Exxon Valdez Oil Spill
Herring Research and Monitoring Program Final Report

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Exxon Valdez Oil Spill Trustee Council Project 21120111
Final Report

W. Scott Pegau
Prince William Sound Science Center
Box 705
Cordova, Alaska 99574

With contributions from: Trevor Branch, Mary Anne Bishop, Alysha Cypher, Beatriz dos Santos Dias, Elaine Gallenberg, Tony Gill, Kristen Gorman, Maya Groner, Stormy Haught, Paul Hershberger, Hayley Hoover, David McGowan, Jennifer Morella, Peter Rand, Kaho Tisthammer, John Trochta, Andrew Whitehead, and Joshua Zahner

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Study History: This work encompasses the projects within the Herring Research and Monitoring program (21120111-A, C, E,G, 21160111-F, 21170111-B and 21170115) and builds on the work completed in the previous Herring Research and Monitoring program (16120111), the Prince William Sound Herring Survey program (10100132), and projects within the Sound Ecosystem Assessment program. The program coordinates with the Gulf Watch Alaska Long-Term Monitoring program (21120114) to better understand the conditions affecting survival and condition of Pacific herring. One product of this project is the synthesis submitted to the *Exxon Valdez* Oil Spill Trustee Council titled, Herring Research and Monitoring Synthesis Report (Pegau and Aderhold 2019). This report draws on the program's annual reports submitted for fiscal years 2017-2020 and final reports from projects (21120111-A, C, E, G, 21160111-F, 21170111-B and 21170115).

Abstract: This report contains a description of the activities that took place in the Herring Research and Monitoring Program between fiscal years 2017 and 2021. The program was made up of seven projects designed to address the goal of improving predictive models of Pacific herring (*Clupea pallasii*) stocks through research and monitoring. The project examining the genetics of herring was later added to the program. The program was made up of a mix of monitoring projects (fish condition, aerial surveys, disease surveys, and acoustic surveys) designed to provide inputs to the predictive model, and process studies (disease, movement, and genetics) that help scientists understand aspects of the herring life history. An age-structure-analysis model is used to estimate population levels and examine factors influencing recruitment and mortality. This report provides highlights from the various projects and a reader should expect to find more detail in the individual reports. The report focuses on how each of the projects contributed to the overall programmatic objectives.

Key words: *Clupea pallasii*, disease, genetics, movement, Pacific herring, Prince William Sound, surveys.

Project Data: References and links to data collected within this program are provided in the individual project reports.

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.

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TABLE OF CONTENTS

LIST OF FIGURES

EXECUTIVE SUMMARY

Pacific herring (*Clupea pallasii*) are an ecologically, commercially, and culturally important forage fish in Prince William Sound (PWS). The herring population collapsed after the *Exxon Valdez* oil spill and is listed by the *Exxon Valdez* Oil Spill Trustee Council (EVOSTC) as an unrecovered resource. This has led EVOSTC to invest heavily in studies of the Pacific herring to understand the collapse and later the lack of recovery. Beginning in 2009 the research was gathered into a single integrated program which later became the Herring Research and Monitoring (HRM) program. Except for a brief period in the late 1990s, the population has remained at or below the fisheries threshold. In recent years there was a further decline in the population until it reached a low point in 2018. A Gulf of Alaska wide large herring recruitment event occurred when the 2016 year class began to recruit to the spawning biomass. This single large year class has led to the recovery of the PWS herring to the level seen earlier in the 2000s. However, the annual biomass of PWS herring is still at or below the fishery threshold level.

The overall goal of the HRM program is to: **Improve predictive models of herring stocks through observations and research**. The program objectives are as follows:

Objective 1: Expand and test the herring stock assessment model used in Prince William Sound.

Objective 2: Provide inputs to the stock assessment model.

Objective 3: Examine the connection between herring condition or recruitment to physical and biological oceanographic factors.

Objective 4: Develop new approaches to monitoring.

A total of eight individual projects made up the HRM program that was designed to address these objectives using modeling, monitoring, and process studies that were coordinated to build on each other. The modeling project used a Bayesian age-structure-analysis (ASA) model to estimate the population and examine environmental covariates. It also evolved as new information became available to fulfil the program's first objective. The second objective was addressed by using the monitoring projects. These included: continuation of age-sex-length collections, mile-days-milt surveys, acoustic biomass surveys, and disease prevalence and antibody activity collections. Outside funding was used to conduct aerial forage fish surveys that provided an index of age-1 herring abundances that was also incorporated into the model.

The modeling project was also used to address the third objective along with projects examining disease dynamics, genetics, and movement. The modeling project examined environmental covariates to see if they could improve the model mortality or recruitment estimates. Further work was conducted to examine how spawn timing and location has shifted and the conditions that may help explain those changes. We also looked at other herring populations around the

world to determine if the collapse and lack of recovery in PWS is unusual. Research was conducted on how water temperature plays a role in the shedding of viruses and how oil affects the susceptibility to disease. The genetics project sequenced the whole genome of herring from different populations in the Pacific through time to examine the relationship between herring populations and looked for evidence of changes that may have occurred through time and the changes associated with the exposure to oil and diseases. We tagged several hundred herring over a few years using acoustic tags. Receiver arrays at the entrances to PWS along with ones around the spawning grounds were used to detect the fish as they moved around PWS. This information was then combined with information about the fish in a model to examine the conditions that made a fish more likely to migrate out of PWS or return earlier to the spawning grounds.

The disease, genetics, movement, maturity, and coordination projects all contributed to addressing the final objective. A novel antibody activity methodology was developed and tested that provides information about the exposure to a major herring virus. The whole-genome genetics provided much greater detail about herring and how they physiologically change with exposure to various stressors. The movement project demonstrated the ability to tag and track herring by using both moored receiver arrays and receivers mounted on gliders. The maturity project examined the potential of using scale growth to determine if a fish had spawn in a given year to validate the maturity function estimated by the ASA model. The coordination project also contributed to examining methodologies for detecting spawning events that may be missed using the normal survey techniques. These included remote cameras, crowd sourcing, and high-resolution satellite imagery.

An underlying objective of the HRM program has been to share information on the program's observations and findings and to gather information from various sources to help guide our efforts. Sharing of information was accomplished through a Facebook page, short articles in the Delta Sound Connections publication, various scientific and public presentations on our efforts, scientific manuscripts, reports to Alaska Department of Fish and Game, and the National Oceanic and Atmospheric Administration's ecosystem status report. A synthesis of research findings was provided to the EVOSTC. This synthesis built upon earlier syntheses of EVOSTC funded work.

We found that it was possible to expand the ASA model using the new disease information and the aerial surveys of juvenile herring to better predict mortality and recruitment. While at first glance the objective to maintain the time series used by the ASA model may seem simple, the outbreak of the COVID-19 pandemic threatened the collection of all samples. It was through working with local fishermen, cross-training personnel, and the value of being in an isolated community that we were able to ensure all of the necessary samples were collected. This was a major feat of coordination and community involvement that demonstrated the importance of the program to the local community. Maintaining the time series allowed us to observe how the weight and length of herring changed after an unusual warming event in the Gulf of Alaska and subsequent recovery, and how the herring population was able to rebuild after reaching its minimum in 2018. We found a spike in the presence of viral hemorrhagic septicemia virus (VHSV) antibodies in 2015 and that the levels dropped to very low numbers once the 2016 year class recruited to the spawning stock. Acoustic biomass surveys also indicated a rapid decline in the herring population by 2016. Aerial surveys of juvenile herring indicated the strength of the 2016 year class before it recruited to the spawning stock.

We examined many environmental conditions from oceanographic indices to whale numbers and found that only adult pink salmon returns were able to provide improvements in the models estimates of mortality and recruitment. That relationship is weak but significant. We also showed that different metrics of the strength of relationship led to different interpretations of the results. Lower temperatures were found to increase the length of time that the VHSV was shed and therefore increased the potential spread of the disease. We were not able to identify the means of spread of *Ichthyophonus* but have found promising new leads to test. Modeling of disease dynamics is an important step towards fully incorporating the new disease information in the ASA model. The tagging work showed that there were preferred migration routes out and into PWS and that larger fish were more likely to migrate than smaller fish. Smaller fish were more likely to return near to the spawning grounds in the fall than larger herring. We were surprised to find that in some instances herring larvae exposed to oil were less susceptible to VHSV.

The disease, genetics, tagging, and maturity work also involved the development of new methodologies to succeed, addressing our fourth objective. Our studies showed that the VHSV antibody activity remained detectable for at least three years after exposure to the disease and provides a good measure of previous exposure and the susceptibility of a population to a disease outbreak. Genetics provided insights on population dynamics over time. We were able to use both moored and glider-mounted acoustic receivers to locate tagged fish. We determined that we could not detect changes in maturity associated with changes in scale growth. We also examined different means of detecting spawn and found that the high-resolution satellite imagery can provide a useful tool to detect spawn outside the flight path of the normal surveys when the skies are clear.

The program was able to meet its objectives even with the restrictions that came about from the COVID-19 pandemic. We continue to examine the factors that may be preventing the herring population from recovering to the levels observed in the 1980s. The decrease in the population beginning around 2015 and subsequent recovery associated with the recruitment of the 2016 year class are providing opportunities to test ideas associated with enhanced recruitment events. These large recruitment events appear to be large-scaled with enhanced recruitment observed throughout the Gulf of Alaska.

We continue to believe that PWS herring provides the very best opportunity possible to tease out key factors in predicting changes in recruitment, natural mortality, and spawn timing. Few regions, if any, in the world contain such a rich dataset of biological, oceanographic, and climate indexes that has been maintained for such a long period of time. If fisheries science ever solves these problems, it will be because of the data collected by the HRM and Gulf Watch Alaska programs.

INTRODUCTION

Pacific herring (*Clupea pallasii*), hereafter 'herring', are an ecologically important forage fish and historically have been an economically and socially important fishery in Prince William Sound (PWS). The Pacific herring population in PWS declined from a peak population of approximately 133 thousand metric tons in 1988 to 30 thousand metric tons by 1993. The recovery of the herring population has been the focus of many projects and programs funded by the *Exxon Valdez* Oil Spill Trustee Council (EVOSTC). This has led to several syntheses of information about Pacific herring in PWS (Norcross et al. 2001, Spies 2007, Rice and Carls 2007, Pegau 2013, Herring Research and Monitoring Team 2014, Pegau and Aderhold 2019), many contributions to herring related symposia (e.g., Funk et al. 2001), as well as many research publications.

The PWS herring population remained high for a few years after the 1989 *Exxon Valdez* oil spill but collapsed by 1993 (Fig. 1). Except for two seasons in the late 1990s, the commercial herring fishery has been closed since 1993. A further decline in the population was observed beginning in 2015. Fluctuations in the herring population are expected with or without a herring fishery. What is not expected is the prolonged state of depressed herring stocks in the absence of an active fishery (Trochta et al. 2020). Other factors are thought to be playing a role in keeping the stock depressed including changes in oceanic conditions, predation, salmon hatcheries, and disease (Deriso et al. 2008, Pearson et al. 2012, Trochta and Branch 2021).

The failure of PWS herring to recover is defined by factors that suppress spawning stock biomass and other factors that prevent recruitment events. The factors that prevent an increase in biomass can be different from those that prevent recruitment. For example, predation by whales may reduce herring biomass, but may not be as important in limiting recruitment. Historically, reduced herring stocks associated with earlier fisheries recovered as the result of large recruitment events. However, it is clear that in PWS there has been a long gap in large recruit classes (Fig. 2). While the recruitment in 2019 is not similar to the levels observed in the 1980s, it was from a very small spawning population, so the number of recruits per spawner is the highest on record (Fig. 3). The low recruitment levels have led to a series of studies that examine the early life stage of the Pacific herring. Ward et al. (2017) found a correlation between recruitment and freshwater discharge, but the spawner-recruit relationship remains fairly high so physical conditions does not appear to have limited recruitment since the 1990s.

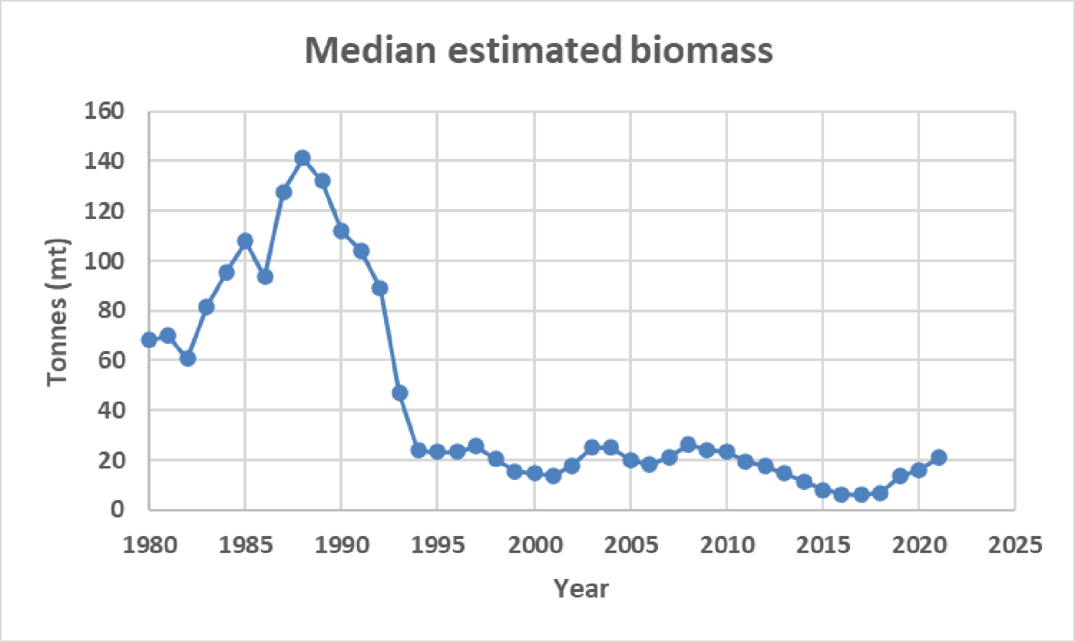

Figure 1. Prince William Sound estimated pre-fishery run biomass from the 2021 age-structured-analysis model run.

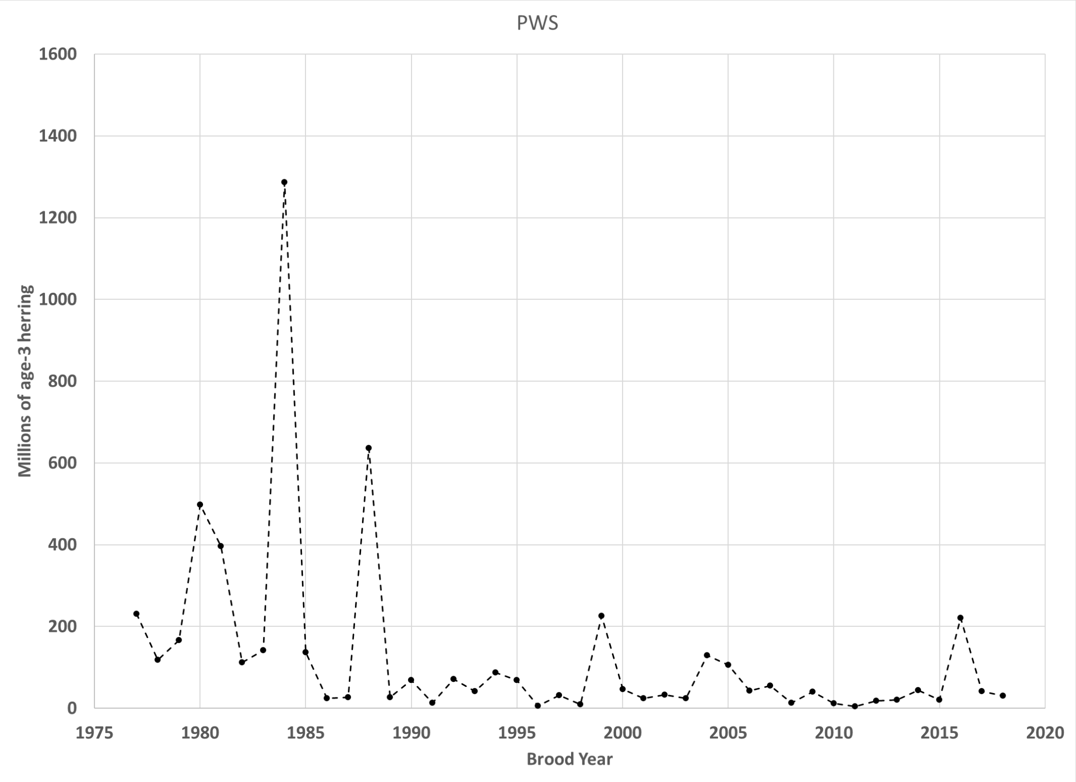

Figure 2. Median estimated number of age-3 fish recruiting to the Prince William Sound spawning stock by brood year based on the 2021 age-structured-analysis model run.

