Pacific herring in Prince William Sound: A synthesis of recent findings

Herring Research and Monitoring Team

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For the Exxon Valdez Oil Spill Trustee Council

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Contents

Executive Summary

The work presented here covers new findings and knowledge acquired since May 2013, when a synthesis of the Prince William Sound Herring Survey program (Pegau 2013) was submitted to the EVOS Trustee Council. While only 18 months have passed between the two synthesis efforts, there has been significant progress towards our understanding of Pacific herring movements, how herring growth and energetic conditions depend on environmental conditions, the prevalence of the disease *Ichthyophonus*, and the use of ice cover by age-0 herring.

Most of the material included in this synthesis comes from findings within the Herring Research and Monitoring (HRM) program. The goal of that program is to improve predictive models of herring stocks through research and monitoring. The program is made up of 20 individual projects that are designed to address four objectives.

1) Provide information to improve input to the age-structure-analysis (ASA) model, or test assumptions within the ASA model.
2) Inform the required synthesis effort.
3) Address assumptions in the current measurements.
4) Develop new approaches to monitoring.

The HRM program is currently half way through its five-year research plan. Not all components are complete, and we do not report on all aspects of the HRM program. When possible we combine results from the HRM program with previous research to develop new understanding of Pacific herring in Prince William Sound.

In addressing the first objective, significant progress has been made in rebuilding the ASA model used by Alaska Department of Fish and Game in a Bayesian framework that allows for estimating the Prince William Sound herring population, including confidence intervals for that estimate. A leave-one-out modeling approach to evaluate the importance of model inputs found that egg deposition, which was the only variable assumed to be an absolute measure of herring abundance, and hydroacoustic biomass estimates are both highly informative for stock assessment purposes.

One of the projects designed to inform the synthesis effort is the imaging of historic Pacific herring scales to determine growth patterns over time. Growth in the first year was found to be strongly correlated to diatom abundance in the Gulf of Alaska, as measured by the continuous plankton recorder in the Gulf Watch Alaska (GWA) program, and to summer water temperatures in Prince William Sound. The relationship with water temperature corresponds to the 18.6 year lunar tidal component and the Pacific Decadal Oscillation.

Several studies address the assumptions underlying measurements being used. Monthly measurements of growth and energetics indicate that the timing of sampling efforts is appropriate for the herring monitoring program. However, the assumed linear decrease in energy over time is not correct and instead decreases exponentially. Samples for fatty acid analysis were not able to show immigration and

emigration of herring. They did show that winter foraging is significant enough to change the fatty acid composition over time. Herring with low lipid levels in November appeared to need to forage and their fatty acid composition changed by March. Fortnightly hydroacoustic surveys in two found significant variations in age-0 herring abundance estimates. The causes of these variations need to be accounted for when interpreting the hydroacoustic surveys for juvenile abundance. Disease monitoring showed that the prevalence of *Ichthyophonus*, a pathogenic protist, is dependent on herring age, which needs to be accounted for when reporting disease prevalence.

Acoustic tagging of adult herring and surveying of juvenile herring with sensors on a remotely operated vehicle provided opportunities to evaluate new approaches to monitoring. Adult herring have a high survival rate when implanted with an acoustic tag. After spawning, adults aggregrated at the southern end of Montague Strait and Hinchinbrook Entrance and left the areas by late June. In September, herring reappeared at Montague Strait and again lingered there for some time.

Using imaging sonar and camera systems mounted on a remotely operated vehicle age-0 herring were found underneath shelf ice within bays during late winter. Size estimates from the sonar were consistent with nearby trawl data. The size of herring under the ice was smaller than in open water.

Combining the research results on growth, energetics, and fatty acids showed regional differences that are consistent with ocean circulation patterns. There are spatial and temporal differences in the $\delta^{13}C$ signature that suggests that food from the Gulf of Alaska is important in determining the condition of juvenile herring. These results indicate that winter foraging occurs when lipid levels reach a critical low. In March, age-0 herring have an energetic content at levels that indicate they are on the verge of death. As a result, age-0 herring are forced to forage and thus be at greater risk to predation.

Our understanding of growth and predation of herring benefits from contributions from the GWA program. The environmental drivers section is providing the data necessary to examine the roll of bottom up forcing on the herring populations. The pelagic component provides information about predation by humpback whales and marine birds, as well as competitors through the forage fish project. The GWA and HRM program are also connected through logistics. The design and implementation of aerial surveys of forage fish were completed with contributions from the HRM and GWA programs. Space is also made available on herring sampling cruises for GWA marine bird surveys. It is through the combined information from the two programs that we can continue to make advances in our understanding of herring in PWS.

The advances in our knowledge about Pacific herring suggest useful avenues of continued research. We recommend maintaining the program goal to improve predictive models of herring stocks through research and monitoring. To achieve this goal will require monitoring of disease prevalence, the spawning biomass using hydroacoustic surveys, and juvenile herring abundance to predict incoming recruitment to the spawning stock. An expanded population model should be developed that can examine different inputs and model scenarios in a manner that can guide future research. We recommend that the research focus be to describe the seasonal distribution patterns of different life

stages of herring. This is needed to ensure we use appropriate data to examine bottom-up forcing. It is also required to understand the overlap with species that are competitors and predators of herring.

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), many contributions to herring related symposia (e.g. Funk et al. 2001), as well as many research publications. This synthesis builds upon previous work, and is not intended to replicate those efforts, but instead to add new insights gained from the Herring Research and Monitoring Program over the last two years.

The PWS herring population remained high for a few years after the 1989 *Exxon Valdez* oil spill, but collapsed in 1993 (Figure 1). Except for two seasons in the late 1990s, the commercial herring fishery has been closed since 1993. 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. 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).

The failure of PWS herring to recover is defined by factors that suppress spawning stock biomass and other factors that prevent punctuated recruitment events. The factors that prevent an increase in biomass can be different than 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. It is clear; however, that in PWS there has not been a large recruitment event in the last twenty years (Figure 2). The low recruitment levels have led to a series of studies that examine the early life stage of the Pacific herring. The synthesis of that work was reported by Pegau (2013).

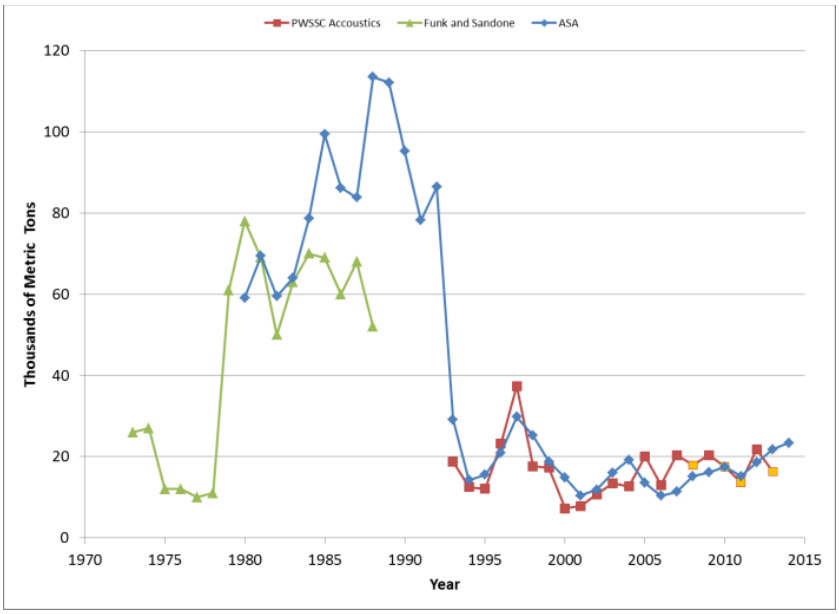

Figure 1. PWS estimated prefishery run biomass from ASA models (green triangles and blue diamonds) and hydroacoustic surveys (red squares). The squares marked in yellow are years that the hydroacoustic estimate is believed to be biased low due to survey conditions. Funk and Sandone (1990) provide estimates of historic herring biomass based on an early version of the Age-Structure-Analysis (ASA) model. It is important to note that the aerial surveys during the early years did not reach all spawning locations in the Sound. The ASA data is from the 2013 run of the model used by ADF&G.

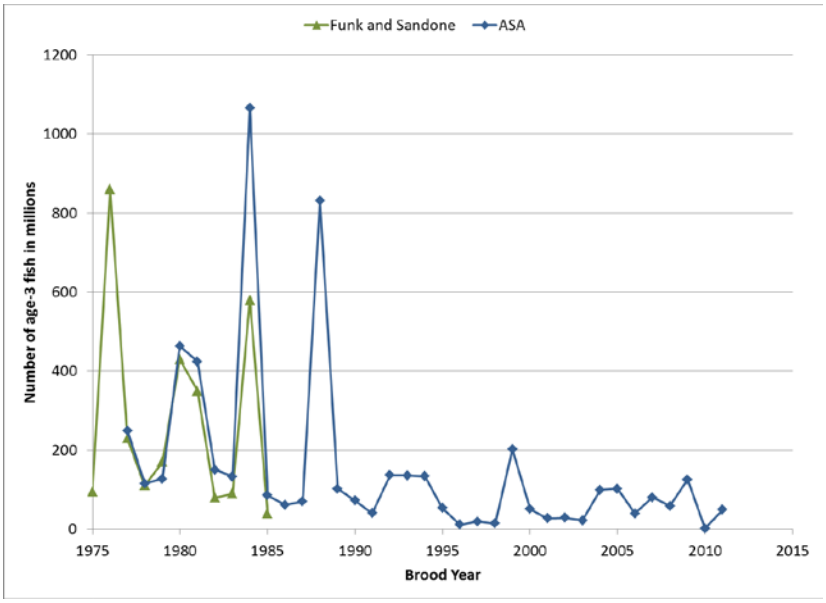

Figure 2. Estimated number of age-3 fish recruiting to spawning stock by brood year. Funk and Sandone (1990) provide estimates of historic herring biomass based on an early version of the Age-Structure-Analysis (ASA) model (green triangles). The ASA data is from the 2013 run of the model used by ADF&G (blue diamonds).

