prey during critical periods (Cushing 1990), but it is uncertain whether shifts in spawn timing are linked to first-year herring survival in Prince William Sound. Variation in spawn timing may compensate for reduced spatial elements of the spawning portfolio, but these dynamics are poorly understood for this herring population. Future work is needed to quantify connectivity between known spawn locations and nursery areas under different oceanographic conditions throughout the spawning season, and to examine how temporal shifts in spawning correspond with variations in timing, magnitude, and duration of the spring bloom that affect prey quality and availability to larval herring. An improved understanding of how spatiotemporal variation in spawning and correspondence with secondary production influences larval dispersal and first-year survival would facilitate incorporating the effects of spawning dynamics on recruitment estimates.

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