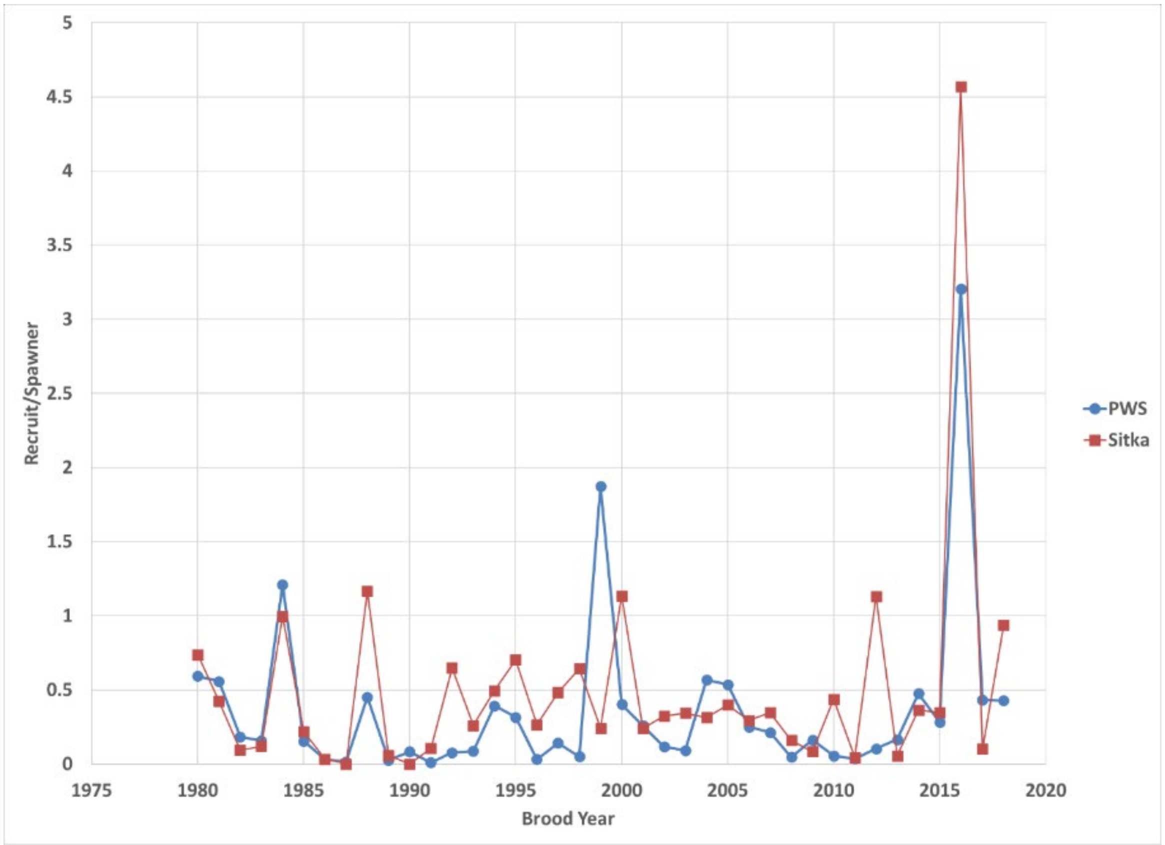

Figure 3. Estimated number of age-3 recruits per number of spawning fish for each brood year based on the 2021 age-structured-analysis model run. Prince William Sound is in blue circles and Sitka in red squares is provided as a comparison.

The Herring Research and Monitoring (HRM) program began in 2012 and was designed to build upon the earlier work completed in the Prince William Herring Survey and Sound Ecosystem Assessment programs. The work was coordinated with the Gulf Watch Alaska (GWA) program that monitors ecological conditions in PWS and other *Exxon Valdez* oil spill affected waters. The HRM program focused on herring in PWS but uses data from other areas to put the PWS findings in context.

OBJECTIVES

This project addresses the Herring Research and Monitoring component of the FY17-21 Invitation for Proposals. The overall goal of the HRM program is to: **Improve predictive**

models of herring stocks through observations and research. The program objectives are as follows:

Objective 1: Expand and test the herring stock assessment model used in Prince William Sound.

Objective 2: Provide inputs to the stock assessment model.

Objective 3: Examine the connection between herring condition or recruitment to physical and biological oceanographic factors.

Objective 4: Develop new approaches to monitoring.

METHODS

The HRM program focused on issues related to herring in PWS. Data from other regions was used to inform the analysis of the results.

Our approach used an integrated set of studies that included modeling, monitoring projects, field-based process studies, and controlled laboratory-based studies. When combined, this approach informs the herring monitoring and modeling efforts by focusing on important population-limiting factors and providing data for the current ASA population model. Aspects of the work are informed by projects within the GWA program, such as monitoring of basic oceanographic conditions, food availability, and predator populations.

The structure of the report is based on the objectives. Many projects addressed multiple objectives and the information from those projects are broken up based on the objective.

Objective 1: Expand and test the herring stock assessment model used in Prince William Sound.

The activities associated with this objective are primarily associated with the modeling work led by Dr. Branch (21120111-C). This project uses a Bayesian formulation of the age structured assessment (BASA) model that builds upon the ASA model run by the Alaska Department of Fish and Game (ADF&G) in the past. The Bayesian formulation naturally weights the input data sources, and better characterizes uncertainty through estimating Bayesian posteriors (Muradian et al. 2017). In addition, the assessment model was used to determine which historical data sets were the most informative given the trade-off between information gain and cost (Muradian et al. 2019).

The BASA model continued to evolve since it was published. The BASA model now also fits to aerial surveys of age-1 school sizes and runs with a state-of-the-art, vastly more efficient estimation algorithm called the No-U-Turn-Sampler (NUTS), which was programmed into AD Model Builder by Cole Monnahan as part of additional efforts in the Branch lab to improve stock assessment methods (Monnahan et al. 2017, Monnahan and Kristensen 2018, Monnahan et al.

2019). This allows a much broader array of sensitivity tests to be run on the model in a Bayesian context and facilitates rapid evaluation of alternative models. A sensitivity analysis was conducted on the maturity schedule incorporated into the model.

One area of improvement for the BASA model is the incorporation of disease information. There is the potential to use novel antibody detection data collected by the disease project (Hershberger, 21120111-E) to better inform the mortality associated with Viral Hemorrhagic Septicemia Virus (VHSV) outbreaks. We conducted a simulation analysis to test the accuracy and precision of estimates of annual infection rates and disease mortality from simulated antibody data (Trochta 2021). The analysis included a model of the truth that simulated more realistic disease dynamics by combining an epidemiological and an age-structured population model; and an estimation model simplified from BASA that takes antibody data as input and estimates time-and-age varying mortality due to disease. This simulation assisted in the incorporation of VHSV antibody data into the BASA model. Age-specific antibody data from 2012-2020 from project 20120111-E were input into BASA. Using the equations from our simulation study, we estimated population-level infection, mortality, and immunity from VHSV. There remain questions regarding how to best interpret aspects of the antibody data, so their incorporation into the model has not been finalized.

Objective 2: Provide inputs to the stock assessment model.
This objective was addressed through the monitoring projects of the HRM program.

Monitoring components are designed to address objective 2 by providing data used within the ASA model to estimate the PWS herring population or collecting information we believe will allow for advances in the ASA model. Below is a brief description of the methods used by the monitoring projects. Individual project reports provide more information about the methods and results. The methods are also discussed in greater detail in chapter one of Pegau and Aderhold (2019). The project number and principal investigator for each project are provided in the description of their methods.

Age-Sex-Length study and aerial milt surveys (21160111-F, Morella): This project continued the time series on herring condition and spawning activities that the longest datasets used by the ASA model. Fish are collected prior to and during spawning events and the age, sex, length, weight, and gonad maturity. These fish collections are referred to as ASL samples. Samples are stratified by area, time, and gear. Sample sizes (n=450) are set to estimate the age composition of each sample to within ±5% of the true proportion 90% of the time assuming no more than 10% of the scales are unreadable. Herring are 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. The age is determined by reading the growth annuli on a scale collected from the fish. The data are used by the ASA model and research examining how the condition of herring changes through time.

The project also flies the coastline of PWS to record the length of coast with herring milt observed. The flights also record information on major predators, such as whales and sea lions. The milt is classified by whether it is active, drifting, or dissipating along with a metric of how intense the spawn is based on the color of the water. The start and end points are recorded in an electronic tablet for determination of the miles of milt observed each survey. Surveys begin prior to the expected spawn to record any herring schools or marine mammal activity that may indicate that spawn will begin soon. The surveys continue throughout the spawning season. The number of miles of active spawn are summed up to provide an annual estimate of mile-days-milt.

Disease in the adult population (21120111-E, Hershberger): Disease prevalence is included in the PWS ASA model. Three or more samples of 60 adult herring were collected during the ASL sample events. These samples were processed to determine the prevalence of Viral Hemorrhagic Septicemia (VHS), Viral Erythrocytic Necrosis (VEN), and Ichthyophoniasis. Diagnostic techniques for these pathogens followed standard procedures. Beside tracking the prevalence of VHS, the blood plasma is analyzed for the presence of antibodies that indicate that the herring have been exposed to the VHS virus (seropositive). The antibody information provides a better indication of the exposure history than is available from prevalence measurements. Up to an additional 300 herring were sampled to provide better identify how the disease prevalence or seropositive data is related to the age of the herring.

Acoustic biomass surveys (21120111-G, Rand): The Prince William Sound Science Center (PWSSC) conducted acoustic biomass surveys in the region of the main spawning stock and surveyed fish found along Montague Island. The presence of whales and other predators were used to help identify areas with herring and daytime transects were used to confirm the presence of herring schools. Surveys were then conducted at night when the herring were higher in the water column. To collect acoustic data, a BioSonics 120 kHz digital single-beam transducer was mounted down-looking on a towfin and a zig-zag path was taken to cover aggregations of fish. Whenever possible the populations were surveyed multiple times to provide an error bound on the estimated biomass.

Juvenile index aerial surveys (Pegau): These surveys were supported by the Prince William Sound Regional Citizens' Advisory Council but the results are incorporated into the ASA model so we provide information on them in this report. The entire coastline is flown at 1000 feet in June each year and the fish species, school size, and number of forage fish schools were logged. The observed forage fish are dominated by herring and sand lance. The herring are aged to age-1 or age-2+. The number of age-1 schools, weighted by the school size, is then used as an index of juvenile herring, which is incorporated into the ASA model to provide an estimate of potential new recruitment into the spawning stock.

Objective 3: Examine the connection between herring condition or recruitment to physical and biological oceanographic factors.

Several studies contributed to our efforts to meet this objective.

Modeling and stock assessment of Prince William Sound herring (21120111-C, Branch): Work began with a global herring meta-analysis (Trochta et al. 2020) that examined the collapse and recovery from 64 herring populations. This analysis was done to determine if the collapse and recovery exhibited in PWS herring is unusual.

The BASA model was used to conduct an in-depth analysis of the potential effects of ecological factors on PWS herring recruitment and mortality (Trochta and Branch 2021). The Pareto-smoothed importance-sampled leave-one-out cross-validation (PSIS-LOO) was used as different environmental variables were incorporated as covariates in the mortality and recruitment portions of the model. Covariates included: VHSV and Ichthyophonus prevalence, summer upwelling, North Pacific Gyre Oscillation (NPGO), Pacific Decadal Oscillation (PDO), pink salmon (*Oncorhynchus gorbuscha*) returns, hatchery pink salmon releases, Gulf of Alaska arrowtooth flounder spawning biomass, walleye pollock (*Gadus chalcogrammus*) spawning biomass, number of age-1 pollock, humpback whales (*Megaptera novaeangliae*), freshwater discharge, first-year scale growth increment, and the 1989 regime shift. These were compared to a null model in which none of the covariates were incorporated. Two general approaches were used to evaluate support for each covariate, computing posterior probabilities of estimated effects and Bayesian model selection. For Bayesian model selection, the Deviance Information Criterion (DIC), Watanabe Akaike Information Criterion (WAIC), Posterior Predictive Loss (PPL), and Pareto-smoothed importance-sampled leave-one-out cross-validation scores PSIS-LOO criteria were examined.

An analysis of the spawning patterns in PWS was conducted (McGowan et al. 2021) to examine changes in spawn distribution and timing. The mile-days-milt data from the herring spawn surveys (project 21160111-F) from 1973 to 2019 were examined. Survey coverage and spawning data were divided into 10x10 kilometer grid cells. Grid cells were assigned a binary value based on the presence of spawn within the cell. The spatial patterns of spawn were characterized at interannual and decadal scales. The spawning population age structure, commercial catch, and shoreline oiled by the *Exxon Valdez* oil spill data were examined within each region through time as potential covariates with changes in distribution. A multivariate, autoregressive, state-space (MARRS) model was used to examine changes in the spawn timing.

The analysis of spawn distribution and timing was followed by an analysis of population, environmental, and climatological factors that may be associated with the changes (Dias et al. 2022). A variety of potential drivers of these timing shifts were examined including:
1) population factors—aerial survey biomass index (mile-days of milt), mean age, and condition factor; 2) environmental variables—satellite derived PWS March and April sea surface temperature, PWS modeled freshwater input, winter, fall and spring downwelling index, winter and fall meridional and zonal winds, and Gulf of Alaska fall, spring and winter sea surface temperature; and 3) climatological variables—multivariate El Niño Southern Oscillation (ENSO) index, PDO, Pacific/North American teleconnection pattern (PNA), NPGO. Included in the covariates was an analysis to identify regime shifts in spawning biomass and surplus production

in herring, using the sequential t-test analysis of regime shift (STARS) approach (e.g., Rodionov 2004, Vert-pre et al. 2013).

Disease in the adult population (21120111-E, Hershberger): Research included an examination of herring in PWS to determine the potential source of the VHS virus in the region. Herring recovering from VHSV were examined to determine if they continued to shed the virus and how any shedding might be related to water temperatures.

The source of *Ichthyophonus* in herring remains unknown. Several potential routes of transmission were examined in the laboratory. Captive reared Specific Pathogen Free (SPF) sentinel herring (age 1+) were cohabitated with *Ichthyophonus*-infected donor herring under four simulated environmental conditions: 1) ambient seawater, 2) ambient seawater with low salinity events, 3) chilled seawater, and 4) chilled seawater with low salinity events. To examine if an intermediate host existed in the prey items of herring, ethanol-preserved zooplankton from PWS (22120144-G, Campbell) were screened for *Ichthyophonus* by qPCR using specific primers. Additionally, herring and pollock eggs were examined to determine if they carried the *Ichthyophonus* parasite fed to herring in the lab to determine if they could transmit the disease. Furthermore, a time series of herring collected in the Cordova harbor were examined for temporal changes in *Ichthyophonus* prevalence that may help indicate an exposure route.

Laboratory exposure of herring to two additional diseases (*Vibrio anguillarum* and *Vibrio ordalii*) were conducted to determine if these diseases may also be important in the herring population.

Annual herring migration cycle (21160111-B, Bishop): We captured and acoustic-tagged adult Pacific herring in PWS while in prespawning aggregations during April over a period of four years, 2017-2020. All captures and tagging took place at the southeast PWS spawning grounds, except for 2019 when a small number of fish were tagged at northern Montague Island. Details describing herring capture, handling, and tagging methods are fully described in (Eiler and Bishop 2016). Briefly, fish were captured using barbed fishing jigs and then placed in a holding tank (770 L capacity). Individual fish were then transferred to a circular tub and anesthetized, weighed, measured (standard length) and placed in a tagging cradle. We made a small incision along the ventral midline to determine sex and to surgically implant an acoustic transmitter. Post-surgery, both tagged and untagged (i.e., not sedated, measured, or tagged) herring from the capture event were held together in a tank to ascertain when tagged herring had recovered from sedation and exhibited normal swimming and schooling behavior. Tagged and untagged herring were released together near a herring school. All capture procedures and protocols were approved by the PWSSC Institutional Animal Care and Use Committee.

We implanted into herring either a V9 or V8 transmitter (Models V9-2x, V9-2x-BLU-1, or V8-4x, 69 kHz; Innovasea, Halifax, Nova Scotia, Canada). A series of receivers (Models VR2W, VR2AR, and VR3; Vemco, Halifax, Nova Scotia, Canada) were deployed in the southeast PWS spawning grounds to monitor the movements of acoustic-tagged herring. Depending on the year and season, from 8 April 2017 through 9 May 2022, a total of 6 to 10 receivers were deployed in six arrays within PWS. One array (Port Gravina) was deployed throughout the duration of the study. Four arrays (Cedar, Canoe Pass, Redhead 1, and Redhead 2) were initially deployed mid-September 2018, while the Johnstone Point array was deployed September 2019. While most array receivers were deployed within 2 km of the shoreline (min = 368 m), Redhead 1 and Redhead 2 in Orca Bay were 7.3 km and 3.8 km from shore, respectively. Receiver data were downloaded 1-2 times a year through 9 May 2022.

We examined post-spawning movements for all four tag years (2017-2020), including detections at entrance arrays from April 2017 through June 2021. Logistic regressions were used to examine the variables (weight, length, condition, sex, age, and tag year) associated with the fish movement. Additionally, this information was examined to determine relationships with residency time in the Gulf of Alaska, seasonal mortality, and spawning site fidelity using a multistate mark-recapture framework and logistic regression.

Genomic mechanisms for lack of recovery (21170115, Whitehead): Exposure experiments were used to examine how exposure to oil and disease factors influenced survival and genetics. Fish from multiple populations were used, so that we could test for evolved differences in Pacific herring sensitivity to oil and virus exposures. We included fish from PWS, Sitka Sound, and Puget Sound. We exposed embryos to a range of very low concentrations of oil. These exposures captured the range of concentrations that Pacific herring were exposed to in PWS in 1989 and 1990 spawning seasons. We tested whether this range of concentrations impacted fish development, with particular focus on the heart, cardiovascular system, and immune system. We collected gene expression data to offer deep insight into the molecular and cellular process that are affected by these exposures. After exposure during embryo development, we transferred these fish to clean water and raised them for many months until they had matured to juvenile stage, at which time their immune system is fully developed. We then challenged fish with virus. We compared virus sensitivity responses (mortality) between fish that had been exposed to oil when they were embryos to those that had not been exposed to oil. This was to test whether exposure to oil during a brief period of very early development impaired the later-life function of the immune system. Since much of the immune system matures after fish have hatched, we also performed oil exposures on larval fish to test for impacts on immune development and function. We repeated all of these experiments in fish from two additional populations – Sitka Sound and Puget Sound. Comparisons between populations allowed us to test hypotheses about how different ecological, environmental, and evolutionary processes have shaped Pacific herring sensitivity to oil and viral infections.

Objective 4: Develop new approaches to monitoring.

Constant refinements are undertaken to improve our understanding and monitoring of herring in PWS. Again, several projects included efforts to address this objective.