Beginning in 2012 the Exxon Valdez Oil Spill Trustee Council (EVOSTC) funded the Herring Research and Monitoring program. The goal of that program is to improve predictive models of herring stocks through research and monitoring. The program is made up of twenty individual projects that are designed to address four objectives:

1) Provide information to improve input to the age-structure-analysis (ASA) model, or test assumptions within the ASA model.
2) Inform the required synthesis effort.
3) Address assumptions in the current measurements.
4) Develop new approaches to monitoring.

These objectives are being pursued using a combination of monitoring and process studies. This report synthesizes the knowledge gained over the past two years, building upon Pegau (2013) and examines new findings where the two efforts overlap.

Adult herring population modeling

ADF&G age-structure-analysis model

The goal of herring research currently being conducted in PWS is to improve predictive models of herring stocks through research and monitoring. The predictive model of herring stocks currently being used is an age-structured assessment (ASA) model and is described below (Hulson et al. 2007). The model used by Alaska Department of Fish and Game (ADF&G) is a standard implementation of an ASA model (Quinn and Deriso, 1999), modified to include the impact of disease on mortality (Quinn et al. 2001). Least squares errors are minimized for the difference between observation and model values of recruitment, initial abundance in the first year, maturity, gear selectivity, a milt calibration coefficient, a hydroacoustic calibration coefficient, and disease coefficients. This minimization is done in MS Excel using the Solver add-in.

Pre-fishery total abundance $N_{a.t}$ starts with recruitment and initial abundance parameters (in millions of fish). The model is given by:

$$N_{a+1,t+1} = \left[\left(\left(N_{a,t} - \left(C_t^s \Theta_{a,t}^s + C_{a,t}^g + P_k C_{a,t}^P\right)\right) S_{a,t}^{\frac{1}{2}}\right) - C_{a,t}^{\frac{f}{b}}\right] S_{a,t+1}^{1/2}$$

The pre-fishery population decreases as a result of four commercial fisheries (s, seine; g, gillnet; p, pound utilization; f/b, food and bait), and natural mortality (expressed in terms of survival S). S is a function of age and year to accommodate disease prevalence. Because the food and bait fishery occurred in the fall and the other fisheries in the spring, survival is expressed in half-year intervals. The catch in the *i*th fishery at age *a* in year *t* ($C_{a,t}^i$) is estimated from the age distribution from the seine fishery, multiplied by a gear selectivity coefficient and the total catch by that fishery. The P_k value for proportion of impounded herring killed is set to 0.75.

The full set of equations associated with the model and a full description of parameters is provided in Appendix 1.

Survival is calculated based on an assumed fixed background mortality that is adjusted annually for disease prevalence. From 1980-1992, mortality is assumed at a fixed value of 0.25 (S = 0.779) except for age-9 and older where S=0.25. From 1993 to present, mortality is adjusted for disease prevalence and is separated into two age groups (ages 3-4, and ages 5-8). The survival of age-9 and older fish is set to 0.567 times the survival of the age-5 through 8 group. The 1993 mortality values were adjusted to account for the crash in the population. Disease prevalence data is multiplied by a factor to account for the portion of the fish expected to die in the half-year (Marty et al. 2003). The primary difference is that Viral Hemorrhagic Septicemia (VHS) is considered the source of disease mortality in ages3-4 and *Ichthyophonus* is the source of mortality in ages5-8. A change in the approach to determining disease prevalence occurred in 2007 and the mortality factor for *Ichthyophonus* used by the model remains at the 2004 level.

The final input necessary to run the model is an initial abundance estimate of age-3 herring each year and age-3 through age-5 in 1980. For hindcasts, these estimates provide initial conditions for the model but do not represent the actual size of the cohort each year, which is estimated by the model. An accurate estimate of the incoming age-3 cohort is necessary for predicting the expected spawning biomass.

The model estimates the seine age composition ($\Theta_{a,t}^{S}$), spawning age composition ($\Theta_{a,t}^{SP}$), mile-days of milt (L_t), egg deposition(E_t), hydroacoustic biomass (H_t), Ricker spawner-recruit (R_t). The model minimizes the residual sum of squares of the difference between modeled estimates and observed values. The mile-days of milt, egg deposition, hydroacoustic biomass, and recruitment parameters are log transformed prior to determining the residual sum of squares. A weighting function is applied to each variable. The current weighting functions are:

Egg surveys	0.25
Mile-days of milt	1.00
Seine age composition	0.25
Spawn age composition	1.00
Acoustics Surveys	0.25
Ricker spawner-recruit	0.03

This weighting reflects the perception that fishery age composition and egg deposition data have not been collected in several years and may have low precision. There is no evidence of a Ricker spawner-recruit relationship and the non-zero weight is selected to prevent the recruitment estimates converging at zero.

The observed variables are associated with the spawning biomass. To move from the observed spawning stock numbers to the total pre-fishery number requires an estimate of the number of fish that have not recruited to the spawning biomass. This is done using maturity functions. Maturity is not

measured, but estimated from the age-composition data. Analyses of residuals suggest a change in the maturity function after 1997. The assumed maturation proportions are provided in Appendix 1.

Since the fisheries threshold is based on the biomass and the model calculations are in numbers of fish a conversion is required. For a given age class and year the pre-fishery spawning biomass is calculated using

$$PB_{a,t} = w_{a,t} mat_{a,t} N_{a,t}$$

where $w_{a,t}$ is the observed weight-at-age in year *t* and $mat_{a,t}$ is the maturity at age *a* in year *t*.

Updated age-structure-analysis model

Currently ADF&G manages Prince William Sound herring based on results of the Excel-based Age-Structured Assessment (ASA) model. The model is run every year to determine if the adult biomass is greater than the 22,000 t (about 20,000 metric tonnes or mt) that is the threshold for opening the commercial fishery. Parameters in the ASA model are estimated by minimizing sums of squares between the model estimates and the various data sources.

There are new efforts underway to integrate all the relevant herring data in an updated assessment framework (see Tables 2.1-2.5 from Muradian's MS thesis, Appendix 2). The key features of the new assessment model are (1) it is implemented in AD Model Builder (Fournier et al. 2011) which offers fast, reliable, model-fitting capabilities, (2) diverse data inputs are weighted using likelihoods instead of sums of squares, allowing for statistically sound weighting of datasets, and (3) the model is contained in a Bayesian framework that allows us to estimate uncertainty around each model output, which is not possible in the existing ASA model.

The updated ASA model incorporates or fits to the following data collected in Prince William Sound: age composition in the survey (Figure 3), catches, biomass trends from the ADF&G hydroacoustic surveys, Prince William Sound Science Center hydroacoustic surveys, mile-days of milt, and egg-deposition surveys (Figure 4), weight-at-age measurements, disease prevalence data that directly affects natural mortality estimates, and fecundity data. In pulling together all of these datasets, the updated ASA model synthesizes many of the research products coming out of the broader project.

One additional capability of the updated ASA model is that it can estimate the additional variance that needs to be added to the reported standard errors of each data point, such that all time-series of data are consistent with each other and the model. Such additional variance comes from year-to-year factors (migration, proportion of population available to the surveys) that, in effect, increase the overall variability for a survey time series.

The key advance of the updated ASA model is its ability to estimate uncertainty in the estimates of pre-fishery biomass, recruitment, and exploitation rate (Figure 5). We present draft results that will continue to change as the model inputs and structure are revised. Initial indications are that biomass has been slightly higher during 2008–2013 compared to 1999–2007, with about a 50-80% probability of

being below 20,000 mt in these recent years. Biomass in 2013 was estimated to be 19,000 mt (95% interval 11,800–30,000)

Some factors to bear in mind for the updated ASA model (which also apply to the existing ASA model), are that egg deposition estimates (Figure 4, top-right) are treated as an absolute measure of spawning biomass. By this, we mean that model estimates of numbers of herring at spawning age are multiplied by eggs produced at each age (fecundity) and then fitted to the egg deposition surveys. In the model we do estimate the additional variance to be added to the egg deposition surveys, which increases the uncertainty associated with the egg deposition data. The model in essence is trading off better fits to the mile-days of milt surveys against worse fits to the egg deposition data in the late 1980s (Figure 4 top left, top right).

The updated ASA model has several advantages over the current ASA model. Most important is the statistically-based likelihood-weighting of different data sources, which replaces the current method of fixing the weight assigned to each time series. Additionally, the updated ASA model allows us to estimate the probability of biomass being above or below management thresholds (Figure 5 top right) instead of focusing solely on the best mean estimate.