Disease in the adult population (21120111-E, Hershberger): Methods for a plaque neutralization test (PNT) were optimized for the detection and quantification of VHSV neutralizing activity in the plasma of Pacific herring. The PNT was complement-dependent, as neutralizing activity was attenuated by heat inactivation; further, neutralizing activity was restored and enhanced by the addition of exogenous complement from specific pathogen-free Pacific herring. Optimal methods included the overnight incubation of VHSV aliquots in serial dilutions (starting at 1:16) of whole test plasma containing endogenous complement. The resulting viral titers were then enumerated using a viral plaque assay in 96 well micro plates. The end result is the seropositive data provided that indicates prior VHSV exposure.

After optimizing the antibody assay and demonstrating its ability to detect antibodies for extended periods post-exposure in the laboratory, the next step was to demonstrate the usefulness of the assay in wild herring by determining whether the assay correctly identified their deduced prior exposure histories. Exposure histories were deduced using a unique principle involving VHS and Pacific herring, whereby wild herring confined into net pens or laboratory tanks often (but not always) experience VHS epizootics. It can be deduced that any group of herring experiencing a VHS epizootic under these conditions was previously naïve to VHSV and did not possess herd immunity at the time of capture. In contrast, any group of herring failing to undergo a VHS epizootic under these confinement conditions most likely survived prior exposure and was demonstrating herd immunity. Utilizing this principle, we repeatedly collected groups of juvenile Pacific herring from various locations, transported them alive to the laboratory, and subsampled their VHSV antibody levels at the time of capture. Their exposure histories were deduced by confining them into laboratory tanks and observing whether a VHS epizootic ensued.

Annual herring migration cycle (21160111-B, Bishop): The approach for successful tagging of herring was developed by this project. Briefly, fish were captured using barbed fishing jigs and then placed in a holding tank (770 L capacity). Individual fish were then transferred to a circular tub and anesthetized, weighed, measured (standard length) and placed in a tagging cradle. We made a small incision along the ventral midline to determine sex and to surgically implant an acoustic transmitter. Post-surgery, both tagged and untagged (i.e., not sedated, measured, or tagged) herring from the capture event were held together in a tank to ascertain when tagged herring had recovered from sedation and exhibited normal swimming and schooling behavior. Tagged and untagged herring were released together near a herring school.

Additionally, we expanded from the moored arrays of detectors to using a glider mapping along a route to detect fish as they returned towards spawning grounds. This technique is described in Cypher et al. (2023). An Innovasea VRC-2 acoustic receiver was mounted on a Teledyne Webb Slocum glider that was deployed three times in southeast PWS. A series of range tests were conducted to determine the ability to detect tagged fish. Tags were moored at three depths and the glider conducted multiple transects past the moored tags. Detection efficiency was calculated from the number of transmissions heard by each receiver out of all known transmissions.

Genomic mechanisms for lack of recovery (21170115, Whitehead): To address how the population genetics varied through time, we collected tissue samples from PWS from multiple times in the past, including 1991, 1996, 2006, and 2017. We sequenced whole genomes from each of ~60 individual fish per year. We then explored how the genetic attributes of the population changed over time, immediately after the *Exxon Valdez* oil spill but before the collapse, after the collapse, and for two decades following the collapse during which time there has been little recovery. To distinguish the influence of these environmental impacts from other factors, we collected similar data from two other Alaska populations of Pacific herring that did not experience oil spills, disease epidemics, or population collapses (from Togiak Bay and Sitka Sound). With sophisticated new computational tools, we scanned genome sequences for the impacts of natural selection and population decline across successive time periods. Furthermore, we collected similar data from 2017 for three other populations that span the geographic range of Pacific herring in North America – from Central British Columbia, Canada, Puget Sound, Washington, and San Francisco Bay, California. These additional samples allowed us to test for the ecological and evolutionary forces that have shaped genetic variation through space and time in this important species.

Studies of reproductive maturity (19170111-D, Gorman): To address the project's objectives, adult herring were collected seasonally in PWS between 2017 – 2019. In the lab, each processed fish was measured for the following metrics: standard length (millimeters, mm), fork length (mm), total length (mm), and whole-body weight (g). Sex of each processed herring was recorded. Gonads of both males and females were removed and measured for weight (g). A gonadosomatic index was calculated following: GSI = (gonad weight/whole-body weight) x 100. Gonad maturation was additionally scored using Hjort Index criteria. For female herring, a small mid-section of the ovary was dissected and preserved in 10 % neutral buffered formalin (VWR) for slide mounting and pathology analysis to discern maturity states. Mounted scales were aged and scale growth was measured. Scale images from an existing image library (Moffitt and Haught 2018) were used to examine potential changes in maturation through time. Four years (1984, 1988, 1999, and 2005) were selected to examine and scales from 60 males and 60 females were used. The scale growth was fit to determine if there was evidence of bimodal growth patterns.

Program coordination (21120111-A, Pegau): The potential to bias mile-days-milt values too low because weather hampers flying or spawn might occur in areas outside of the survey path has led to attempts to find other techniques that might assist the determination of spawn events and extent. These techniques include the use of local observers, deployment of remote cameras, and use of satellite imagery. Local observers include seeking out observations from other people in the area and deploying a crew to a remote location to watch for spawn events and call if one occurred. Cameras were also deployed that took an image every six hours and sent it via satellite to allow monitoring for spawn events. Lastly, high-resolution, visible satellite imagery from

Planet and Sentinel were used to look for spawn events by scanning for evidence of spawn in the images.

RESULTS

Objective 1: Expand and test the herring stock assessment model used in Prince William Sound.

The BASA assessment model provides good fits to the mile-days of milt survey, age-1 aerial survey, hydroacoustic survey, and the historical egg deposition surveys that provide anchor points for absolute biomass. The assessment estimates that spawning biomass has recovered to 18,100 mt (95% interval 12,100–27,800 mt) in 2021 from its lowest point of 5,400 mt in 2018 (Fig. 4).

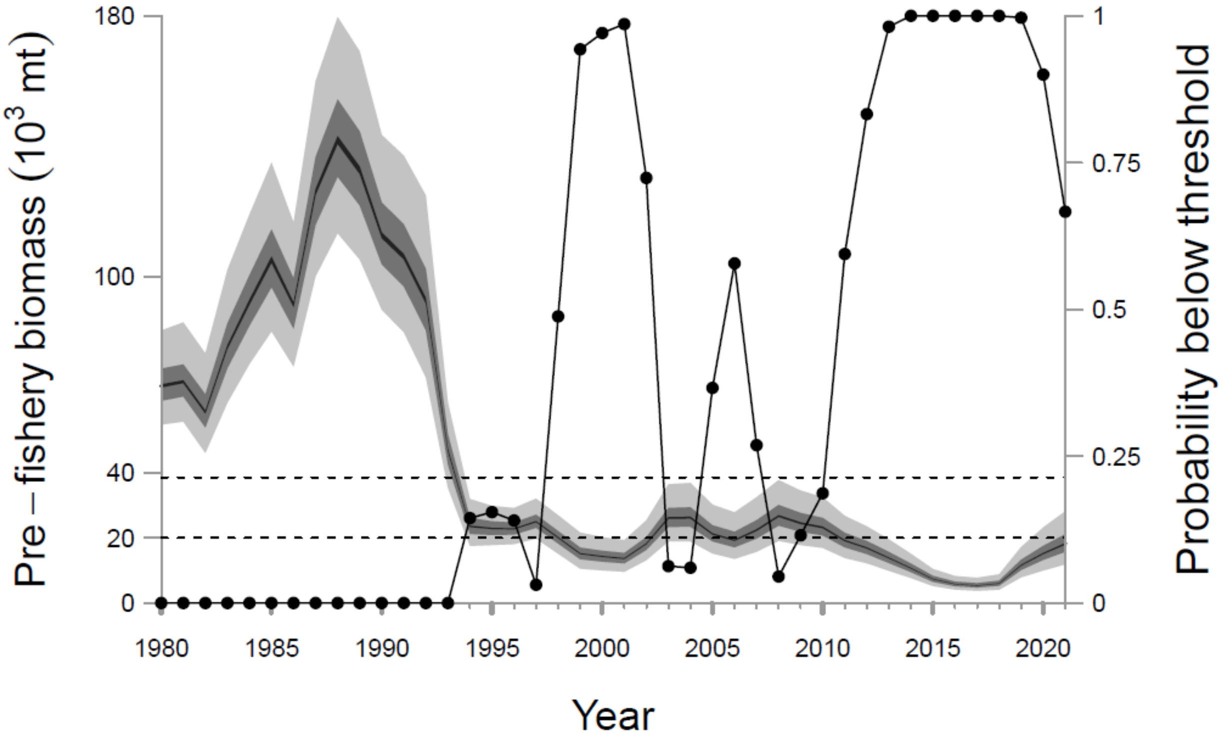

Figure 4. The median pre-fishery biomass along with the 60 and 95% (shaded) confidence intervals plus the probability that the estimate is below the regulatory fisheries threshold value (circles).

Stock assessment models fitted to the resulting simulated seroprevalence data were able to produce unbiased estimates of biomass, recruitment, and disease infection rates, which exceed the performance of the model when seroprevalence data are excluded (Trochta et al. 2022).

The inclusion of the age-1 herring aerial surveys has allowed the model to include ages less than age-3, which was the youngest class in earlier versions of the model. The model fit to the age-1 surveys is good but has large ranges due to the relatively short duration of the age-1 aerial surveys.

Objective 2: Provide inputs to the stock assessment model.

Age-Sex-Length study and aerial milt surveys (21160111-F, Morella): The aerial survey effort for mile-days of milt remained high throughout this study (Fig. 5). The mile-days of milt rapidly declined in 2015 and continued to decline until reaching a minimum in 2018. With the recruitment of the 2016 year class to the spawning stock beginning in 2019, the mile-days of milt have built up to near the level seen in 2014. The maps of spawn locations show the contraction in the spawn area through 2018 and then the expansion as the 2016 year class began to recruit to the spawning stock. Beginning in 2019 the population has been dominated by the 2016 year class (Fig. 6). This has led to several new spawning areas being used, primarily in Eastern PWS.

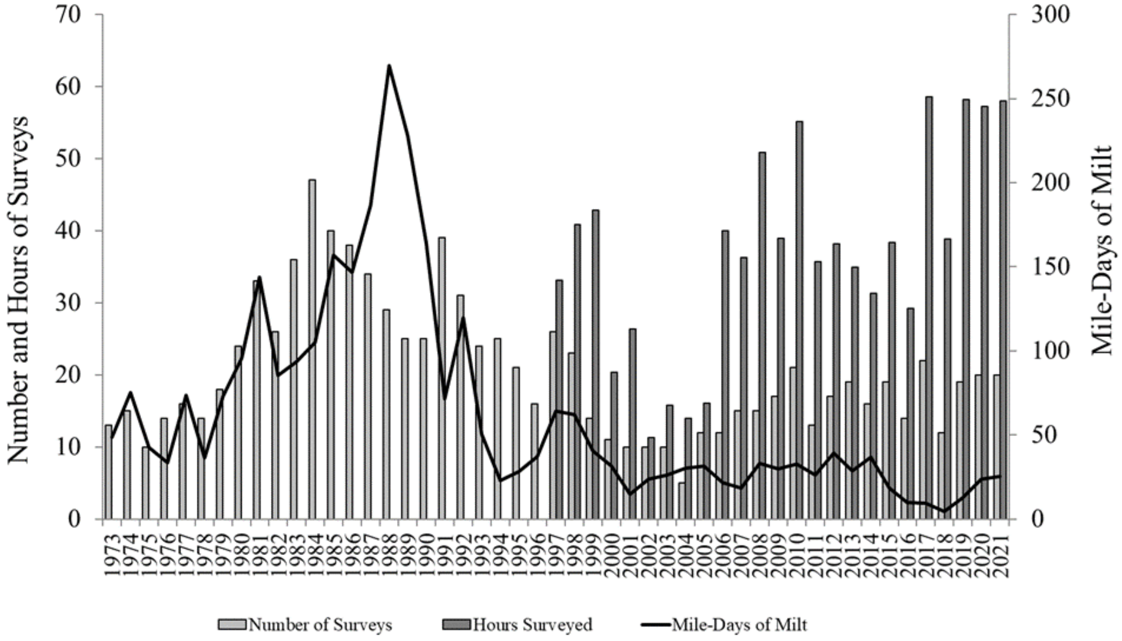

Figure 5. The number of surveys (light bars), hours of surveys (dark bars), and detected mile-days of milt (line) are provided.

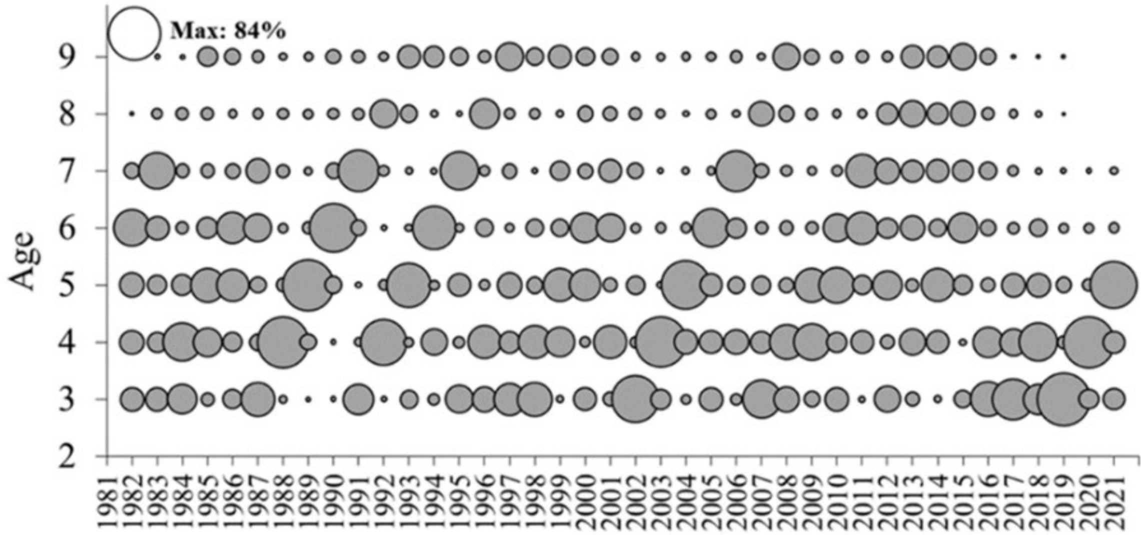

Figure 6. Spring herring age composition by year 1982-2021. The size of the circle denotes the percentage of the population at that age.

At the same time as the mile-days of milt was decreasing the condition of the herring was also decreasing. Weight at age for older fish began decreasing in 2016 and had a minimum for all ages in 2020 (Fig. 7). The decrease in weight at age is most obvious in older fish. The fluctuations in weight at age of the youngest (age-3) fish remains fairly constant in recent years. Beginning in 2021 the condition of the herring has begun to improve and is nearing the historical average.

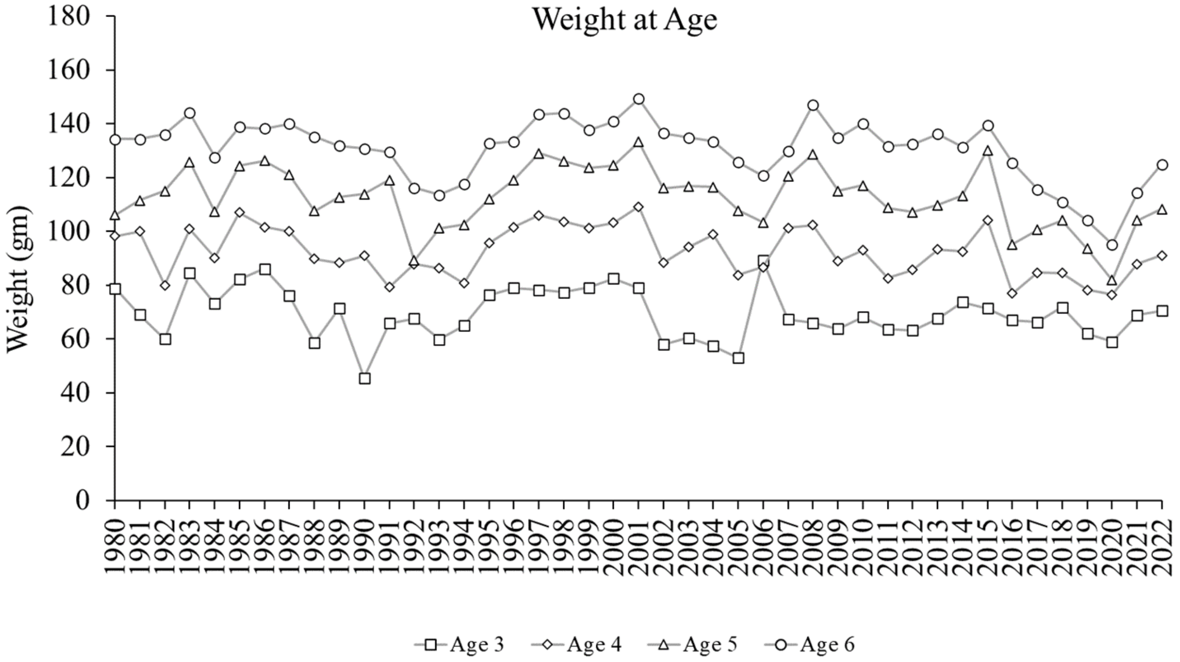

Figure 7. Weight at age by year from 1980 to 2022.