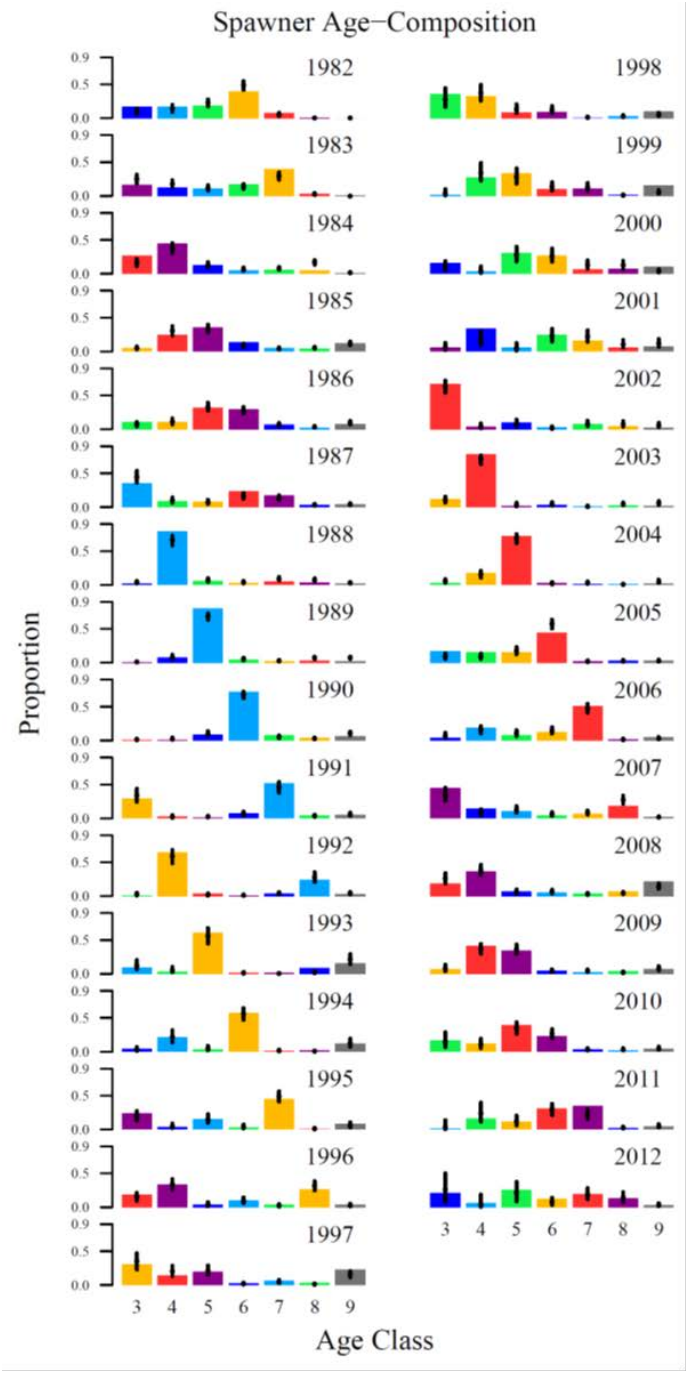

Figure 3. Updated ASA model fits (points; lines indicate 95% intervals) to the spawning age composition data (bars) from 1982-2011, showing the strong influence of a few dominant year classes entering the model at age 3. Each color represents an individual cohort.

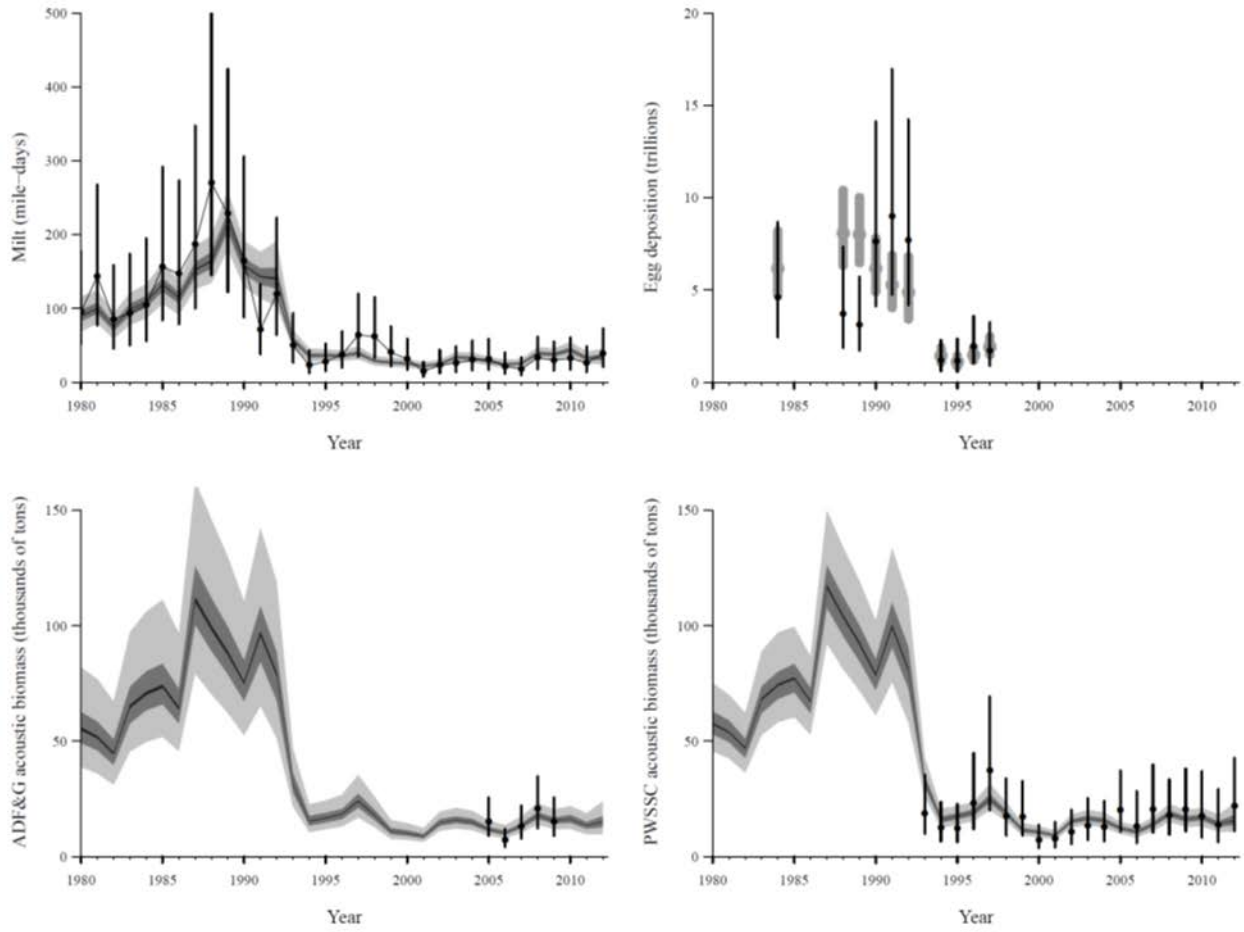

Figure 4. Draft model fits to four time series relating to abundance: mile-days of milt, egg deposition, ADF&G hydroacoustic estimates (mt), and PWSSC hydroacoustic estimates (mt). In each panel, solid circles and lines represent the mean and 95% intervals of the data (including additional variance estimated in the model), while shaded lines show model estimates of biomass (light gray = 95% interval, darker gray = 50% interval, black line = median).

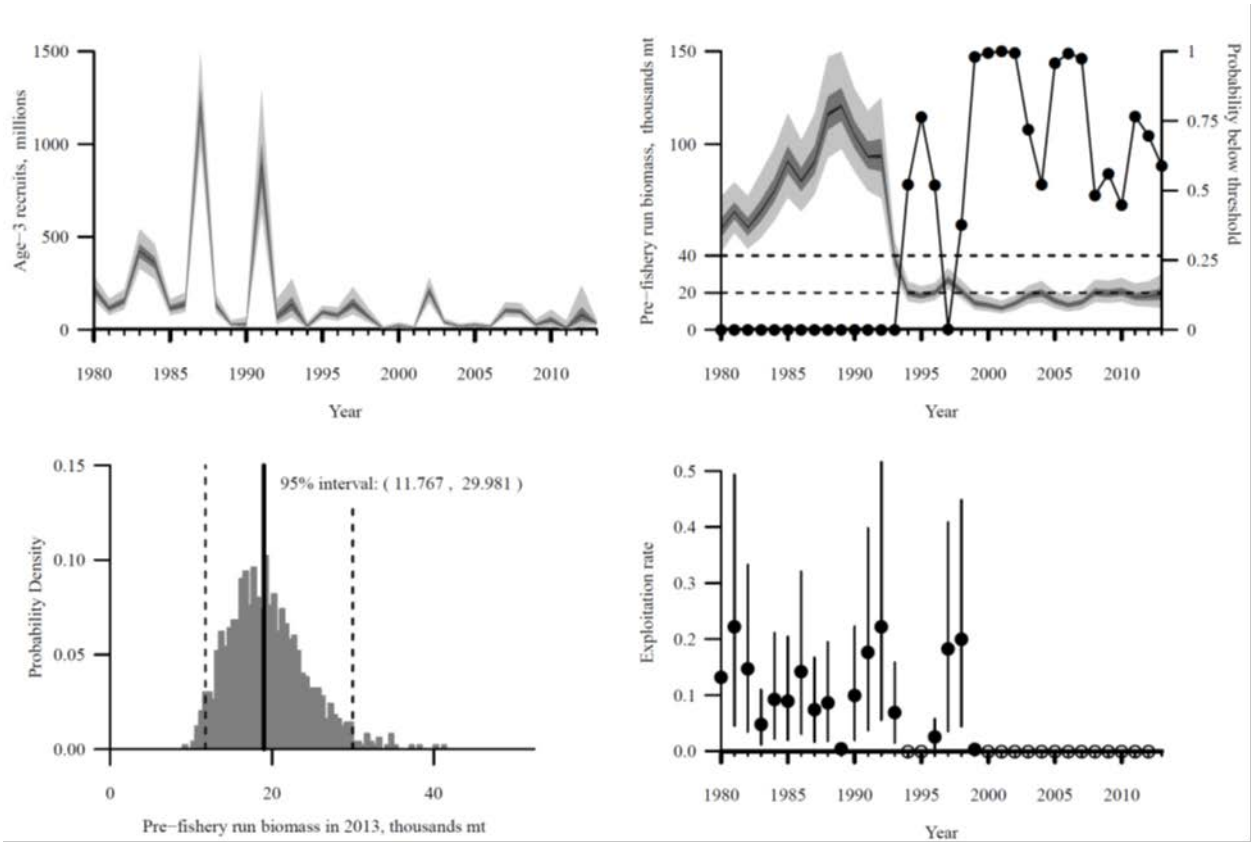

Figure 5. Draft results from the updated ASA model demonstrating the uncertainty estimates that come out of the Bayesian framework. The panels show estimated recruitment at age 3 (top-left), pre-fishery biomass (top-right bands), the probability that pre-fishery biomass is below 22,000 t (top-right points), estimated pre-fishery biomass in 2013 (bottom-left) and exploitation rate in each year (bottom right, open points show fishery closures).

In the next phase of the modeling project, the updated ASA model is used to assess the impact of different datasets on obtaining precise model outputs. We employ a leave-one-out approach, where each major type of data (disease, age-composition, mile-days of milt, proportion female, fecundity, egg deposition, hydroacoustic surveys) is left out, and the ASA model rerun to estimate pre-spawning biomass. The mean relative error is then calculated, using the full model representing the "truth". This general approach is repeated 1000 times, each time using the updated ASA model as an "operating model" that simulates a realistic suite of data (minus one dataset), which are input to the updated ASA model to examine the precision of the resulting biomass estimates. Preliminary estimates show that the egg deposition survey data and the hydroacoustic survey data are both highly informative for stock assessment purposes; and their omission results in substantial bias in the stock assessment. It is important to note that the egg deposition survey was the only variable treated as an absolute measure of herring abundance by the model.

The next phase of the modeling effort will examine the costs of collecting each type of data compared to the return on investment, as measured by the mean relative error. We expect that by this measure the hydroacoustic survey will outperform the much more expensive egg deposition survey, justifying the discontinuation of the egg deposition survey in the late 1990s.

Growth, energy, and the environment

Herring are known to be highly seasonally variable in their energetic composition (Vollenweider et al. 2011). Further, first winter survival of herring can be extremely low (Norcross et al. 2001); however, physical (ocean-climate) and biological drivers of variation in energy density and subsequent links with early life stage survival are not well understood. Age-0 herring have been collected since 2007 to examine energetic content before and after winter (Kline 2013).

Assumptions related to the seasonal sampling include: 1) sampling occurs when energy content is at its highest and lowest, 2) feeding does not occur through the winter, and 3) the energy loss through the winter is constant (Kline 2013). Monthly sampling from September 2011 through June 2012 was used to examine the seasonal sampling assumptions. Sampling included measuring energy density, herring lipid content as an index of stored energy, RNA/DNA ratio as a growth index, the isotopic ratios of carbon ($^{13}C/^{12}C$, $\delta^{13}C$) and nitrogen ($^{15}N/^{14}N$, $\delta^{15}N$) that provide an integrative proxy of trophic linkages (Peterson and Fry 1987), fatty acids as an indicator of feeding, and diet analyses. Together, these analyses enabled a more complete investigation into juvenile herring winter energy budgets, connection to environmental conditions, and mortality risks.

Monthly energy changes

Energetic data collected monthly between September 2011 and June 2012 confirmed that energy stores were depleted throughout the winter months (Figure 6). Considerable energy reserves were built between October and November. By December, energy reserves were significantly reduced, nearly to the levels found in January and February. By March, energy reserves began to rise again. Lipid content follows a similar pattern with a peak in lipids observed in November and a decrease that continues until the lipid level reaches a minimum in the February-March time period. The minimum lipid level is associated with what appears to be a critical level of 1.5% (of wet mass) below which the odds of survival are very low (Sewall, unpublished laboratory data). Growth as measured by RNA/DNA also has a similar seasonal pattern. Growth began decreasing in October as fish dedicated more resources to lipid storage. The RNA/DNA ratio then remained at a level that indicated no growth through March.

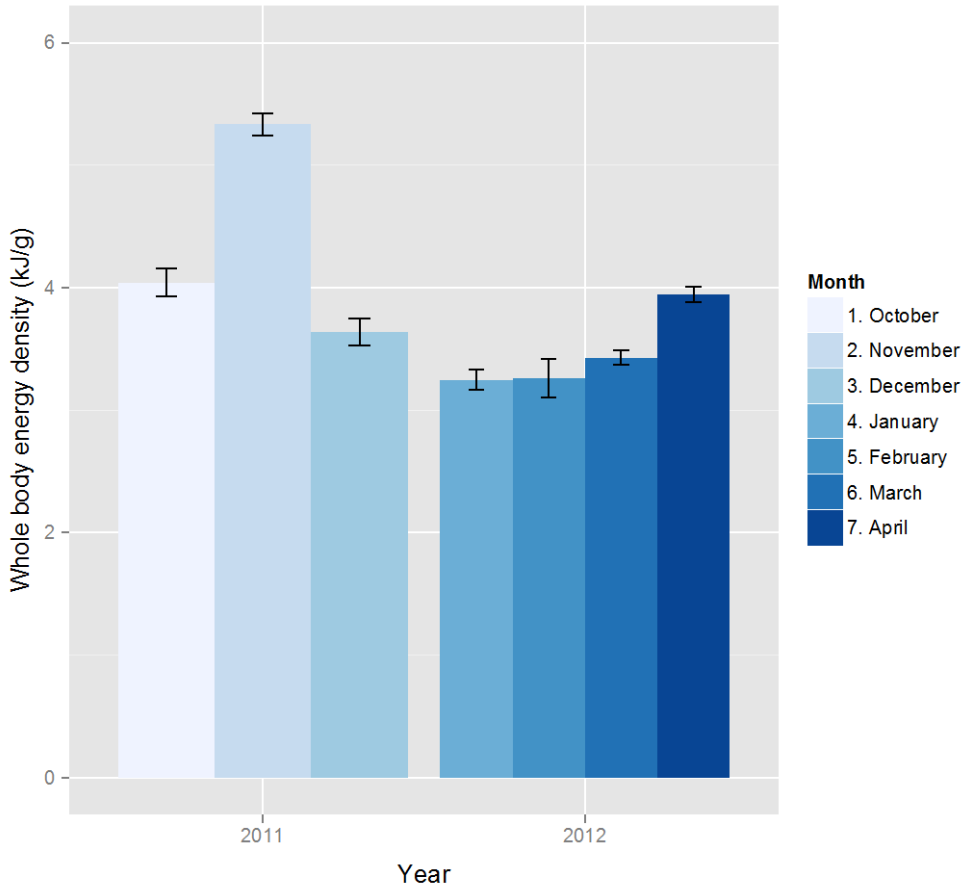

Figure 6. Winter 2011/12 variability in energy density of age-0 herring in Prince William Sound. Error bars are 95% confidence intervals.

Energy density, lipid content, and growth exhibited size dependence in age-0 herring. In the fall, larger herring shifted from growth to lipid storage earlier than smaller herring (Sewall et al. 2013). This increased lipid content leads to a higher energy density. Higher lipid content also allows the fish to remain above the critical lipid level longer in the spring. This is reflected in an apparent increase in size of age-0 herring beginning in February. There is no indication of growth from the RNA/DNA ratio at that time. Therefore, the increase in size is likely to be caused by size-dependent mortality that occurs as smaller fish reach the critical lipid level.

Since smaller fish tend to have lower lipid content they are more dependent on feeding throughout the winter. This is evident based on stomach content analysis of herring collected during winter (Table 1). Mean mass of stomach contents as a percentage of fish body mass tended to increase from December through February, which likely reflects greater reliance on dietary energy as lipid stores were decreasing. Size-dependent foraging may be evident in the fatty acid composition observed in March. Fatty acid composition is conserved during fasting, but measurements of fatty acid composition in

March show a change in composition indicating foraging during the winter. Fish with higher lipid content in March were found to have a fatty acid composition similar to that in November (Figure 7), indicating that those fish are not foraging. Fish sampled in spring with lipid levels near 1.5% show the greatest change in composition. This level was previously found to be associated with increased stomach fullness in juvenile herring sampled in spring (Sewall et al. 2013) and mortality in laboratory studies.

Table 1: Percent empty stomachs observed in age-0 herring captured in Simpson Bay, Prince William Sound, Alaska. *Herring caught by cast net and gillnet in May 2012 that were pooled in the field. Fish captured by castnet tended to be smaller than those caught by the gillnet used.

	Castnet		***Gillnet***	
Month	**% Empty**	**N**	**% Empty**	**N**
Sep 2011	0	60		
Oct 2011	0	20		
Nov 2011	0	30	70	10
Dec 2011	0	20		
Jan 2012	0	20		
Feb 2012	12.5	16		
Mar 2012	0	10	0	10
May 2012	25*	20 *		
Jun 2012	0	20		
Total	5.93	236		

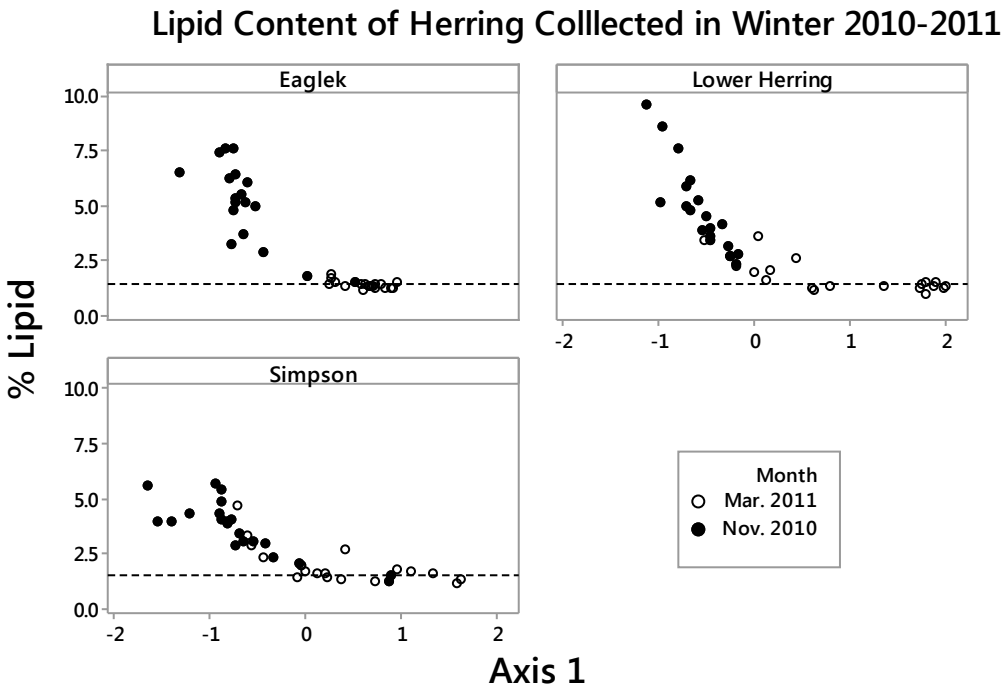

Figure 7. Relationship between MDS axis 1 score and the lipid content of juvenile herring sampled during winter 2010-2011. Horizontal line in plots indicates 1.5%, the critical level required for survival under laboratory conditions.