Disease in the adult population (21120111-E, Hershberger): Diseases metrics being monitored include the prevalence of VHS, VEN, and *Ichthyophonus*. Blood plasma samples were tested for the presence of VHSV antibodies (seropositive results) to indicate prior exposure to VHSV. The VHS and VEN prevalence data does not show any significant prevalence of these viruses during the collection period. The seropositive values show an increase in values that peak in 2015 at 25% of the population. The values decreased to very low levels beginning in 2019 and have remained at those low values (Fig. 8). The overall seropositive results are driven by the seropositive value in the age-5+ age class. A peak in the seropositive results in the age-3-4 age class occurred in 2015 and drove the higher overall values seen that year (Fig. 9)

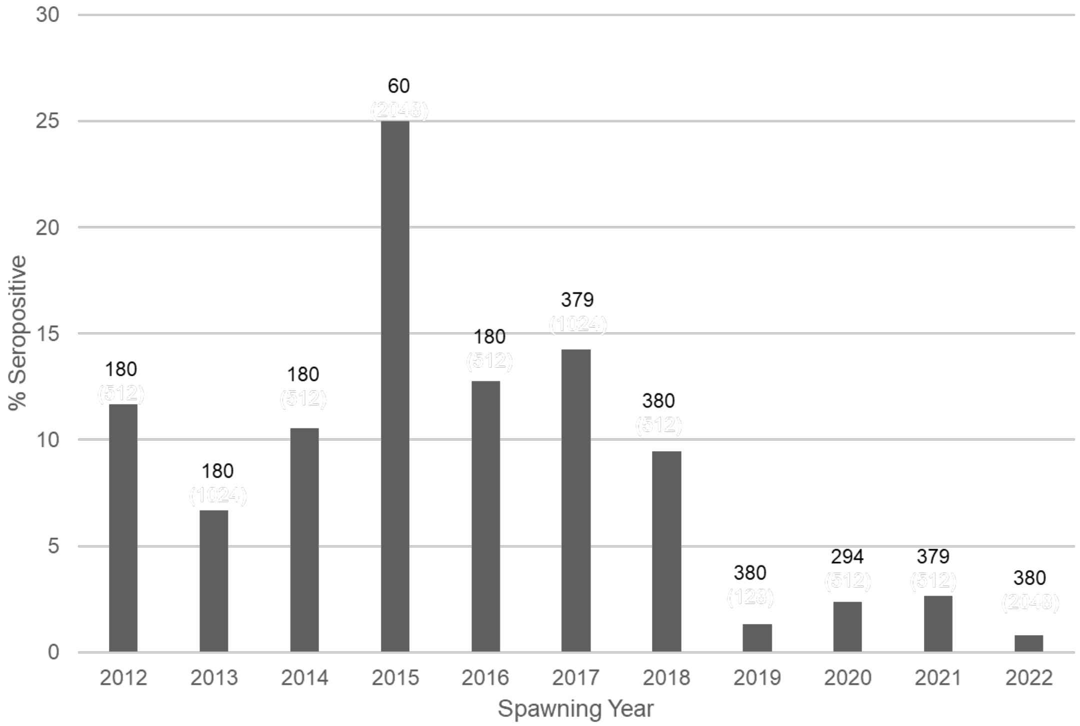

Figure 8. Viral hemorrhagic septicemia virus neutralizing antibody presence (seropositive) data by year. The number above the bar is the number of fish sampled.

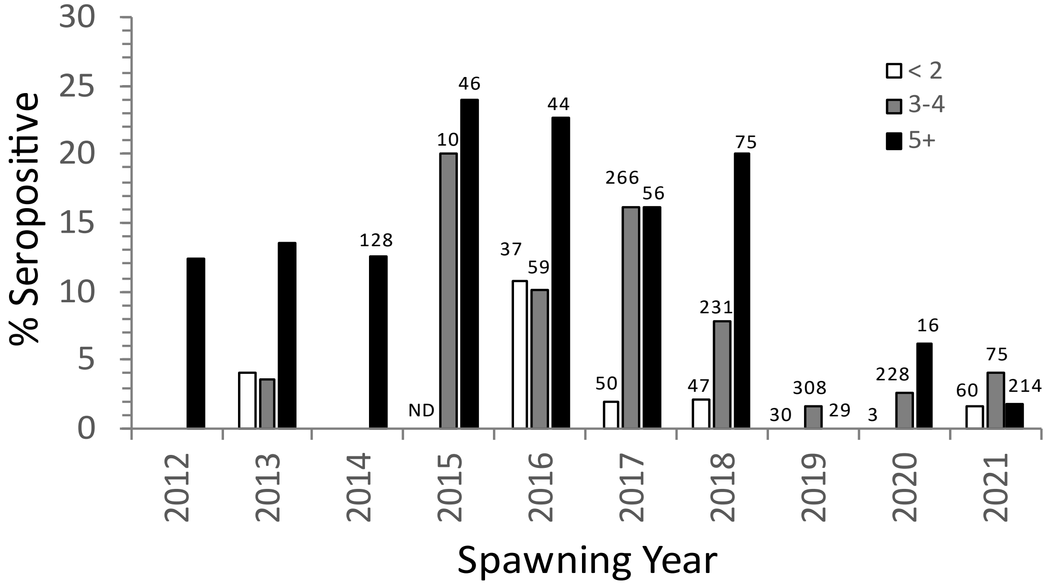

Figure 9. Viral hemorrhagic septicemia virus seropositive data for different age classes of herring by year.

Ichthyophonus prevalence is separated by fork length (Fig. 10). *Ichthyophonus* prevalence generally increases with fork length (a proxy for age). The prevalence in PWS is to that found in Sitka Sound herring.

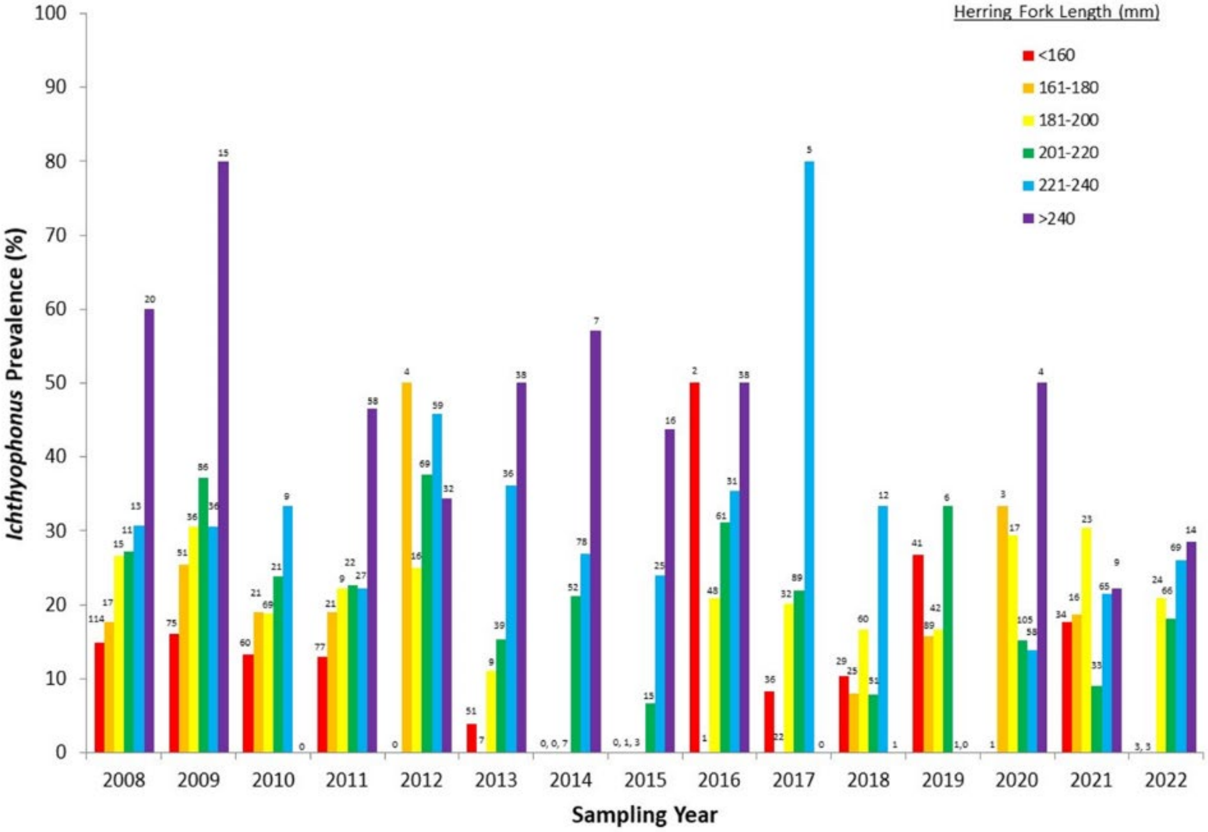

Figure 10. Prevalence of Ichthyophonus infected herring in each herring size class from Prince William Sound. Numerals above the bars indicate sample size (n).

VEN was not detected in the prevalence surveys.

Acoustic biomass surveys (21120111-G, Rand): The biomass estimates over the course of the study (2017-2021) ranged from a low of 3,646 mt (2018) to a high of 18,245 mt (2020, Fig. 11). The majority of the biomass was measured in Port Gravina in all years except 2019, a year when biomass measured at Hawkins Island (near Canoe Pass) exceeded that measured in Port Gravina. The proportion of the total biomass attributed to Port Gravina ranged from a low of 21% (2019) to a high of 97.5% (2017). We observed herring aggregations in six separate regions over the course of this study (Port Gravina, Hawkins, Double Bay, Rocky Bay, Zaikof Bay, and Stockdale Harbor). The survey years of 2019 and 2020 were marked by a more even distribution of biomass across the regions (particularly 2019), whereas the other survey years were dominated by estimates in Port Gravina. The tendency for the spawn distribution to be centered in the eastern part of PWS is consistent with the description by McGowan et al. (2021). These authors documented a spawn distribution that contracted away from historical aggregations in the western part of PWS following the collapse of herring abundance in the 1990s. Result here indicate that the spawning abundance during the period (2017-2021) remains highest in the eastern portion of PWS.

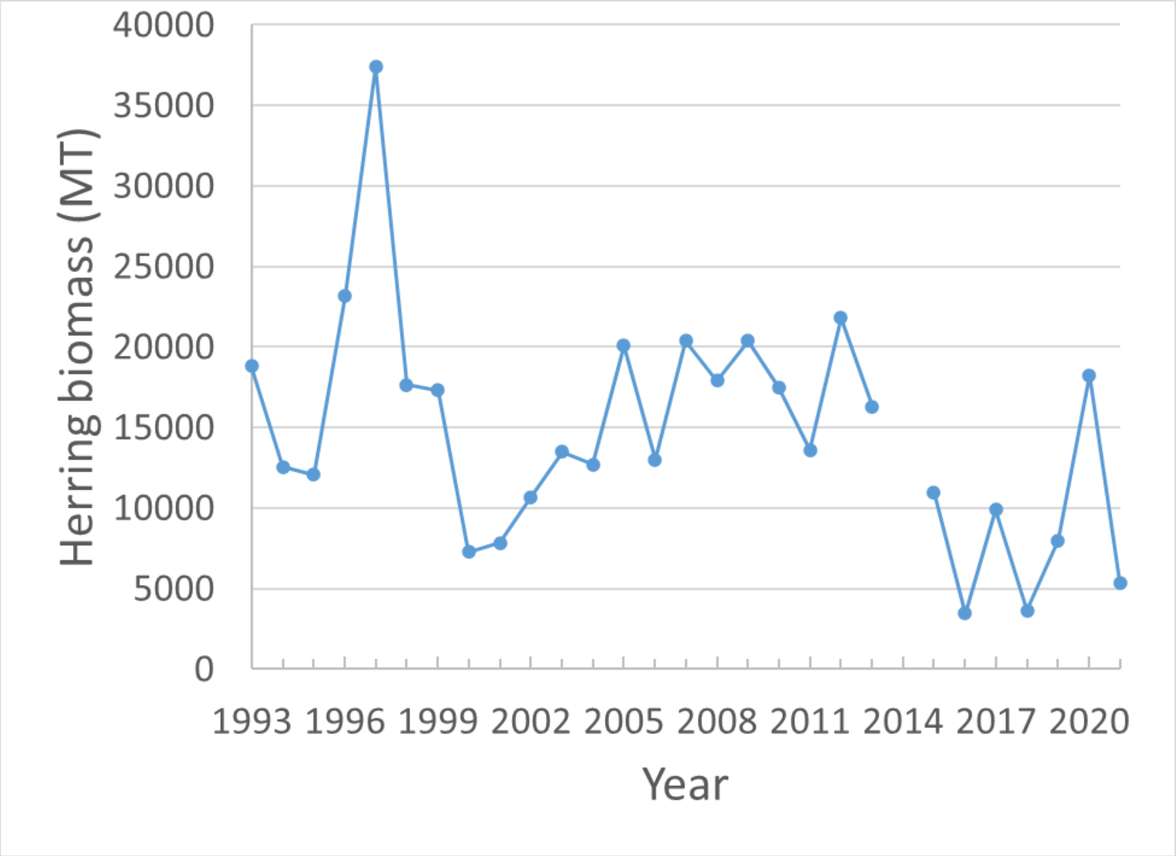

Figure 11. Herring biomass estimates in metric tons (mt) produced from Prince William Sound Science Center acoustic surveys during 1993-2021. Note that no estimate of herring biomass was produced in 2014 owing to an inability to survey fish that were very close to shore.

Juvenile index aerial surveys (Pegau): Age-1 herring make up the majority of the observed forage fish schools. They are followed by age-2+ herring and Pacific sand lance (*Ammodytes hexapterus*).

The distribution of age-1 herring tends to be highest in eastern PWS near the spawning grounds and along Knight Island passage. There were interannual differences in the distribution.

Throughout the ten years of observations age-1 herring have been found almost everywhere in PWS. The adult herring were not as regularly observed but were more likely to be found south of Glacier Island and at the southern end of Knight Island and the passages into the Gulf of Alaska. Sand lance were concentrated on Middle Ground Shoal with some schools observed in other areas, particularly the Naked Island group.

Large numbers of age-1 herring were observed in 2017 and 2021 (Fig. 12). The number of schools have been normalized to the small school equivalent to account for interannual differences in the distribution of school sizes. The large number of schools observed is consistent with the herring recruitment peaking every four years. Large herring recruit classes around the Gulf of Alaska include the 2012 and 2016 year classes, although the 2012 year class was not large in PWS. This four-year cycle in recruitment was also seen in the 1970s and 1980s (Williams and Quinn 2000).

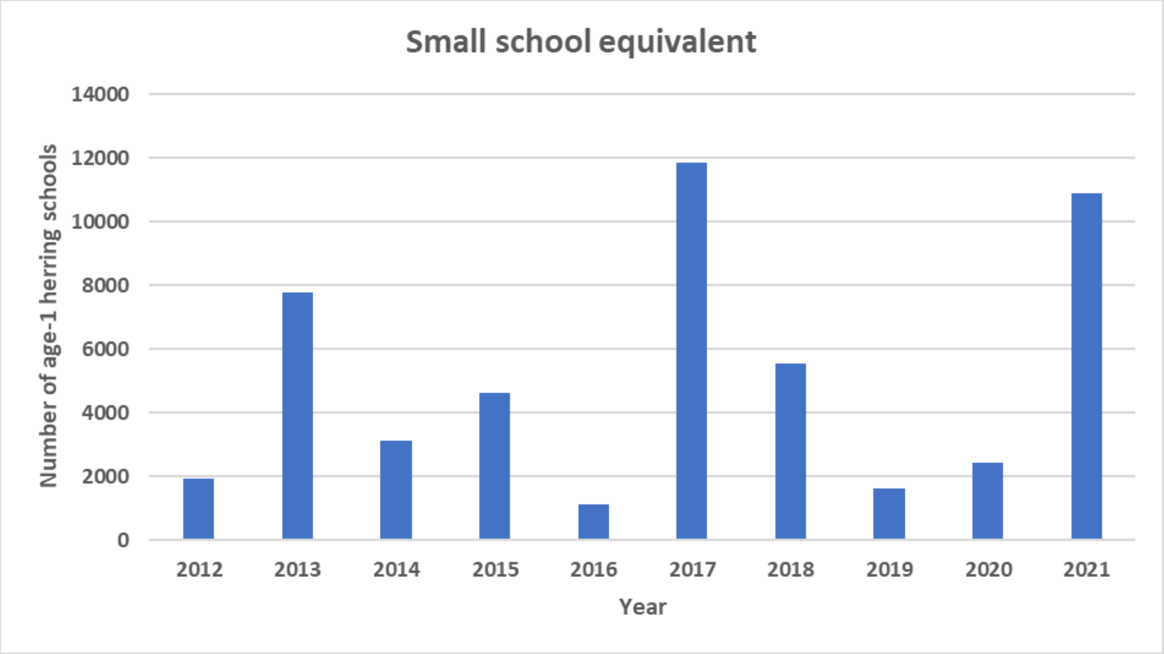

Figure 12. The number of age-1 herring schools after normalizing for the size of the schools. The 2016-year class was observed as age-1 fish in 2017.

Objective 3: Examine the connection between herring condition or recruitment to physical and biological oceanographic factors.

Modeling and stock assessment of Prince William Sound herring (21120111-C, Branch): Fourteen covariates were tested to examine for the existence of a relationship between either recruitment or mortality with that covariate. Only one covariate, pink salmon return, was supported across more than two Bayesian model selection criteria (for 3 of 4 criteria) showing an association with higher adult herring natural mortality (Fig. 13, Trochta and Branch 2021). There was ambiguous support for other fixed effects on natural mortality (walleye pollock and the NPGO) and recruitment (hatchery-released juvenile pink salmon and a 1989 regime shift).

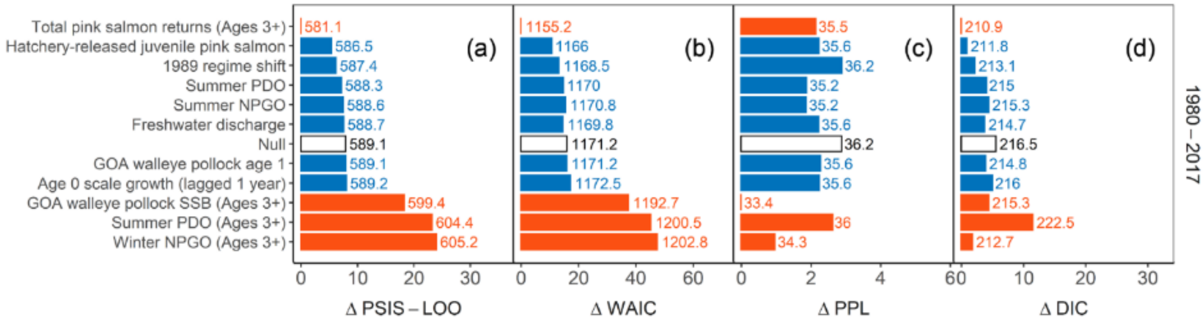

Figure 13. Model selection values for covariates explaining natural mortality (red) or recruitment (blue), for four model selection criteria (panels). Better models have smaller values than the Null model. The criteria are Pareto-smoothed importance-sampled leave-one-out cross-validation scores (PSIS-LOO), Watanabe-Akaike Information Criterion (WAIC), posterior predictive loss (PPL), and Deviance Information Criterion (DIC). PDO = Pacific Decadal Oscillation, NPGO = North Pacific Gyre Oscillation; GOA = Gulf of Alaska; and SSB = spawning stock biomass. From Trochta & Branch (2021).