The assumption that November is the peak of energetic density is supported by the monthly data. There appears to be an increase in energy density in March, but it is not significantly different from that in February (Figure 6). The lipid content in March remains at the minimum level.

Decreases in energy density were not constant over time as previously predicted (Kline 2013). Instead there was a rapid decrease in energy as lipids were consumed that flattened out as the lipid levels reached a critical minimum. Stomach content and fatty acid data indicate that foraging occurs throughout winter, suggesting that smaller fish with lower lipid content are more likely to need to forage.

Seasonal, interannual, and spatial energetic variability

There is considerable seasonal variability in whole body energy density of age-0 herring. Fish collected in November are more energy dense than fish collected at the end of winter in March (Figure 8). This reflects the over-winter energetic strategy of juvenile herring where fish build energy reserves prior to winter that are needed to fuel basic maintenance metabolism until feeding can begin in earnest in the spring.

Energy density data from November 2010 represent the extreme low value while that from November 2012 and 2013 represent the extreme high energy density values in the current time series. However, subsequent sampling in March yielded different results as the March time series indicated that 2009 – 2011 were years of low energy density, while 2007 and 2013 were years of high energy density. During years with low whole body energy density (WBED) in March WBED is approximately 3.3 kJ/g. This may be a result of the fish reaching their minimum lipid levels and may represent a critical energy density below which the probability of mortality is high. The critical WBED observed in the field measurements is similar to that report by Paul and Paul (1998) for laboratory studies (3.2 kJ/g). The slight difference between field and laboratory observations is likely due to the field observations being live fish and the laboratory ones the WBED at death.

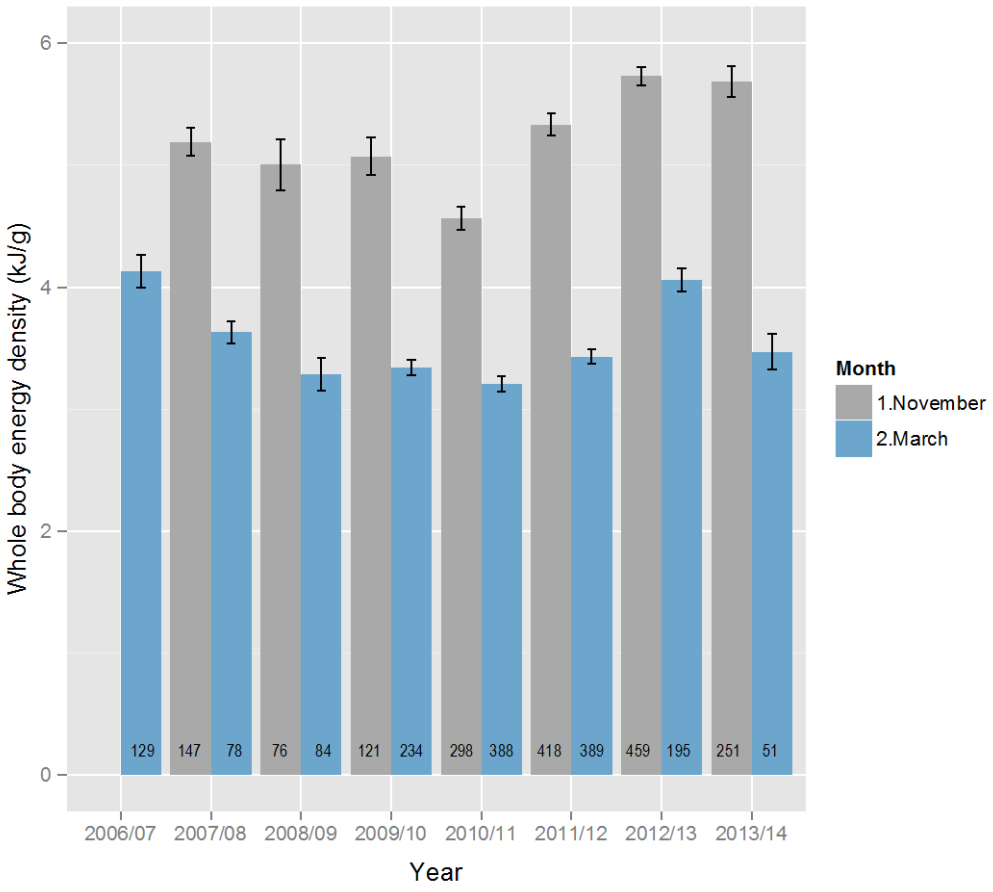

Figure 8. Seasonal variability in energy density of age-0 herring in Prince William Sound. Error bars are 95% confidence intervals. Sample sizes are noted at the bottom of each bar.

During the time period of these observations, the 2009 brood year had the largest recruitment to the spawning stock (Figure 2). The energetic density data from that brood year is not different from the weak recruitment of the 2010 and 2011 brood years. This result does not support energetics being a

good predictor of recruitment. The 2012 brood year that is significantly higher in energetic content in both November and following March has yet to recruit to the spawning stock.

Variability in stable isotope signatures of carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$) of age-0 herring has been examined for temporal and spatial variability. Fish collected in November consistently had depleted $\delta^{13}C$ signatures as compared with fish collected in March (Figure 9). Signatures of $\delta^{15}N$ showed little variability that might be associated with seasonal differences in energetics. Signatures of $\delta^{13}C$ significantly predict energy density with all years and collections sites pooled where fish with depleted $\delta^{13}C$ signatures had higher energy density (Figure 10). The relationship was stronger for fish caught in November than in March. Further, fish caught in November had a greater portion of individuals with more depleted $\delta^{13}C$ signatures as shown by the distribution of data points to the left of -20 $\delta^{13}C$ (Figure 10). A negative relationship between $\delta^{13}C$ signatures and energy density exists for all months and years when examined separately. In the years with the greatest energy density the $\delta^{13}C$ signatures were all less than -20 $\delta^{13}C$.

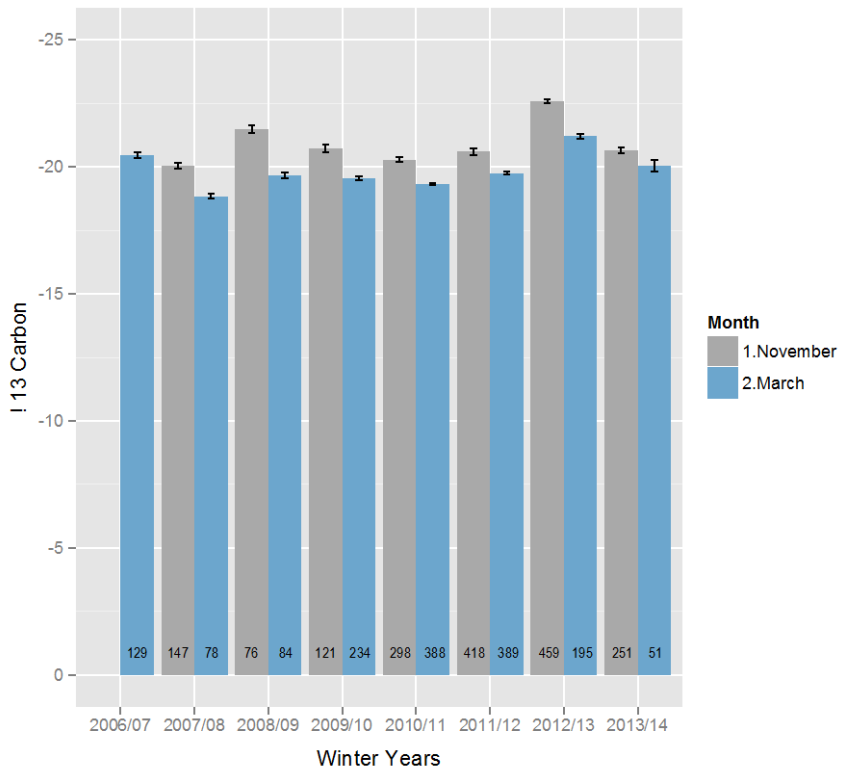

Figure 9. Seasonal variability in $\delta^{13}C$ signatures of age-0 herring in Prince William Sound. Error bars are 95% confidence intervals. Sample sizes are noted at the bottom of each bar.

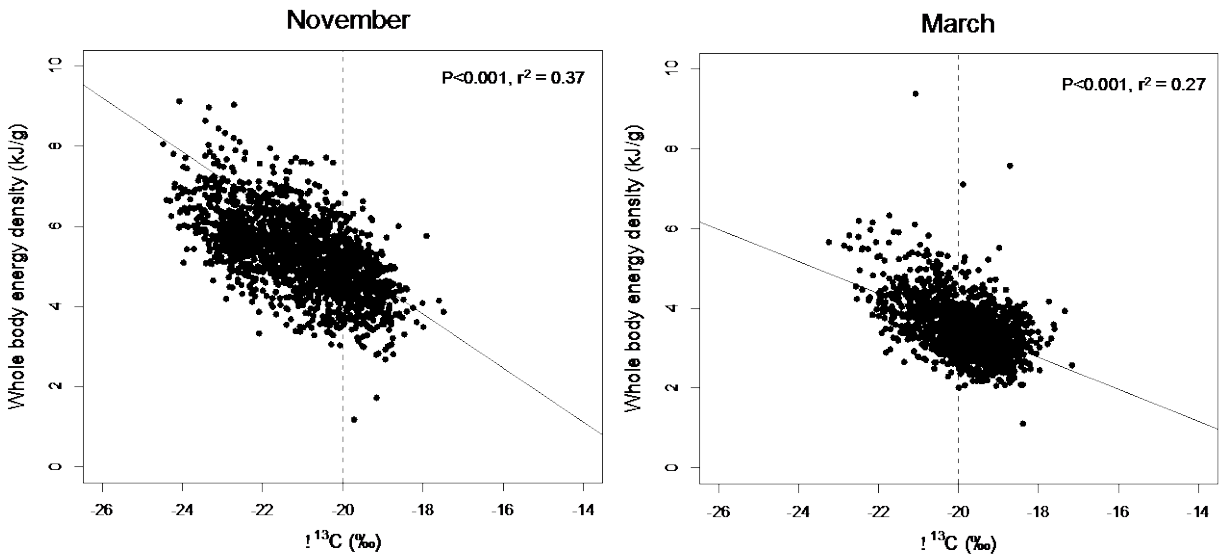

Figure 10. Seasonal variation in energy density of age-0 herring as predicted by δ^{13}C signatures of fish tissues. Data are pooled across all years (2007-2014).

Kline (1997) indicated that carbon in plankton originating from the Gulf of Alaska (GoA) is relatively depleted in δ^{13}C in comparison with PWS. Foraging during the winter on zooplankton in PWS may then lead to the enrichment of δ^{13}C between November and March. This is consistent with the preliminary results from analysis of fatty acid content.

Differences in diet affect the fatty acid composition of herring. During fasting the fatty acid composition remains constant, therefore changes in fatty acid composition are an indication of foraging. Analysis of fatty acid compositions using multi-dimensional scaling (MDS) indicates that there can be major shifts in composition between November and March (Figure 11). A major change in fatty acid composition occurred in Eaglek Bay. In November 2010 signatures of δ^{13}C among herring in Eaglek Bay were <-22 suggesting herring were foraging on plankton originating in GoA while in March 2011 signatures increased to >-22, suggesting that herring foraged on plankton originating in PWS. In Simpson Bay that same winter the δ^{13}C value was >-22 in both months, which is consistent with the smaller change in fatty acid composition observed.

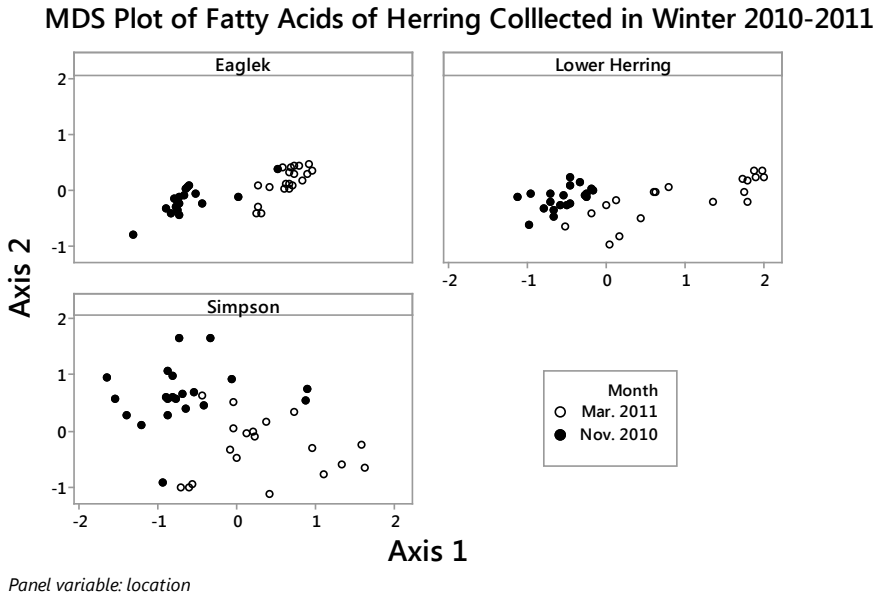

Figure 11. MDS plot of the fatty acid compositions of herring collected during the winter of 2010-2011.

Regional differences are observed in the fatty acid composition. The MDS analysis of data Eaglek, Lower Herring and Simpson bays revealed a difference in the fall of 2011 between Simpson and the other two bays (Figure 12). This indicates that diet composition in fall varied between the east and west parts of the Sound, but on the west side there was little evidence of a spatial difference in diet. This is consistent with the δ^{13}C value observations (Figure 13) where samples from the western Sound tend to have depleted δ^{13}C signatures in comparison with other regions suggesting that it receives more influence from the GoA.

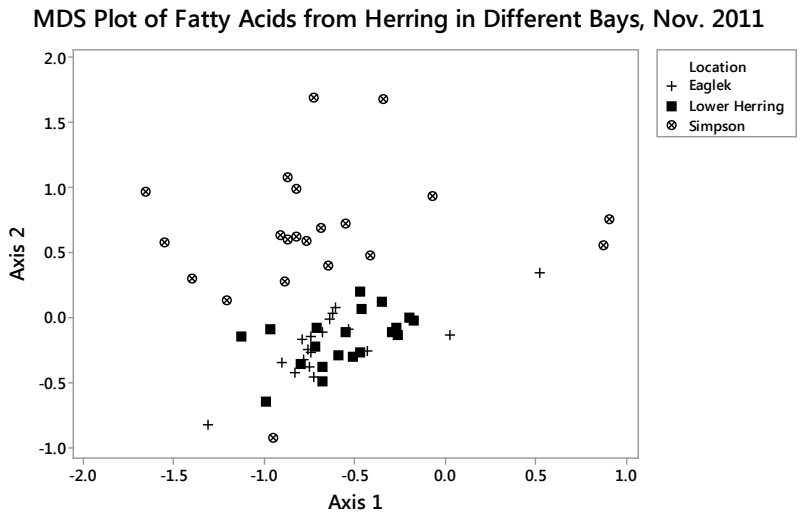

Figure 12. Fatty acid compositions of herring from three bays in PWS in November 2010.

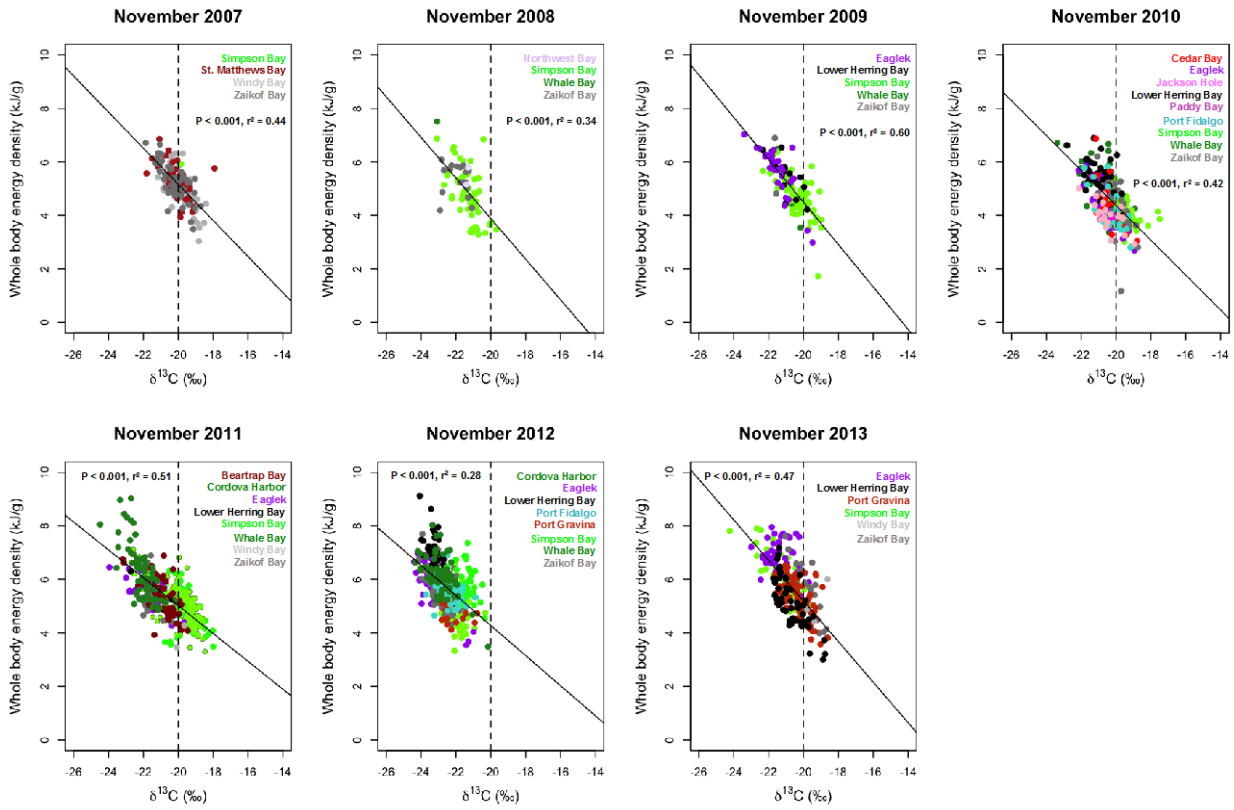

Figure 13. Temporal and spatial variation in November energy density of age-0 herring as predicted by $\delta^{13}C$ signatures of fish tissues.

Historical growth

Since the 1970s the Alaska Department of Fish and Game has been archiving scales from fish collected during the spawn. Recently a project was undertaken to image the scales and then measure the growth increments between annuli. Sixty scales were selected for each of three age groups (4, 5, and 6) each year from 1985 to 2013. Scales were selected so that approximately half were from female fish and half from male to check for gender biases in growth.

First year scale growth of all three age classes were positively correlated when the age was adjusted to the brood year. The growth increments in the first year were found to be normally distributed and independent of gender. This allows for the pooling of all data from a given brood year.

A visual examination of first year growth increments and biomass (metric tons) from the ADF&G age structured model would suggest that growth was negatively correlated with biomass until 2003 (Figure 14). The correlation among all years is very weak; however, for years prior to 2003, first growth by age and biomass are all moderately correlated (-0.63 to -0.65) and significant ($p<0.002$). This suggests density dependent growth prior to 2003. After 2003 almost all of the herring spawn has occurred on the east side of Prince William Sound and almost all of our scales are from the east side. Density dependent

growth could still be a factor if herring larvae from eastern PWS are rearing in a limited number of bays. The apparent relationship may also be caused by other environmental conditions.