Disease in the adult population (21120111-E, Hershberger): Processes that allow VHSV to persist in the marine environment remain enigmatic, owing largely to the presence of covert and cryptic infections in marine fishes during typical sub-epizootic periods. As such, marine host reservoirs for VHSV have not been fully demonstrated, nor have the mechanism(s) by which infected hosts contribute to virus perpetuation and transmission. Here, we demonstrated that, after surviving VHS, convalesced Pacific herring continue to shed the virus at a low rate for extended periods. Viral shedding from VHS survivors occurred at longer durations in cooler water and a recurrence of viral shedding among fully recovered individuals coincided with seasonal temperature declines. Further, exposure of previously naïve conspecific sentinels to this shed virus can result in infections for at least 6 months after cessation of overt disease (Fig. 14) Transmission potential from viral shedding was not necessarily dependent on the magnitude of the disease outbreak, as prolonged transmission occurred from two groups of donor herring that experienced cumulative mortalities of 4% and 29%. The results further suggest that the virus persists in association with the gills of fully recovered individuals and long-term viral shedding or shedding relapses are related to cooler or decreasing water temperatures. Cumulative mortality due to the VHS virus was found to increase at lower water temperatures (Fig. 14).

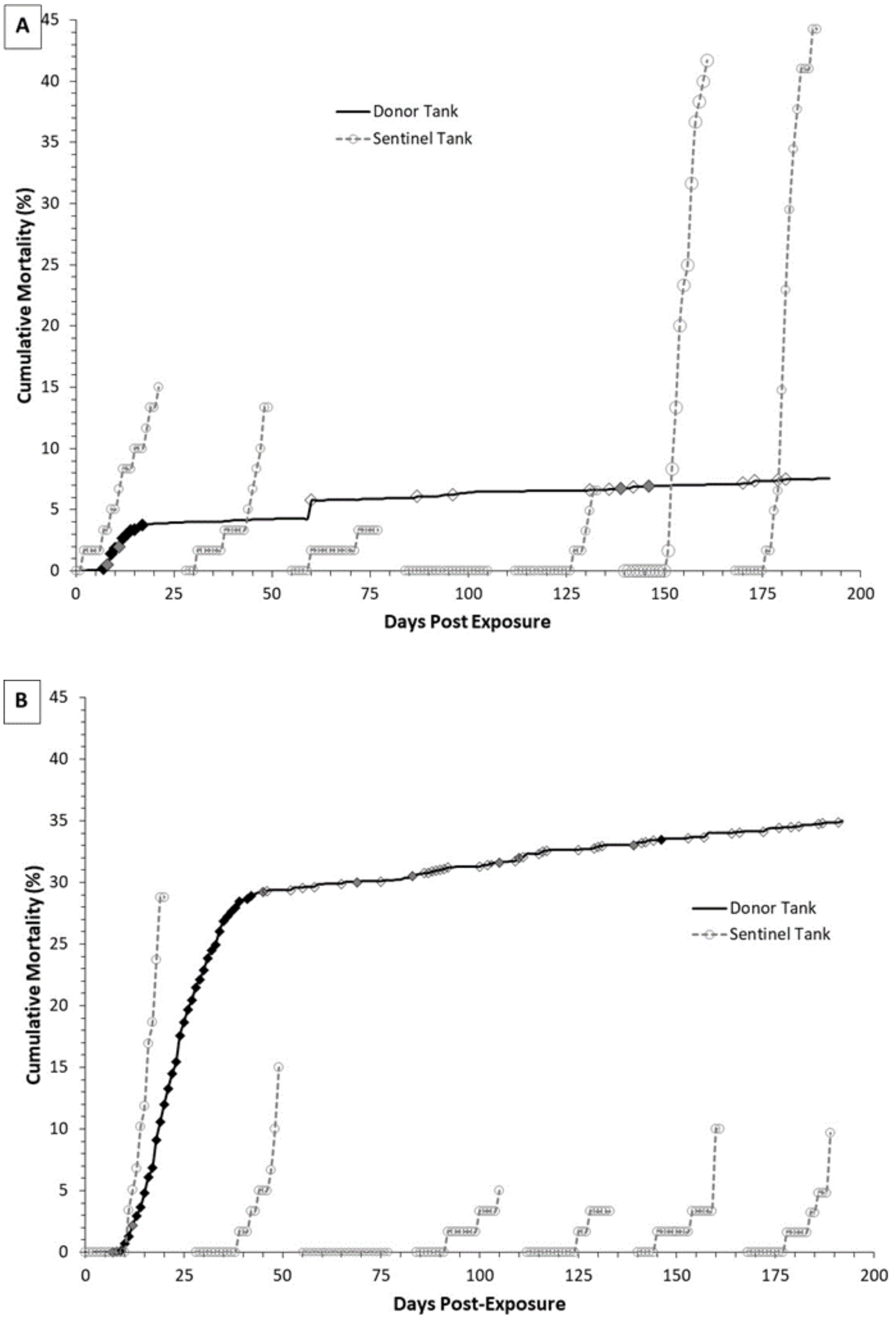

Figure 14. Cumulative mortalities in the viral hemorrhagic septicemia (VHS) virus treatments at ambient (A) and chilled (B) temperatures. The mortality anomaly in the ambient treatment (A) on 60 d was caused by a low oxygen event after a disruption in seawater supply. Results for the negative control groups are not displayed, as cumulative mortalities in the donor colonies were 1.3% (ambient) and 0.4% (chilled), and cumulative mortalities in the sentinel control groups were 0-10%. VHS virus was not detected in any mortalities or survivors in the negative control groups (donor or sentinels) by RT-qPCR or plaque assay.

The source of *Ichthyophonus* in herring remains unknown. Several potential routes of transmission were examined in the laboratory. Captive reared SPF sentinel herring (age 1+) were cohabitated with *Ichthyophonus*-infected donor herring under four simulated environmental conditions: 1) ambient seawater, 2) ambient seawater with low salinity events, 3) chilled seawater, and 4) chilled seawater with low salinity events. In all cases there was no evidence of the ability to transmit the disease through cohabitation. We were not able to detect *Ichthyophonus* in the zooplankton that are the natural prey of herring.

A time series of herring collected in the Cordova harbor showed a sharp increase in infection prevalence during the spring (Fig. 15). The cause of the sharp increase remains to be identified but may be related to one of the following:

1. An exodus of healthy herring from the harbor during the spring, leaving the infected herring behind if they are too sick to participate in the outmigration.
2. Increased infection pressures resulting from offal discharges when the fish processing plants become active in the spring.
3. Other disease co-factors that may occur in Cordova harbor, including exposure to biofouling contaminants (e.g., tributyltin or copper-based paints), limited food availability, temperature differences, etc.).

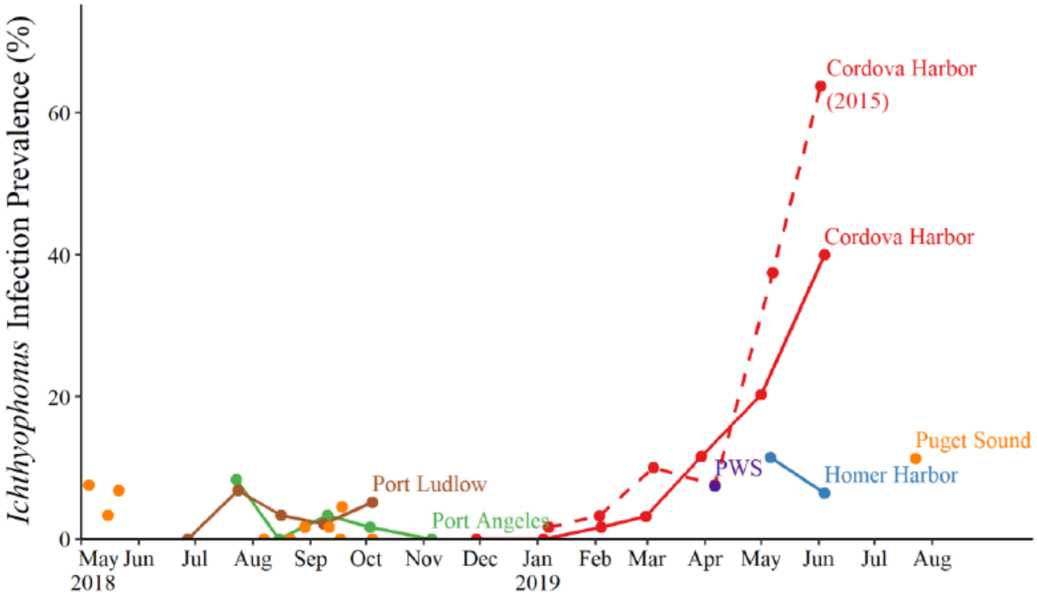

Figure 15. Ichthyophonus infection prevalence in age-0 herring from various locations throughout the northeast Pacific, including Cordova Harbor, throughout the year (May 2018 – Aug 2019).

Annual herring migration cycle (21160111-B, Bishop): We estimated the probability that the first detection at a Gulf of Alaska entrance array would occur at either Montague Strait (MS) or the nearby Southwest Passages (SWP). Initially, we used the data set comprised of the 235 known-age fish, however, no variable was found to be significant. Because age was not shown to significantly affect the probability compared to the null model ($\chi^2 = 0.47$ on 1 d.f., $p = 0.49$), analysis continued with all 517 fish detected at the entrance arrays. Both weight and standard length were found to significantly affect the probability of a first detection at MS/SWP. Continuing the analyses using weight, a univariate model was found to be significantly better than the null model ($\chi^2 = 15.44$ on 1 d.f., $p < 0.001$) and a model with both weight and tag year was found to be marginally better than the model with weight alone ($\chi^2 = 6.7$ on 3 d.f., $p = 0.08$). Both models found that as weight increased, the probability of first detection at MS/SWP over Hinchinbrook Entrance (HE) increased. The model with tag year additionally found that the overall probability varied somewhat year to year, with 2020 having the lowest overall probability of a first detection at MS/SWP (Fig. 16).

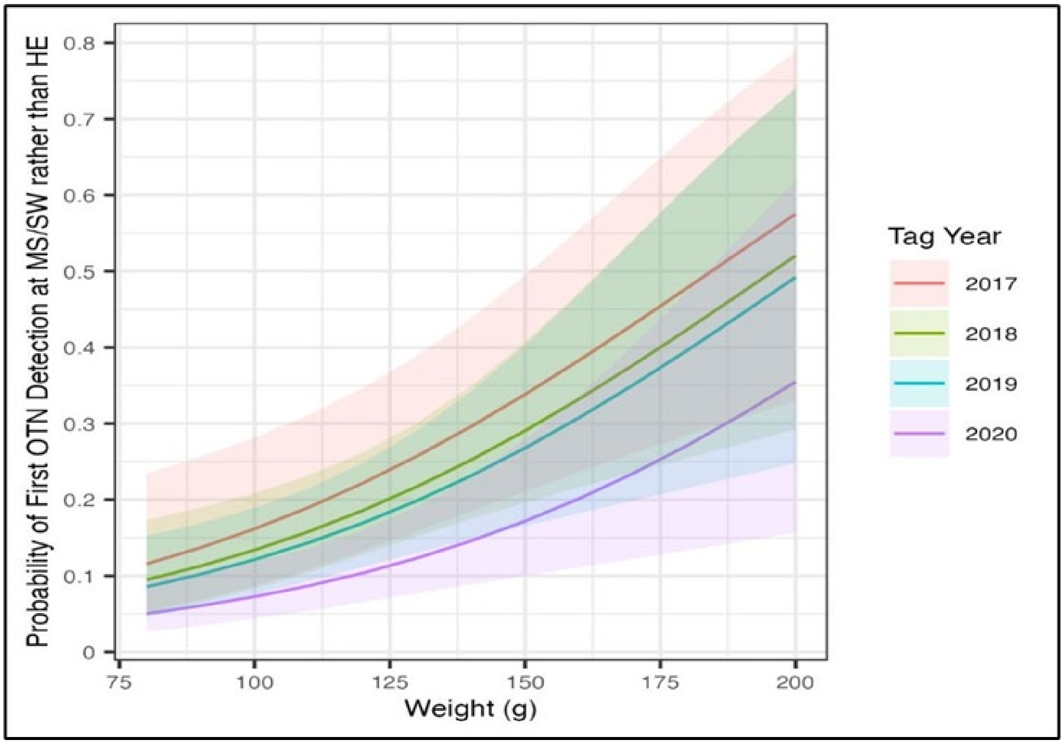

Figure 16. Using a model from 517 fish detected at a Gulf of Alaska Ocean Tracking Network (OTN) entrance arrays in the year after tagging, it was estimated that the probability of a first array detection at Montague Strait (MS) or Southwest Passages (SWP) rather than Hinchinbrook Entrance (HE) increased as weight increased, and that the overall probability varied based on the tag year with 2020 tag year fish having an overall lower probability of first detection. The relationship between weight and odds of leaving was estimated to be the same for each year.

We used multiple linear regression to understand the factors influencing residency time in the Gulf of Alaska. After averaging the top three models, results indicated that the interaction of length and exit array had a significant effect on the Gulf of Alaska residency time. Sex was also included in this averaged model but was not found to be significant. Standard length positively affected average Gulf of Alaska residency time for fish exiting from HE, but not for fish exiting from MS/SWP. For condition and weight models, no variables were found to significantly affect average residency time in the Gulf of Alaska.

Based on detection data from all PWS arrays, 32 of a possible 164 herring (19%) returned early (between September and November) to the southeast PWS spawning grounds. There was compelling evidence that the probability of an early return was related to fish weight (χ_1^2= 6.5, p = 0.011) and length (χ_1^2= 6.86, p = 0.009) with smaller herring significantly more likely to return than larger herring. Conversely, there was little evidence that condition was associated with the probability of an early return (χ_1^2= 0.44, p = 0.51). It was estimated that an increase in weight of 10 g was associated with a 25% decrease (95% CI: 4 – 40) in the odds of being detected at the southeast PWS spawning grounds between September and November. Similarly, an increase of 10 mm in length was associated with a 43% decrease in the odds of being detected (95% CI: 11 – 63). On a probabilistic scale, an 80 g herring would have a 0.39 probability of being detected (95% CI: 0.22 – 0.60) compared to 0.04 for 175 g herring (95% CI: 0.01 – 0.17) while a 190 mm herring would have a detection probability of 0.43 (95% CI: 0.23 – 0.66) compared to 0.05 for a 240 mm herring (95% CI: 0.01 – 0.16).

Genomic mechanisms for lack of recovery (21170115, Whitehead): Though water concentrations of ∑PAH (polycyclic aromatic hydrocarbons) were nearly uniform for all three populations of herring used (Fig. 17A and 17D), accumulated body burdens differed between populations. PWS and Sitka Sound (SS) fish had similar body burdens of PAHs by 10 days post fertilization (dpf) (Fig. 17B and 17C), but the WA population fish had lower overall ∑PAH concentrations in their tissues, and a shift in the profile of PAHs compared to the Alaska populations (Fig. 17E). This suggests that metabolism and elimination of PAHs may be greater in WA fish compared to Alaska fish. Indeed, metabolism of PAHs during embryogenesis is apparent; the temporal profile of PAH accumulation, which was characterized in only PWS fish, showed accumulation up to 4 dpf, followed by a substantial decrease between 4 and 10 dpf, despite exposure to constant PAH concentrations in the external waters over this exposure period.

The earliest time point during development where circulation is detectable, indicating early stages of cardiovascular system development, is 4 dpf in Pacific herring. Pericardial edema, which is a sensitive indicator of crude oil impacts on the developing cardiovascular system, was not affected by oil exposures by 10 dpf (p>0.05), even in the highest dose. This indicates that our range of exposure concentrations was very low. Once fish are hatched and no longer coiled within the embryonic chorion, it is possible to orient individual fish such that different dimensions of heart morphology may be reliably measured. We characterized heart morphology at 1 day post hatch (dph). At our medium dose (64.5 ng/g, 0.53 µg/L) and higher, the area of the posterior ventricular outgrowth was significantly reduced ($p<0.05$) by oil exposure compared to controls in PWS and SS fish. We found that the oil exposure impact on heart morphology varied between populations (significant dose-by-population interaction, $p<0.0001$), where the two Alaska populations (PWS and SS) were more sensitive than the WA population.

Numerous changes were observed in transcriptional responses related to the exposure to oil. Due to the complexity of these changes, we refer readers to the project report (Whitehead 22170115) for details on the topic. The largest differences occurred between the Alaska populations and the one from Washington used in these tests. Transcriptional responses to oil varied between populations, where the two Alaska populations (PWS and SS) were most similar, and the WA population was most different. This is consistent with population variation in their susceptibility to oil-induced cardiac injury (Fig. 10). Though the number of genes showing a conserved transcriptional response to oil increased with developmental age (Fig. 14A), population-dependent responses showed the reverse pattern where the earliest stage had the most transcriptional responses distinguishing WA fish from the other populations. This suggests that the mechanisms responsible for the reduced toxicity observed in WA fish compared to AK fish included those induced by oil very early in development.