It is important to note that there is no relationship between growth and recruitment. Survival of juvenile herring is expected be dependent on growth. The lack of a correlation between growth and recruitment may indicate that larval retention into the nursery grounds is a more important factor than survival in setting up future recruitment.

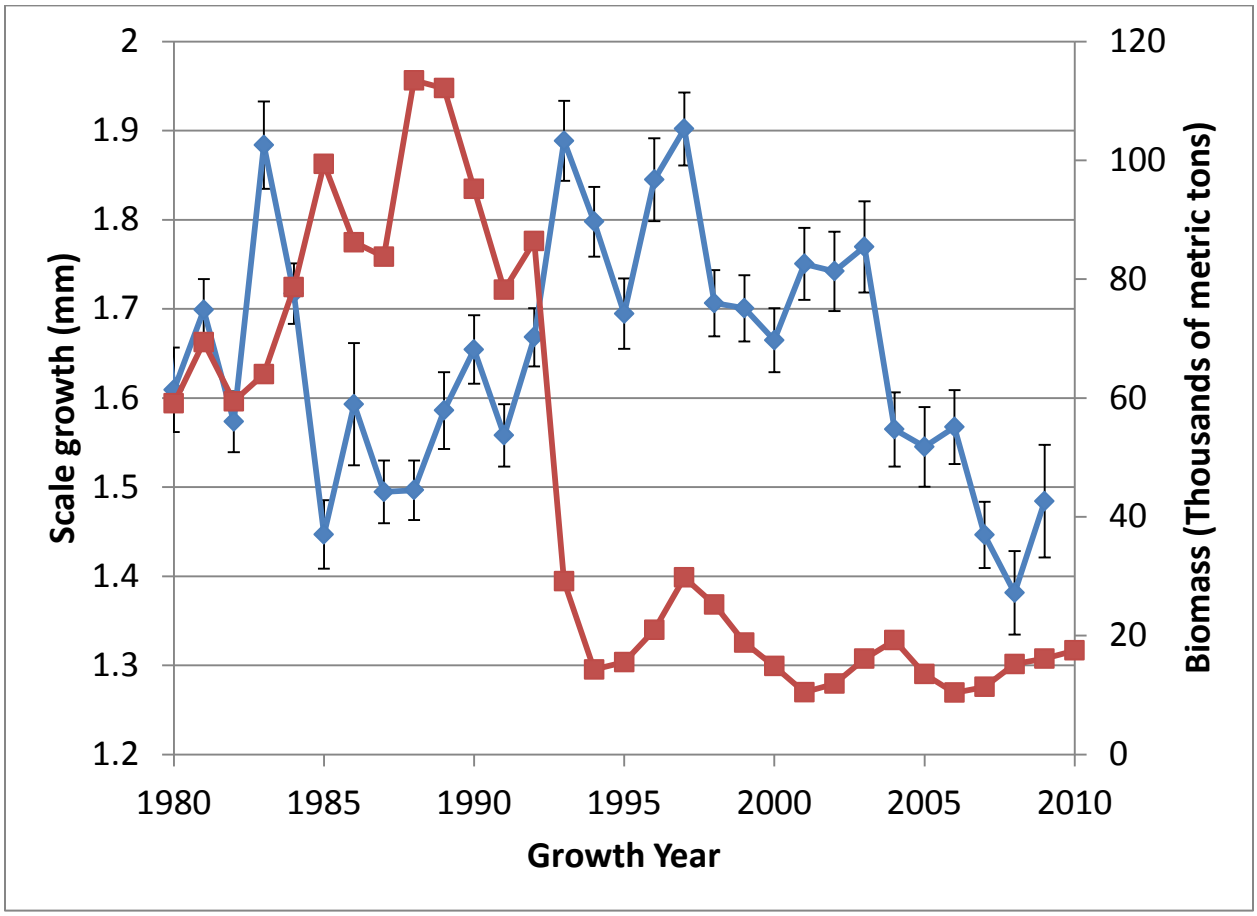

Figure 14. First year scale growth increments (blue diamonds) and age structured model estimates of prefishery run biomass (red squares). The x axis (year) represents the year when the first year of growth occurred and the paired biomass estimate for that year.

Connections to environmental conditions

The temporal and spatial variability in $\delta^{13}C$ values and fatty acid composition may be associated with water exchange from the Gulf of Alaska (GoA) into PWS. Previous work has indicated that carbon originating from the GoA in comparison with PWS is relatively depleted in $\delta^{13}C$ as shown by a $\delta^{13}C$ gradient among plankton in the region (Kline 1997). In general fish with depleted $\delta^{13}C$ signatures tend to be more energy dense; therefore water exchange from the GoA into PWS may be an important factor in determining the energy density of age-0 herring. There are seasonal changes in the $\delta^{13}C$ signatures

(Figure 10) that suggests seasonal differences in GoA water input. Spatial patterns in the $\delta^{13}C$ signatures suggest that most of the GoA water input is along the deeper trench in western PWS (Figure 15).

These patterns are consistent with input of GoA water at depth during relaxation of downwelling winds that occurs in the summer (Halverson et al. 2013). This deep water exchange carries zooplankton with the GoA carbon signature. Since the deep channel in PWS runs along the western shore it is expected that locations along this channel would benefit the most from the influx of deep water. In 2008 and 2012; however, the depleted $\delta^{13}C$ signatures were found throughout PWS in November. The extension of the depleted $\delta^{13}C$ signatures into Simpson Bay in those years is likely to require another mechanism for obtaining Gulf of Alaska water.

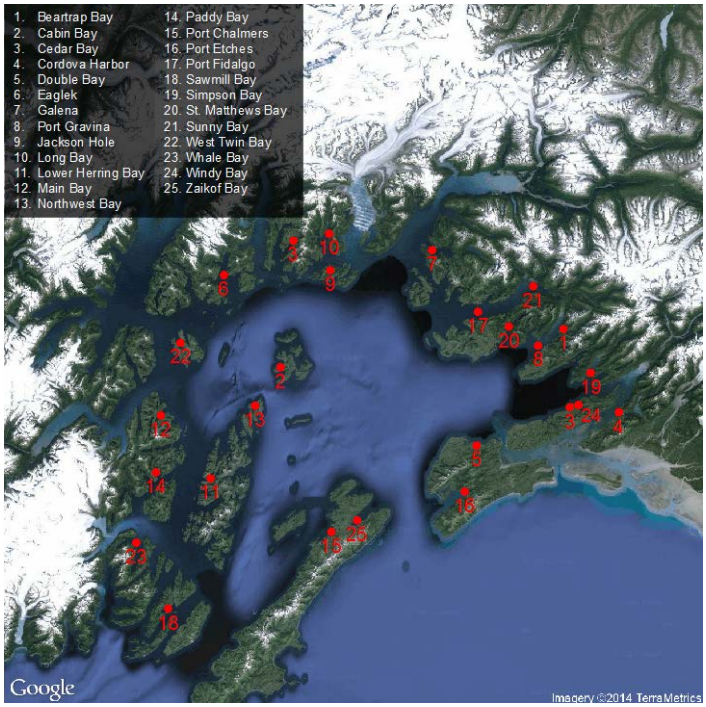

Figure 15. Sampling locations for juvenile herring condition monitoring throughout Prince William Sound. Deeper water is indicated by darker blue colors. Image produced in the R language environment (R Core Team 2014) using the ggmap package.

The scale growth data provides an opportunity to examine connections between historical growth patterns and environmental conditions. The longest environmental data sets in the region are of water temperature. First year growth by age from scale growth increments show weak positive correlations with the Pacific Decadal Oscillation (PDO) ($r= 0.39$ $p=0.04$). A slightly better positive relationship is observed between growth and summer (the average of July and August) water temperature measured in Cordova ($r=0.50$ $p<0.01$; Figure 16). This time period is right after the larvae metamorphose into juveniles and scale formation begins. The correlation is heavily impacted by the three warmest years on record. Removing those three years increases the correlation to ($r=.79$). This result is consistent with the increased growth rates of Atlantic herring with temperature (e.g. Oeberst et al. 2009) or

temperature may be a proxy for another environmental condition, such as prey abundance, quality, or growth timing (Mackas et al. 2007). A little surprising is the strength of the relationship between the growth increment and the 18.6 year lunar nodal tide cycle (Figure 17). However, the lunar nodal tidal cycle has been associated with oceanographic temperature variability in the region (Royer 1993). Therefore, the relationship between herring growth and the lunar nodal tide component may just represent the water temperature fluctuations.

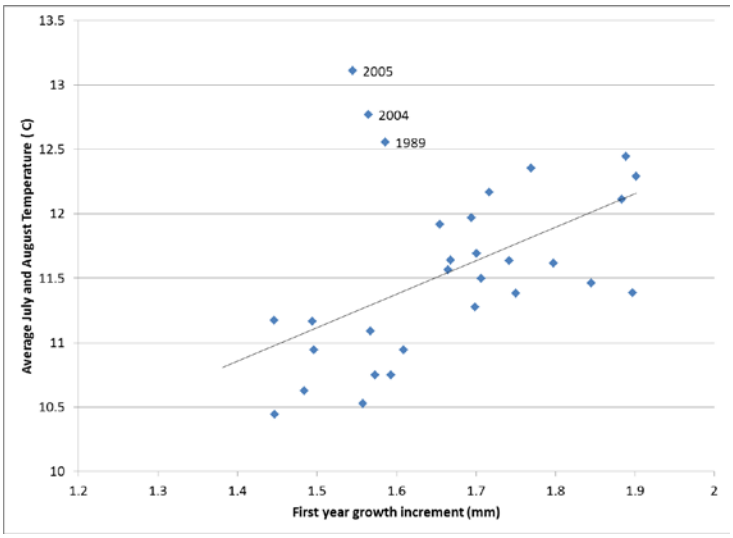

Figure 16. First year scale growth has a positive correlation to summer (July and August) average water temperature.