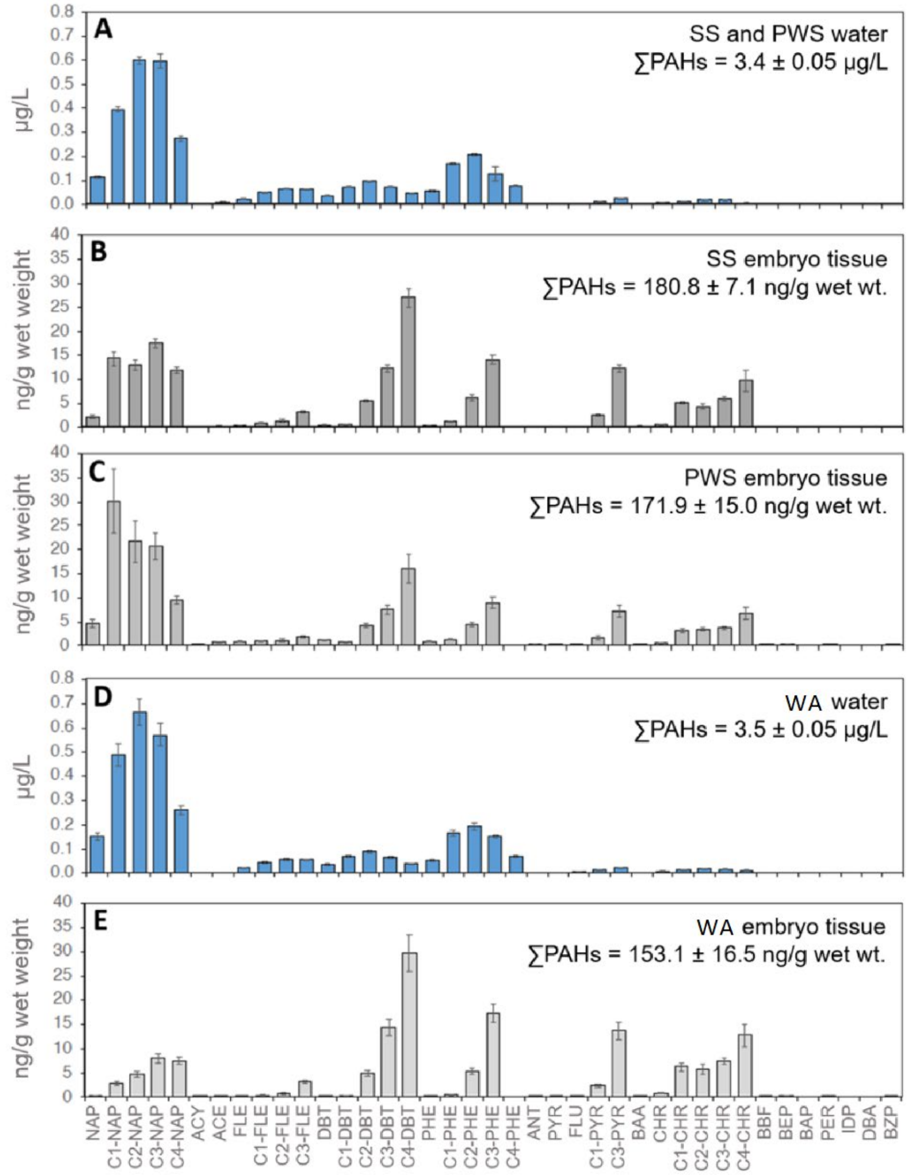

Figure 17. Water and tissue polycyclic aromatic hydrocarbons concentrations for two exposure experiments. A-C: water and tissue concentrations for the first experiment that included both Alaska populations (Prince William Sound (PWS) and Sitka Sound (SS). D-E: water and tissue concentrations for the second experiment that included the Washington (WA) population. A and D show water concentrations in µg/L for the two exposure experiments, and B, C, and D show tissue concentrations in embryos from the high dose at 10 dpf in ng/g wet weight for each of the three populations. Analytes included naphthalene (NAP), acenaphthylene (ACY), acenaphthene (ACE), fluorene (FLE), dibenzothiophene (DBT), phenanthrene (PHE), anthracene (ANT), pyrene (PYR), fluoranthene (FLU), benz[a]anthracene (BAA), chrysene (CHR), benzo[b]fluoranthene (BBF), benzo[e]pyrene (BEP), benzo[a]pyrene (BAP), perylene (PER), indeno[1,2,3-cd]pyrene (IDP), dibenz[a,h]anthracene/dibenz[a,c]anthracene (DBA), benzo[ghi]perylene (BZP) in addition to their alkylated homologs indicated as C1-, C2-, etc.

Additional testing examined the response of fish exposed to oil when later challenged with VHSV. VHSV virulence was high, causing 70%-80% mortality over 21 days. This level of virulence did not vary between populations and did not depend on whether fish had been exposed to oil many months before during embryogenesis (Fig. 18A). In a follow-up experiment fish from only the PWS population were briefly exposed to oil during a different stage of early life: as larvae they were exposed to oil for 20 days starting at 2-weeks post-hatch. These fish, and control no-oil exposed fish, were subsequently raised to juvenile stage in clean water then exposed to VHSV. Virulence (mortality) was reduced in fish that had been briefly exposed to oil during early larval development (Fig. 18B). The molecular mechanisms that underlie response to VHSV, including in fish that had been exposed to oil as larvae, are not reported here since analysis is still incomplete, but this work is ongoing.

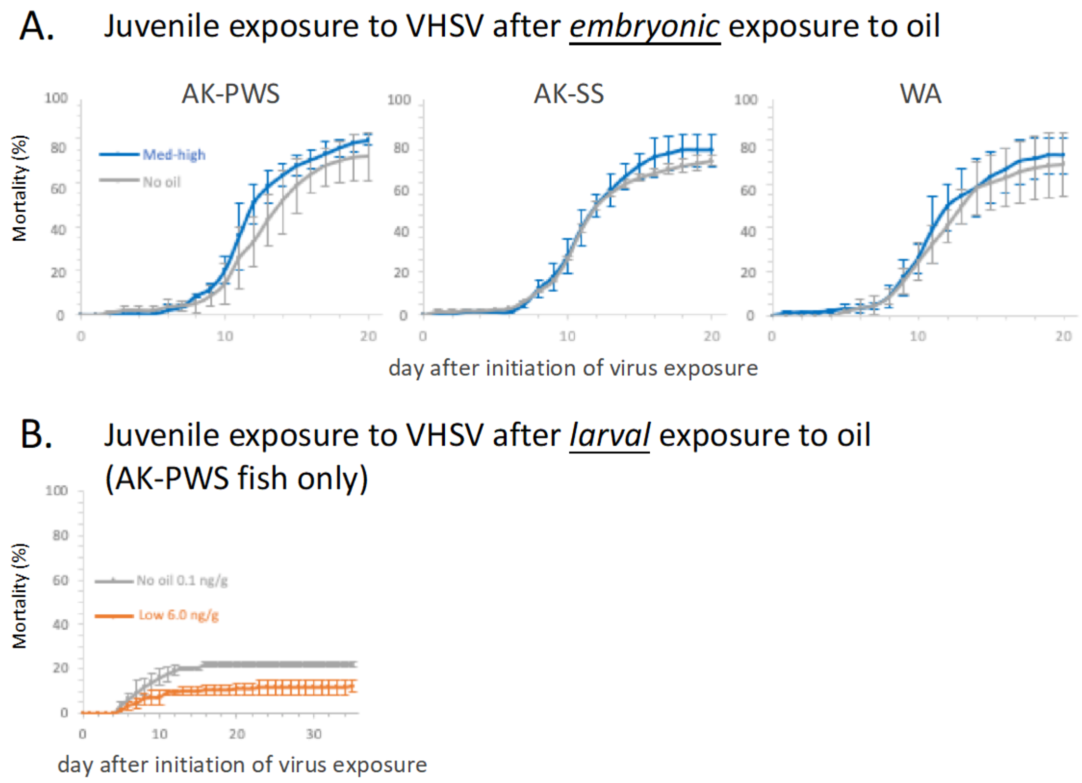

Figure 18. Mortality of post-metamorphosis juvenile Pacific herring in response to viral (VHSV) exposure. A: Mortality for fish from each of three populations (Prince William Sound [AK-PWS], Sitka Sound [AK-SS], and Washington [WA]) for fish that had been exposed to oil during embryogenesis (blue lines) and control fish that had not been exposed to oil (grey lines). B: Mortality for fish from the AK-PWS population that had been exposed to oil as larvae for three weeks starting two-weeks post-hatch (orange line) and controls not exposed to oil (grey line).

Objective 4: Develop new approaches to monitoring.
Constant refinements are undertaken to improve our understanding and monitoring of herring in PWS. Again, several projects included efforts to address this objective.

Disease in the adult population (21120111-E, Hershberger): A major breakthrough was the development of the methodology to detect the influence of VHSV antibodies in the serum. This approach allows us to not only detect what fish are currently sick (prevalence measure) but what part of the population had been exposed and survived. Serum neutralizing activity was virus-specific, as plasma from VHS survivors demonstrated only negligible reactivity to infectious hematopoietic necrosis virus (IHNV), a closely related rhabdovirus. Among Pacific herring that survived VHSV exposure, neutralizing activity was detected in the plasma as early as 37 d post-exposure and peaked approximately 64 d post-exposure. The onset of neutralizing activity was slightly delayed at 6.0 ºC relative to warmer temperatures (8.5 and 12.0 ºC); however, neutralizing activity persisted for at least 345 d post exposure in all temperature treatments.

For the neutralizing antibody assay to functionally apply to the population level, it is important to understand the kinetics of antibody production and persistence. For example, if antibodies are detectable for at least 1-year post-exposure, then annual herring surveillances should be adequate to detect whether VHSV exposures occurred since the previous annual stock assessment. A long-term study to evaluate the persistence of detectable VHSV antibodies was completed. Briefly, SPF Pacific herring were exposed to VHSV during a single waterborne challenge and neutralizing antibodies were assessed at monthly intervals after exposure. Fish were subsamples at monthly intervals post-exposure and assessed for the presence of detectable antibodies. The experiment was terminated approximately three years after the herring were exposed to VHSV. Neutralizing antibodies were detected as early as 28d post-exposure and persisted throughout the duration of the 3 yr study (Fig. 19).

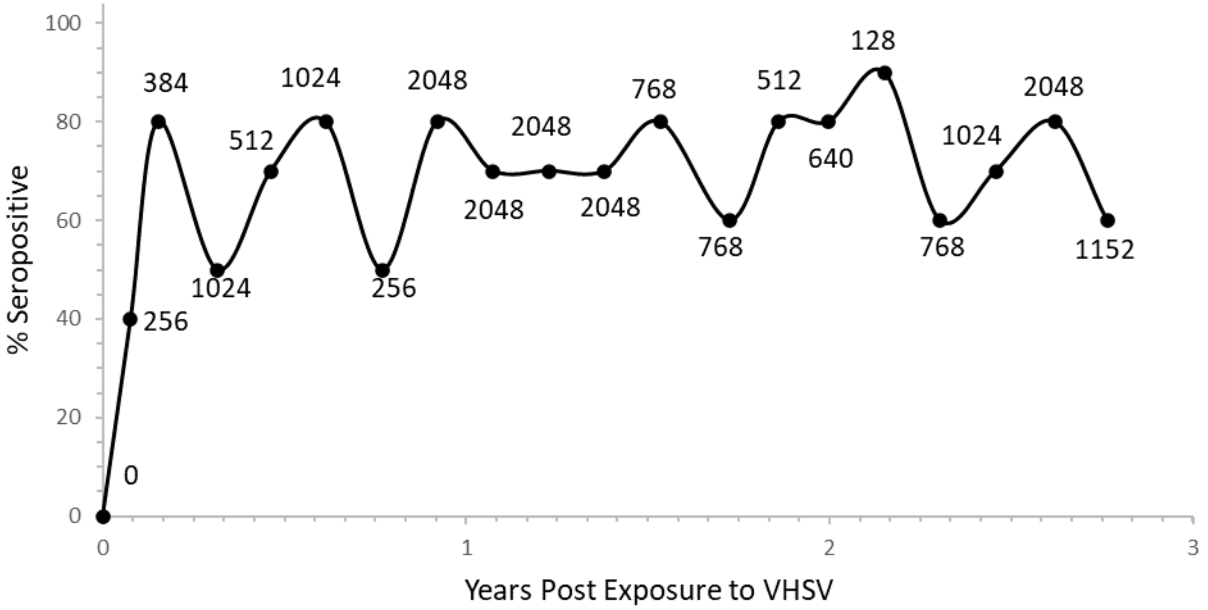

Figure 19. Persistence of detectable neutralizing antibodies in herring that survived viral hemorrhagic septicemia virus (VHSV) exposure. Numerals associated with each data point indicate the median antibody titer among seropositive individuals, reported as the reciprocal 50% inhibitory dilution – ID50 (titer range: 64 - 2,048). Sample size (n) = 10 fish at each subsampling interval. None of the specific pathogen-free negative controls (n = 10 / sampling date) tested positive on any of the subsampling dates (data not shown). Note: these results reflect the novel (optimized) plaque neutralization methods.

Exposure histories were deduced using a unique principle involving VHS and Pacific herring, whereby wild herring confined into net pens or laboratory tanks often (but not always) experience VHS epizootics. It can be deduced that any group of herring experiencing a VHS epizootic under these conditions was previously naïve to VHSV and did not possess herd immunity at the time of capture. In contrast, any group of herring failing to undergo a VHS epizootic under these confinement conditions most likely survived prior exposure and was demonstrating herd immunity. Utilizing this principle, we repeatedly collected groups of juvenile Pacific herring from various locations, transported them alive to the laboratory, and subsampled their VHSV antibody levels at the time of capture. Their exposure histories were deduced by confining them into laboratory tanks and observing whether a VHS epizootic ensued. If an epizootic did not ensue, it could be inferred that either:

> 1) The population survived prior exposure and was refractory to the disease (in possession of herd immunity).

2) The population was never previously exposed, remained susceptible, and had no herd immunity; however, viral carriers were not present among the captured individuals, so exposure to VHSV did not occur in the tanks. This possibility was eliminated by further exposing these groups to known amounts of VHSV under controlled conditions.

Susceptible Groups: It was concluded that six of these herring groups were largely naïve to VHSV at time of capture and did not demonstrate herd immunity when they were collected because classic VHS epizootics (characterized by mortalities accompanied by high VHSV prevalence and tissue titers) ensued after their confinement into the tanks. The day 0 antibody profiles generally support this conclusion, as seropositives at the time of capture were typically low (≤3%).

Refractory Groups: It was concluded that three groups survived prior exposure to VHSV and demonstrated herd immunity when they were collected because VHS epizootics did not ensue after their confinement into laboratory tanks, nor did they occur after subsequent exposure to known amounts of virus. The Day 0 antibody profiles generally supported this conclusion, as seropositives at the time of capture were much higher (26-33%) than in the susceptible groups.

Ambiguous Group: One group of susceptible herring (Protection Island, Oct 4, 2018) returned relatively high antibody levels (27%), indicating that they survived prior exposure. However, laboratory confinement indicated that these fish were still susceptible when they were introduced to the laboratory. This ambiguity may reflect a mixed school demonstrating differing exposure histories.

Annual herring migration cycle (21160111-B, Bishop): This project developed the approach to successfully tag and track herring using both moored receiver arrays and receivers mounted on a glider. We acoustic-tagged 726 Pacific herring in Prince William Sound during April 2017-2020 and post-release detected 96% of the fish. Most fish detected that were only on the spawning grounds had a final detection occurring within one month of release suggesting mortality or tag shedding. Over 70% of the tagged fish departed from the tagging grounds and by 16 July had been initially detected at one of the Gulf of Alaska entrance arrays: HE, MS, or one of the four SWP. Fish were observed as they moved in and out of PWS past the receiver arrays and later as they returned to the spawning grounds.

Overall, the glider-mounted VR2C detected 65.7% of all acoustic transmissions that occurred during transects where within 1 km of the transmitter mooring. When the glider-mounted VR2C was within 515 m range of the transmitter mooring, it had slightly higher detection efficiency for the surface transmitter (83.8%, p=0.02) than the mid-water (72.7%) and bottom transmitters (75.5%). By comparison, the stationary receivers (M1_1, M2_1, and M2_2) had variable detection efficiency for transmitters that was unexplained by distance alone. The detection efficiency of the VR2AR at the bottom of the transmitter mooring (M1_1) was 98.5% for the bottom tag (5 m above) in comparison to 26% for the surface tag (120 m above), despite the distance between receiver and surface transmitter being within range (<500 m) to expect high detectability based on previous range tests for the OTN (Eiler and Bishop 2016). By contrast, the bottom receiver (M2_1) of the receiver mooring detected 64.7% of surface transmitter pings and had the highest detection efficiency for the mid-water transmitter (68.9%, 504.2 m) and lowest for the bottom transmitter (47.5%, 500.1 m). The mid-water column receiver (M2_2) had the lowest overall detection efficiency for all three transmitters, detecting 28% and 11% of transmissions from the surface and bottom transmitters, respectively.

During the three glider deployments the VR2C detected herring that were acoustic tagged in 2019 and 2020 in Port Gravina, Orca Bay, and MS. Over the course of an 89-day deployment, the glider detected 30 herring transmitters, 3 implanted in 2019 and 27 in 2020. Although the glider was originally directed to pass within 1 km of detected herring transmitters, the results of the range test indicate that 0.5 km is a more suitable range for determining if a herring transmitter is shed or alive. Therefore, of the 30 herring detected (Fig. 20), 14 were re-detected within a 0.5-km range on at least two separate passes, which occurred on separate days in all instances. Because these herring transmitters remained in one area for the duration of the study, they were designated as shed, meaning that the herring either ejected the tag after implantation or experienced mortality.

Of the remaining 16 herring transmitters detected, 8 were designated as alive, and the remaining 8 were designated as undetermined. Herring were designated as undetermined when detections occurred during one time period and the area was not re-surveyed within a 500 m range. For the herring designated as alive, 6 were detected during one event in one location, but re-surveying of the area within 500 m did not result in a re-detection, indicating that the animal moved away from the area. Lastly, there were two herring detected in two separate locations, demonstrating a movement within the interior of PWS, by 14.8 and 59.5 km. The herring that traveled 59.5 km was first detected in eastern PWS near the mouth of Port Gravina on April 19th, 2021, and re-detected in MS on May 5th, 2021.

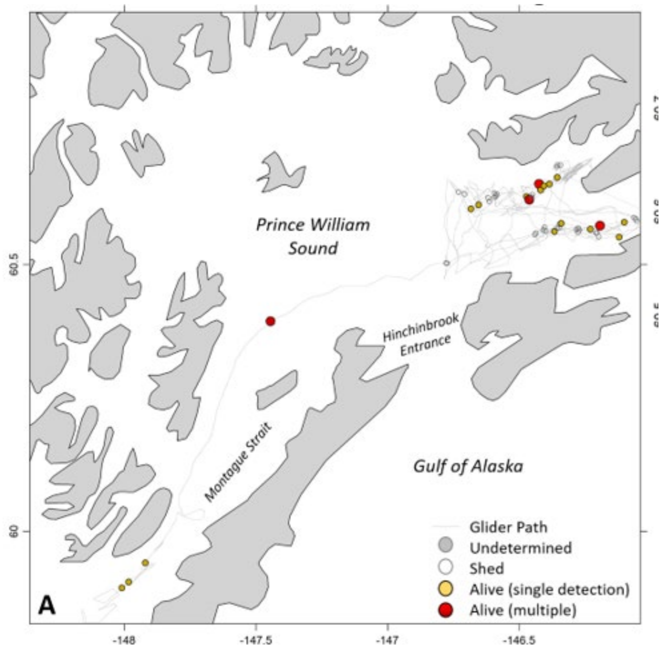

Figure 20. Location of herring tags and the inferred status of the herring from the glider detections.

Genomic mechanisms for lack of recovery (21170115, Whitehead):

We collected whole genome sequences from 892 samples from 14 population groups (sorted by location and year) using low-coverage whole genome sequencing, resulting in per-individual average depth coverage of 1.061x. After read mapping, sites were filtered to genotyping level of 0.5 for each population and year combination. After filtering steps, a total of 330,482 loci were included in the subsequent analyses.

Strong population structure was detected between Togiak Bay and the rest of the herring populations (Pairwise Fst: 0.125-0.198), suggesting limited gene flow across the Alaska Peninsula. Of the remaining populations between the Gulf of Alaska and California, the California population was most distinct from the rest (Pairwise Fst: 0.030-0.0325), while small differentiation was detected between the Gulf of Alaska and Washington (Pairwise Fst: 0.0088-0.011). This population structure was also supported by the results from NGSadmix, which estimates individual admixture proportions. The results from NGSadmix and subsequent evaluation by Clumpak showed that three primary ancestral clusters, with minimal gene flow from the Togiak Bay population to others.

PCA (PCAnsgd) and model-based admixture (NGSadmix) analysis showed no substantial changes in genetic structure over time within a population. Genome-wide pairwise Fst values showed little change over time within each population (Fst: 0.0066-0.0117). However, the Fst values within PWS population (0.0081-0.0117) were higher than SS (0.0066-0.0103) and Togiak

Bay (0.0067-0.0104) populations, indicating relatively greater genetic variance in the PWS population over this time period.

Temporal covariance revealed signatures of natural selection whereas more traditional PC-based selection scans did not. No significantly selected loci were identified from PC-based genome-wide selection scans between years within any of the three (PWS, Sitka Sound, Togiak Bay) populations. Temporal covariances revealed that the PWS population showed a signal of genome-wide positive selection (adaptive responses) over time, whereas other populations (Togiak Bay and Sitka Sound) did not (Fig. 21). Since the program that we used to detect linked selection using allele frequency covariances was established based on the assumption of non-overlapping generations, we assessed how overlapping generations might have impacted the observed patterns of temporal covariances using simulations in SLiM. Both overlapping and non-overlapping generation models produced highly similar covariance patterns, consistent with valid application of this analysis for Pacific herring.

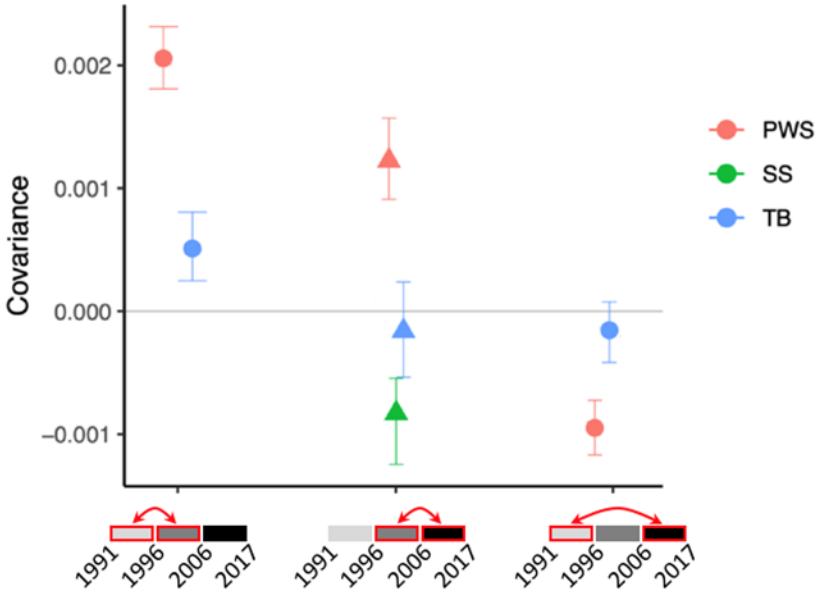

Figure 21. Positive temporal covariances, indicating the influence of polygenic selection, were detected for the Prince William Sound (PWS) population across the first three time periods and the second three time periods. Negative covariance for the PWS population over the whole time period (1991/1996 to 2006/2017) indicated switching selective regimes over time. Slightly positive (Togiak Bay [TB] 1991/1996 to 1996/2006), zero, or negative temporal covariances were detected for all other populations (e.g., Sitka Sound [SS]), indicating limited signal of polygenic selection, or signal of selection that could not be distinguished from genetic drift.

Studies of reproductive maturity (19170111-D, Gorman): Examination of ovaries for post-ovulatory follicles showed that they were only evident until July. This was before any maturation began so there was no time when both herring with the follicles and maturing fish were observed together. By November there was evidence of maturation in preparation for the upcoming spawning season. There were some age-2 herring with post-ovulatory follicles.

Bayesian clustering analysis and density plots did not find consistent evidence of bimodal growth in male or female herring during the four years examined. The times that had some evidence of a bimodal structure it was driven by a small number of fish.

Program coordination (21120111-A, Pegau): Our test of remote cameras found that it was difficult to get them high enough to easily detect the presence of spawn. What was obvious in the images were the changes in bird activity associated with spawning events. We find that expanding our efforts to reach people flying over or working near spawning grounds is a good means to get information on spawn events that occur at unusual times or locations. Most times these reports can lead to a flight to confirm the presence of spawn. High-resolution, visible satellite imagery has proven very effective at detecting and delineating spawn events (Fig. 22). The imagery is limited to clear sky conditions, which are limited in the PWS area. Satellite passes are not always daily, which leads to further gaps in the data. This can be mitigated by using multiple satellite systems.

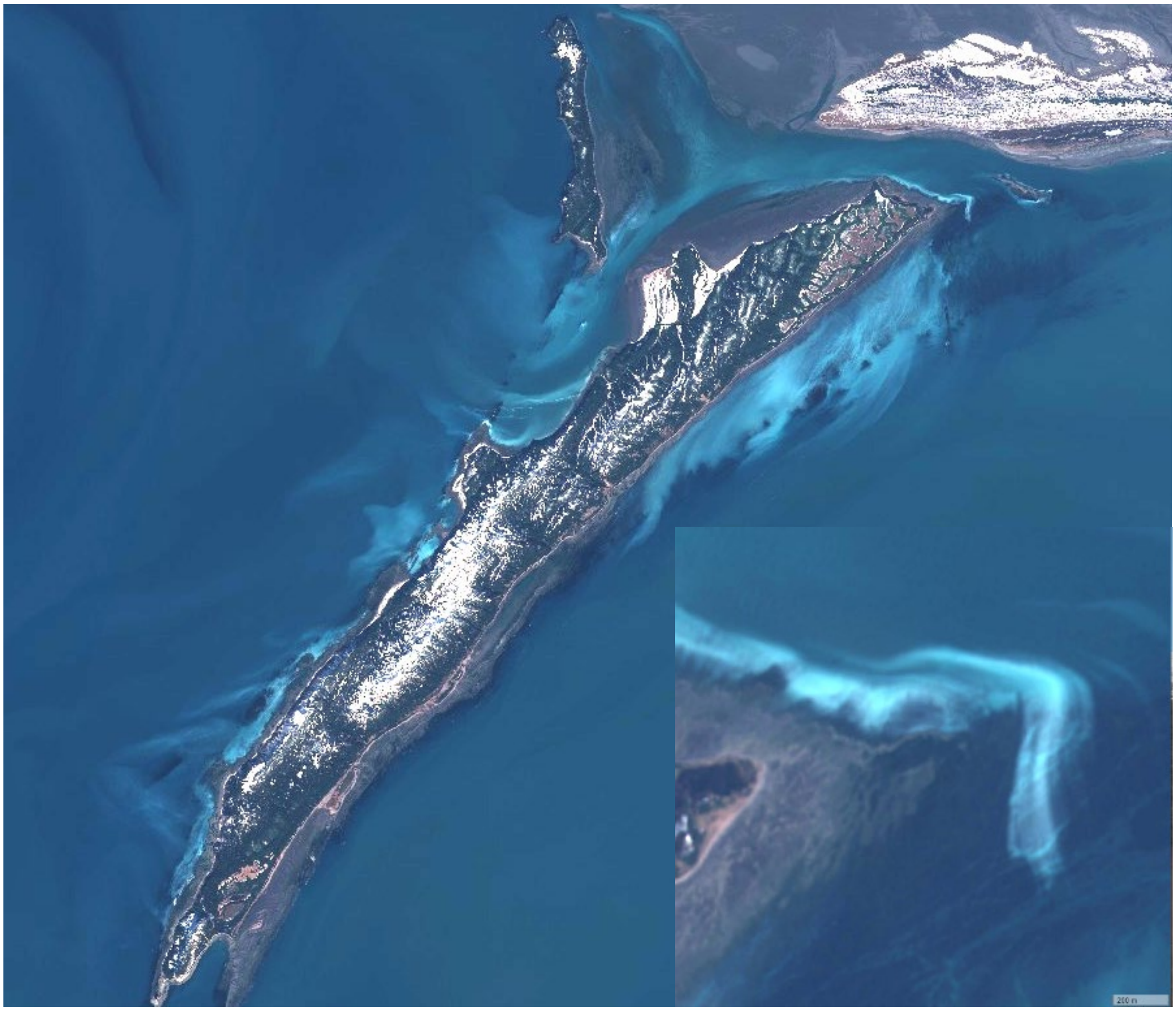

Figure 22. A major spawn event at Kayak Island visible in high-resolution Sentinel satellite imagery. The inset shows a detailed view of the northeast corner of the island.

DISCUSSION

This discussion focuses on how the various projects helped the program meet its objectives. Readers are encouraged to read the individual project reports to get more information on the findings of the individual projects.

Objective 1: Expand and test the herring stock assessment model used in Prince William Sound.

We were able to regularly produce PWS herring stock assessments and provide those assessments to ADF&G, National Oceanic and Atmospheric Administration, and the public. The regular BASA assessment of PWS herring continues to affirm that this population collapsed in the early 1990s and has since remained in a regime with low recruitment, spawning biomass and surplus production. Annual estimates of spawning biomass show a high probability of being below the lower regulatory threshold for reopening the fishery.

The model was expanded to include aerial survey of juvenile herring, which allowed the model to estimate age classes that haven't recruited to the spawning stock. Including the disease data in BASA (Trochta 2021, Trochta et al. 2021) marks a landmark in fisheries stock assessment modelling: the first stock assessment that can estimate the magnitude of disease outbreaks, mortality from disease, and the resulting impact on natural mortality. Current estimates show relatively low disease impact on the population, but also a cautionary note that the proportion of the population with positive seroprevalence is low, suggesting that the population could be susceptible to a VHSV outbreak. The seropositive data suggests that outbreaks of VHS are not regularly detected in the prevalence data.

The original model estimated mortality over two time periods in the data record. A sensitivity test indicated that the model was not significantly improved by estimating separate mortality over two time periods instead of a single period. This led us to use the single estimate of mortality.

Objective 2: Provide inputs to the stock assessment model.

The program continued to provide the inputs used by the stock assessment model. These included the age-weight-length-sex-gonad information provided by the ASL surveys, the mile-days-milt estimates from aerial surveys, acoustic biomass estimates, and disease prevalence data. Through outside funding, we were also able to continue the aerial surveys of juvenile herring that provided the age-1 herring index. 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. We also observed a decrease in weight and length of age that appears to be associated with unusually warm water conditions in the Gulf of Alaska.

Similarly, the past five years (2017-2021) of acoustic monitoring produced a range of total biomass estimates, from a low of 3,646 mt (2018) to a high of 18,245 mt (2020). While biomass was generally greatest in Gravina over the five-year period, we observed a more even distribution of biomass across regions in two years in the study period (2019 and 2020). As documented in other studies (McGowan et al. 2021), the majority of the herring biomass during the spring spawning period over this period was in the eastern region of PWS.

While this may not seem like a hard objective to meet, the pandemic that began in 2020 created significant challenges to collecting the necessary information when national and state travel and workplace restrictions were implemented in an effort to slow the spread of the virus. Many of the restrictions were first enacted as our sampling season began. It was through having existing research efforts sample for those that were not able to collect samples, working with local fishermen to collect samples, cross training of personnel, and the advantage of most personnel being in an already isolated area that the program was able to collect the samples necessary to maintain the existing time series.

Objective 3: Examine the connection between herring condition or recruitment to physical and biological oceanographic factors.

Several projects contributed to this objective. We were able to examine several environmental factors to determine how they impacted the model's fit once the data was incorporated into either the mortality or recruitment terms. Only the adult pink salmon returns led to a weak but significant improvement of the mortality term. In examining the potential between environmental conditions and herring mortality and recruitment, as well as spawn timing, we found that some factors were identified as important by one metric and not by others (Trochta & Branch 2021, Dias et al. 2022). The basic problem is that most fisheries time series are relatively short, interactions are highly complex, and successful high recruitment likely relies on a confluence of multiple factors all being at optimal levels.

Pathogens, such as VHSV and *Icthyophonus*, are influenced by environmental conditions. We were able to demonstrate the herring act as a reservoir for continued spread of the VHS virus. Viral shedding from VHS survivors occurred at longer durations in cooler water and a recurrence of viral shedding among fully recovered individuals coincided with seasonal temperature declines. Further, exposure of previously naïve conspecific sentinels to this shed virus can result in infections for at least 6 months after cessation of overt disease.

We remain unable to identify the transmission mechanism of *Ichthyophonus* but have been able to eliminate mechanisms such as fish-to-fish transmission and normal zooplankton prey. We found that there are areas with higher than typical infection rates exist, but unable to fully understand the cause of the infection hot spots. However, food with *Ichthyophonus* remains one possible explanation.

Tagging studies provided perspectives on the life history of herring. We found that larger herring were more likely to migrate into the Gulf of Alaska and that smaller herring tended to show up near the spawning grounds earlier in the fall and remain in the area overwinter.

Exposure to oil created mixed interactions with pathogens. At low oil exposure fish later exposed to VHSV were less likely to die than fish not exposed to oil. At higher oil exposures the mortality in exposed fish was similar to unexposed fish. Fish that had been exposed to oil were slightly more likely to die when exposed to *Ichthyophonus* later.

Analyses of genetic change through time in Alaskan populations indicates that the PWS population has experienced natural selection over the past three decades following the *Exxon Valdez* oil spill, epidemic, and collapse, whereas the Sitka Sound and Togiak Bay populations have not. Moreover, the regions of the genome subject to the pressures of natural selection are not the same between successive time periods. This indicates that the environment has been changing over time, such that genes that affect fitness in one time period are different from those in another – that selective regimes have been shifting over time. This is consistent with the massive changes in the PWS environment that have unfolded over the past three decades.

Objective 4: Develop new approaches to monitoring.

We were able to confirm that the new approach for measuring VHSV antibody activity is changing our understanding of the disease dynamics. We are now able to demonstrate that the antibody activity can be detected for at least three years after survival from the initial exposure. Therefore, we can use the antibody information to deduce prior exposure and not have to rely on the prevalence data. The antibody information (seropositive) is providing a much different picture of the exposure history in PWS than has ever been inferred from the prevalence data. We have also been able to model the disease dynamics using this new information.

Tagging provided ample information about the movement patterns of herring. We had good success in tagging herring and observing them as they came and went from PWS. Receivers mounted on moorings and gliders provided information about the tagging success and movement of the fish. We were able to examine the typical routes that herring took after spawning and found that larger fish were more likely to leave PWS. There was a tendency for fish to leave through the closest entrance (Hinchinbrook) and move towards the southwest passages. They then returned throughout the fall and winter favoring Montague Strait and the other southwest passages.

We were able to take advantage of advances in genetics to gain a better understanding of changes in the genetic structure of herring in time and space. We were also able to examine biotic responses related to exposure to oil and diseases.

Our results indicated that some age-2 herring had spawned. The current maturity function does not show spawning as occurring until age-3. It is not possible to determine how prevalent age-2 spawning is but there are very few age-2 herring collected with the spawning population. In the scale analysis we did not observe unimodal growth in fish less than three years old, which was unexpected. There was some evidence of bimodal growth in particular age-classes within a year but we did not observe a consistent difference that may indicate changes in annual growth depending on whether the fish was maturing.

We continue to look for additional ways to detect herring spawn that may be missed using our traditional survey techniques. The increasing availability of high-resolution satellite imagery is allowing us to search areas not covered by the survey plane. Satellite imagery remains limited by the number of overpasses and the inability to view through even thin cloud layers.

CONCLUSIONS

The program was able to meet its objectives even with the restrictions that came about from the COVID-19 pandemic. We continue to examine the factors that may be preventing the herring population from recovering to the levels observed in the 1980s. The decrease in the population beginning around 2015 and subsequent recovery associated with the recruitment of the 2016 year class are providing opportunities to test ideas associated with enhanced recruitment events. These large recruitment events appear to be large-scaled, with enhanced recruitment observed throughout the Gulf of Alaska. More local events are becoming evident as well. A large 2012 year class was observed in most locations in the Gulf of Alaska but not in PWS, although early indicators suggested that there should have been a strong recruitment from the 2012 year-class.

The modeling efforts are providing more information about potential mechanisms of recovery and showing the difficulties of identifying the specific sets of conditions that lead to strong recruitment or unusual mortality. Our modeling project to build a model of intermediate complexity (MICE model) that includes humpback whales, pink salmon, pollock, and herring is a next step in the model's evolution. It is also important to examine the management strategies if the population remains closer to the current levels. It may be that our time series starts with an unusually high population, and it isn't realistic to expect it to return to the levels observed in the 1980s. We recognize that the model does not have a mechanism that can adjust to unusual mortality events. We continue to work on the proper way to incorporate the seropositive data to determine if we can then better account for mortality associated with VHSV.

There remains much to be learned about the dynamics of the important herring diseases. When does *Ichthyophonus* cause mortality and how is it transmitted remain open questions. We think that fish eggs may be an important mechanism in the transmission of *Ichthyophonus* that we can test.

We continue to believe that PWS herring provide the very best opportunity possible to tease out key factors in predicting changes in recruitment, natural mortality, and spawn timing. Few regions, if any, in the world contain such a rich dataset of biological, oceanographic, and climate indexes that has been maintained for such a long period of time. If fisheries science ever solves these problems, it will be because of the data collected by the HRM and Gulf Watch Alaska programs.

The importance of the program to the local communities has been evident in the growing interest in following our observations and findings through social media and other outlets. More importantly, the support from fishermen and other people in the area for collection of data and observations that complement the scientific observations. Without this support the program would not have been able to succeed as well as it has.

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Vega, S. L., C. W. Russell, J. Botz, and S. Haught. 2018. 2017 Prince William Sound area finfish management report. Alaska Department of Fish and Game, Fishery Management Report No. 19-07, Anchorage.

Publicly available datasets

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Trochta, J. T., J. A. Zahner, and T. A. Branch. 2022. Model code and data for 2021 Bayesian Age-structure Stock Assessment (BASA) results. Available from: https://portal.aoos.org/#metadata/4aaecfe2-de4b-4b6b-ba8e-bb715d26c6f1/project

Whitehead, A. 2022. Population genomics of Pacific herring across space (from California to Alaska) and through time (for Alaska populations from 1991 to 2017): NCBI BioProject

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Scientific Presentations

Arimitsu, M., M. A. Bishop, D. Cushing, S. Hatch, R. Kaler, K. Kuletz, C. Matkin, J. Moran, D. Olsen, S. Pegau, J. Piatt, A. Schaefer, and J. Straley. Changes in marine predator and prey populations in the Northern Gulf of Alaska: Gulf Watch Alaska Pelagic update 2019. Poster presentation. Alaska Marine Science Symposium, Anchorage, AK, January.

Arimitsu, M., M. A. Bishop, D. Cushing, S. Hatch, R. Kaler, K. Kuletz, C. Matkin, J. Moran, D. Olsen, S. Pegau, J. Piatt, A. Schaefer, and J. Straley. 2021. Heatwave-induced synchrony within forage fish portfolio disrupts energy flow to top pelagic predators. Poster presentation. Alaska Marine Science Symposium, Anchorage, AK, January.

Arimitsu, M., M. A. Bishop, D. Cushing, S. Hatch, R. Kaler, K. Kuletz, C. Matkin, J. Moran, D. Olsen, S. Pegau, J. Piatt, A. Schaefer, J. Straley, and J. Durban. 2022. Changes in marine predator and prey populations in the northern Gulf of Alaska: Gulf Watch Alaska pelagic update 2021. Poster presentation. Alaska Marine Science Symposium, Anchorage, AK, January.

Batten, S., M. A. Bishop, R. Bochenek, K. Boswell, T. Branch, M. Collins, K. Gorman, J. Guyon, R. Heintz, P. Hershberger, S. Moffitt. S. Pegau, P. Rand, F. Sewall, D. Thorne, J. Vollenweider, S. Wilde, and Cordova District Fishermen United. 2017. Prince William Sound Herring Research and Monitoring, Poster presentation. PICES small pelagics conference. Victoria, Canada, October.

Bishop, M. A. 2020. Annual herring migration cycle. Review of the Herring Research and Monitoring Program by the *Exxon Valdez* Oil Spill Trustee Council Science Panel. Oral presentation. February, Anchorage.

Bishop, M. A., T. Branch, K. Gorman, M. Groner, S. Haught, P. Hershberger, S. Pegau, P. Rand, J. Trochta, and A. Whitehead. 2020. PWS Herring Research and Monitoring. Poster presentation. Alaska Marine Science Symposium, Anchorage, AK, January.

Bravo, E., C. Conway, P. Hershberger, J. Gregg, and M. Groner. 2018. Do histological analyses of herring infected with *Ichthyophonus* sp. suggest a shift from endemic to epidemic disease? Poster presentation. Society for the Advancement of Chicanos / Hispanics and Native Americans in Science. San Antonio, TX. October.

Cypher, A. D., P. K. Hershberger, J. Gregg, and J. Incardona. 2020. Influence of embryonic crude oil exposure in overwinter fasting and disease susceptibility in juvenile Pacific herring (*Clupea pallasii*). Online presentation. Alaska Marine Science Symposium. Anchorage, AK. January.

Cypher, A. D., P. Hershberger, N. Scholz, and J. P. Incardona. 2019. Larval cardiotoxicity and juvenile performance are likely contributors to the delayed fishery collapse of Pacific herring after the *Exxon Valdez* oil spill. Poster presentation. Society for Integrative & Comparative Biology Annual Meeting. Tampa, FL. January.

Cypher, A. D., H. Statscewich, R. Campbell, S. L. Danielson, J. H. Eiler, and M. A. Bishop. 2022. Detecting acoustic tagged Pacific herring (*Clupea pallasii*) using an autonomous underwater glider carrying an integrated acoustic receiver in Prince William Sound, AK. Online Presentation. Alaska Marine Science Symposium, January, Anchorage.

Dias, B. S., D. W. McGowan, and T. A. Branch. 2020 Influence of environmental and population factors on herring spawn timing in Prince William Sound. Oral presentation. PICES Workshop VW6, Research priorities for understanding the population dynamics of small pelagic fish in the North Pacific, Vancouver, October.

Dias, B. S., D. W. McGowan, R. Campbell, and T. A. Branch. 2020 What affects spawning phenology of herring (*Clupea pallasii*) in Prince William Sound? Oral presentation. Alaska Marine Science Symposium, Anchorage, AK, January.

Gill, T., T. Linbo, P. Hershberger, J. Incardona, and A. Whitehead. 2019. Interactions between oil exposure and immune function relevant for Pacific herring population collapse. Poster Presentation. Annual Meeting of the Society of Environmental Toxicology and Chemistry. Toronto, ON, Canada. November.

Gray, B. P., M. A. Bishop, S. P. Powers. 2018. Identifying key piscine predators of Pacific herring (*Clupea pallasii*) and walleye pollock (*Gadus chalcogrammus*) during winter months in bays of Prince William Sound, Alaska through multivariate analysis of stomach contents. Poster Presentation. Alaska Marine Science Symposium,January, Anchorage.

Groner, M., E. Bravo, C. Conway, J. Gregg, P. Hershberger. 2019. A quantitative histological index to differentiate between endemic and epidemic ichtyhophoniasis in Pacific herring. Poster presentation. Alaska Marine Science Symposium. Anchorage, AK. January.

Groner, M. L., E. Bravo-Mendoza, C. M. Conway, A. H. MacKenzie, J. L. Gregg, and P. K. Hershberger. 2021. Epidemiology of ichthyophoniasis in Pacific herring in Sitka Sound and Prince William Sound from 2007 – 2018. Online presentation. Alaska Marine Science Symposium. Anchorage, AK, January.

Hershberger, P. K., A. H. MacKenzie, J. L. Gregg, R. Powers, and M. K. Purcell. 2020. Long term shedding of viral hemorrhagic septicemia virus from Pacific herring. Poster presentation. Alaska Marine Science Symposium. Anchorage, AK. January.

Hershberger, P. K., A. H. MacKenzie, J. L. Gregg, M. D. Wilmot, R. Powers, and M. K. Purcell. 2017. Long term shedding of viral hemorrhagic septicemia virus from Pacific herring. Online presentation. 58th Western Fish Disease Workshop. Suquamish, WA. June.

Hershberger, P. K., L. Hart, A. MacKenzie, R, Powers, and M. Purcell. 2017. Quantifying the potential for disease impacts to Pacific Herring. Poster presentation.. Alaska Marine Science Symposium. Anchorage, AK. January.

MacKenzie, A. H., J. L. Gregg, M. D. Wilmot, T. Sandell, D. Lowry, and P. K. Hershberger. 2017. Temporal and spatial patterns of *Ichthyophonus* in Pacific herring throughout the southern Salish Sea. Poster presentation.. 58th Western Fish Disease Workshop. Suquamish, WA. June.

McGowan, D. W. 2019. Spatial and temporal variations in Pacific herring spawning in Prince William Sound. Poster presentation. Alaska Marine Science Symposium, Anchorage,

McGowan, D., and T. A. Branch. 2019. Large multi-decadal space and time shifts in Pacific herring spawning in the Gulf of Alaska. Oral presentation. PICES, Victoria, BC. 21-24 October.

Mena, A. J., J. St. Ledger, A. MacKenzie, J. Gregg, M. Purcell, W. Batts, P. Hershberger, and E. E. B. LaDouceur. 2020. *Ichthyophonus* sp. infection in opaleye (*Girella nigricans*). Poster presentation. International Aquatic Animal Medicine Conference. Tampa, FL. May.

Sitkiewicz, S., B. Harris, P. Hershberger, and N. Wolf. 2017. Impacts of the Parasite *Ichthyophonus* (sp.) on Groundfish Growth and Condition. Poster presentation. Joint Meeting of the American Fisheries Society, Alaska Chapter American Water Resources Association, Alaska Section. Fairbanks, AK. March.

Sitkiewicz, S., B. Harris, P. Hershberger, and N. Wolf. 2017. Effects of the parasite *Ichthyophonus* (sp.) on groundfish growth and condition. Poster presentation. Alaska Marine Science Symposium. Anchorage, AK. January.

Sitkiewiz, S. E., B. P. Harris, P. K. Hershberger, and N. Wolf. 2017. Effects of the parasite *Ichthyophonus* on groundfish growth and condition. Poster presentation. 58th Western Fish Disease Workshop. Suquamish, WA. June.

Sitkiewicz, S., P. Hershberger, N. Wolf, and B. Harris. 2018. Effects of the parasite *Ichthyophonus* (spp.) on Pacific halibut (*Hippoglossus stenolepis*) growth and condition. Poster presentation. Alaska Marine Science Symposium. Anchorage, AK. January.

Stinson, M. E., B. C. Hall, B. C. Stewart, and P. K. Hershberger. 2017. Validation of improved *Listonella* (*Vibrio*) *anguillarum* vaccine in coho salmon. Poster presentation. 58th Western Fish Disease Workshop. Suquamish, WA. June.

Trochta, J. T. 2020. A Bayesian analysis of the utility of ecosystem information in a stock assessment. Oral presentation. Alaska Marine Science Symposium, Anchorage, AK, January.

Trochta, J. T. 2020. The rise of Bayesian: A stock assessment story. Invited talk. American Fisheries Society 150th Annual Meeting, Virtual, September.

Trochta, J. T., and T. A. Branch. 2018. Insights into the dynamics of Atlantic and Pacific herring following population collapse. Oral presentation Alaska Marine Science Symposium, Anchorage, AK, January.

Trochta, J. T., and T. A. Branch. 2019. Evaluating the effects of a changing ecosystem on Pacific herring (*Clupea pallasii*) in Prince William Sound, Alaska. Poster presentation. Alaska Marine Science Symposium, Anchorage, AK, January.

Trochta, J. T., and T. A. Branch. 2020. Challenges to estimating maturity in stock assessment: a case study of Pacific herring in Prince William Sound, AK. Invited talk. Think Tank Seminar Series. School of Aquatic and Fisheries Science, Seattle, WA, April.

Trochta, J. T., and T. A. Branch. 2020. Hard of herring: Detecting effects on herring survival from a noisy environment in the Gulf of Alaska. Invited talk. Alaska Department of Fish and Game, Juneau, AK, February.

Trochta, J. T., and T. A. Branch. 2021. A framework for incorporating and evaluating environmental hypotheses using Bayesian stock assessments. Oral presentation. ICES Annual Science Conference, Virtual, Denmark, September.

Trochta, J. T., and T. A. Branch. 2021. Using Bayesian model selection to evaluate different ecosystem effects on natural mortality in stock assessment of Prince William Sound herring. Oral presentation. Center for the Advancement of Population Assessment Methodology, Workshop on Natural Mortality: Theory, Estimation, and Application in Fishery Stock Assessment Models, Seattle, WA, June.

Trochta, J. T, T. A. Branch, and W. S. Pegau. 2020. Challenges to estimating maturity in stock assessment: a case study of Pacific herring in Prince William Sound, AK. Oral presentation. School of Aquatic and Fishery Sciences Think Tank, Seattle, WA, April.

Trochta, J. T., M. L Groner, P. K. Hershberger, and T. A. Branch. 2021. Using antibody data to quantify disease impacts in fisheries stock assessment. Oral presentation. Alaska Marine Science Symposium, Anchorage, AK, January.

Trochta, J. T., M. L. Groner, P. K. Hershberger, and T. A. Branch. 2020. Using antibody data to improve estimates of natural mortality in fisheries stock assessment. Invited talk. Quantitative seminar. School of Aquatic and Fisheries Science, Seattle, WA, October.

Trochta, J. T., A. MacCall, D. McGowan, and T. A. Branch. 2019. Incorporating spawn surveys in a semi-spatial stock-recruitment model. Oral presentation. Center for the Advancement of Population Assessment Methodology (CAPAM) conference on Spatial Stock Assessment Models, La Jolla, CA, October.

Wendt, C., P. Hershberger, and C. Wood. 2019. Patterns of *Ichthyophonus* sp. infection in age zero Pacific herring. Poster presentation. Alaska Marine Science Symposium. Anchorage, AK. January.

Outreach

Bishop, M. A. 2017. Pacific herring: Once done spawning – Where to next? Delta Sound Connections 2017-18. https://pwssc.org/wp-content/uploads/2017/05/DSC-2017.pdf.

Bishop, M. A. 2018. How to tag a herring. Delta Sound Connections 2018-19. http://pwssc.org/wp-content/uploads/2018/05/DSC-2018-FINAL_WEB.pdf.

Bishop, M. A. 2019. Time to spawn! Delta Sound Connections 2019-20. https://pwssc.org/wp-content/uploads/2019/05/DSC-2019_WEB.pdf.

Bishop, M. A. 2021. O herring, where are thou? Delta Sound Connections 2021-22. https://pwssc.org/wp-content/uploads/2021/06/DSC-2021-LR.pdf.

Bishop, M. A. 2021. Shackleton's Search for herring. PWSSC Breakwater Newsletter, March.

Bishop, M. A. 2022. Early returns: Do herring winter near their spawning grounds? Delta Sound Connections 2022-23. https://pwssc.org/wp-content/uploads/2021/06/DSC-2021-LR.pdf.

Bishop, M. A., and J. W. Bernard. 2021. Acoustic-tagged herring - modeling the unknown. Delta Sound Connections 2021-22. https://pwssc.org/wp-content/uploads/2021/06/DSC-2021-LR.pdf.

Bishop, M. A., and B. Gray. 2019. How to tag a herring and where do they go afterwards? PWSSC Tuesday night lecture series. January, Cordova.

Dias, B. S. 2021. About time. Delta Sound Connections 2021-2022. https://pwssc.org/wp-content/uploads/2021/06/DSC-2021-LR.pdf.

Dias, B. S. 2022. What is causing herring early spawning? Delta Sound Connections 2022-2023. https://pwssc.org/wp-content/uploads/2022/06/DSC-2022-WEB.pdf.

Gray, B. 2019. Ping! Tracking fish using passive acoustic technology. Delta Sound Connections 2019-20. https://pwssc.org/wp-content/uploads/2019/05/DSC-2019_WEB.pdf.

Gray, B. 2018. Herring on the menu. Delta Sound Connections 2018-19. http://pwssc.org/wp-content/uploads/2018/05/DSC-2018-FINAL_WEB.pdf.

Haught, S. 2018. Aerial Surveys of Pacific Herring. Delta Sound Connections 2018-19. http://pwssc.org/wp-content/uploads/2018/05/DSC-2018-FINAL_WEB.pdf.

Haught, S. 2019. Mile-Days of Milt. Delta Sound Connections 2019-20. https://pwssc.org/wp-content/uploads/2019/05/DSC-2019_WEB.pdf.

Hershberger, P. K. 2017. Long term shedding of VHS virus from Pacific herring: Demonstration of a marine reservoir host. Invited talk, Washington State Disease Co-Managers Meeting, Olympia, WA. July 5-6.

Hershberger, P. K. 2018.Causes of Pacific herring mortality: A disease perspective. Annual Science Night invited talk, Prince William Sound Regional Citizens Advisory Council. December 6.

Hershberger, P. K. 2018. The ecology of disease in marine fishes: Insights from Pacific herring. Invited seminar, NOAA – Northwest Fisheries Science Center, Monster Seminar Jam. May 24.

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Principal investigator Trevor Branch communicates widely about science including this project on social media at @TrevorABranch on Twitter. He has 17,400 followers and has posted more than 50,000 times. During this project (February 2017 to January 2022) his tweets were viewed 40.2 million times.