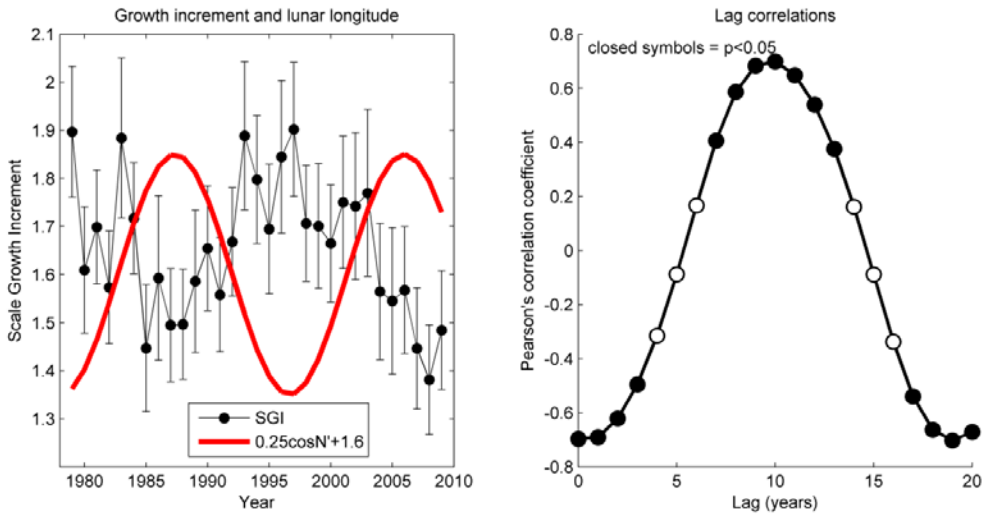

Figure 17. The left panel shows the scale growth increment and the negative of the longitude of the moon's ascending mode (this is scaled to fit on the same y axis as the scale growth increment) associated with the 18.6 year tidal cycle. The right panel shows the lagged correlation of the two. (Figure from Rob Campbell)

Plankton data sets that can be used to compare to the scale growth measurements are very limited. The plankton data collected in PWS under the PWS Herring Survey Program and continued into to the Gulf Watch Alaska program begins after the most recent scale growth information is available. The Continuous Plankton Recorder (CPR) provides measures of zooplankton and large phytoplankton abundances in the surface water in the Gulf of Alaska. Data from several cruises each year are combined to provide annual abundance estimates and anomalies of zooplankton biomass, which is subdivided into large copepod, small copepod, euphausiid/hyperiid, and pteropod components. Phytoplankton measures included a color index, diatom abundance, and dinoflagellate abundances. Phenology and annual abundance indices were calculated using a method proposed by Grieve et al (2005) that relies on cumulative integration. An annual abundance anomaly (Log10, based on the geometric mean of all years) was calculated for each year for the cumulative integrated biomass/abundance at day 300.

CPR data provides ten years of overlap with the scale growth record, but the CPR data is collected in the Gulf of Alaska, which may not be a good representative of conditions within PWS. Keeping that limitation in mind, the annual zooplankton and phytoplankton biomass anomalies are regressed against the scale growth for years 2000 to 2009. The time span covers most of the range of growths observed in the scale data (Figure 14). Regression of the growth versus the total zooplankton biomass anomaly provides a weak positive relationship ($r=0.64$ $p=.05$). No significant relationship is found to the individual zooplankton components that make up the total zooplankton biomass (small copepod, large copepod, euphasiid/hyperiid, and pteropod). By far the strongest relationship observed is between the scale growth and diatom abundance anomaly ($r=.91$ $p< 0.01$; Figure 18).

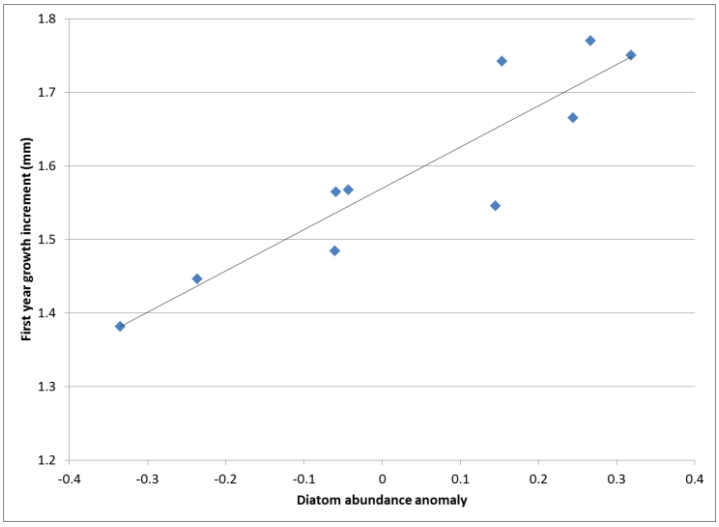

Figure 18. First year growth increment from herring scales versus diatom abundance anomaly determined from Continuous Plankton Recorder data collected in the Gulf of Alaska from 2000 to 2009. It should be noted that the data includes 2004 and 2005, which were anomalous in the temperature data.

While herring are zooplanktivores, there are a couple of possible explanations to why the growth may be most strongly related to diatom abundance. One possibility is that changes from a diatom dominated system to a dinoflagellate based food web lead to a change in the fatty acids of the zooplankton that the herring are feeding on (Litz et al. 2010). This suggests that the quality of food is important for growth. The instantaneous growth of larval herring has been found to be positively correlated to the essential fatty acids contained in diatoms in Atlantic herring (Paulsen et al. 2013). It has also been found that diatoms can be an important food source for larval herring (Friedenberg et al. 2012). Presumably the abundance of diatoms leads to more rapid growth of larval herring allowing a more rapid shift to larger prey and hence longer time for growth after scales form.

Disease research

A leading hypothesis for the explanation of the sudden decline in the PWS herring population is mortality associated with a disease outbreak that may have been exacerbated by the large population at the time and poor nutrition (Pearson et al. 1999, Marty et al. 2003). Research after the population decline focused on the impact of viral hemorrhagic septicemia virus (VHSV) and *Ichthyophonus* on the adult herring populations. The early emphasis was on documenting the prevalence of these diseases in the adult population and incorporating these data into herring population models (Marty et al. 2003). Recent research has expanded to studies intended to understand the fundamentals of the disease processes, including factors influencing transmission and susceptibility and the inclusion of screening for viral erythrocytic necrosis (VEN). A recent overview in our understanding of these diseases was provided in Pegau (2013). Subsequently a synthesis of our knowledge about *Ichthyophonus* was completed by Hershberger et al. (in preparation). A draft of that synthesis is provided as Appendix 3.

Ichthyophonus is perhaps the most ecologically and economically significant pathogen of wild marine fishes throughout the world, based on its low host specificity, broad geographic range, and recurring association with epizootics that result in massive fish kills and population-level impacts (reviewed in Burge *et al.* 2014). Details regarding the epizootiology of *Ichthyophonus* in herring remain largely uninvestigated, including its geographic range, seasonal and interannual persistence, and differences in infection prevalence within and between genetically distinct host metapopulations. The synthesis of Hershberger et al. examines these knowledge gaps using data from prevalence surveys over the past 11 years. They found that *Ichthyophonus* occurred in herring throughout the eastern North Pacific, but not in populations as far south as San Francisco. The prevalence of *Ichthyophonus* was not consistent in herring throughout the range where it is present. Large differences in prevalence were detected on smaller spatial scales, such as Puget Sound. There was also large annual difference in the infection prevalence at a single location.

One commonality among populations throughout involves a direct relationship between the prevalence of *Ichthyophonus* infection and host size and age. For example, the annual spring infection prevalence in Prince William Sound increased with size class from 15-60% in 2008, 16-80% in 2009, 13-33% in 2010, 13-47% in 2011, and 4-50% in 2013; the trend was less apparent in 2012, where data from the smallest

size classes were likely confounded by small sample sizes (Figure 19). It is important to consider this *Ichthyophonus* pattern with herring age / size when surveying wild populations. For example, a standard 60 fish sample from a population may contain a biased age / size distribution due to sampling gear / techniques; this size bias is subsequently reflected in the reported *Ichthyophonus* infection prevalence for the population (Holst 1996). Therefore, it is recommended that future *Ichthyophonus* prevalence in herring populations be reported by age / size class rather than as a single prevalence from a geographic stock / location; further, it is recommended that this relationship be scaled to the overall population age / size distribution and incorporated into an updated ASA model.

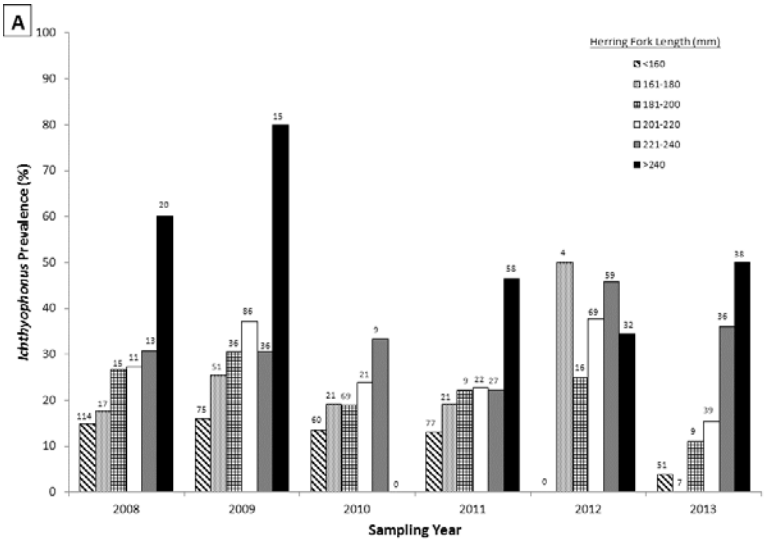

Figure 19. Ichthyophonus infection prevalence in each size class of Pacific herring collected from Prince William Sound, AK during the spring. Numerals above the bars indicate sample size (n).

The widespread distribution of *Ichthyophonus* in herring throughout the west coast of North America provides some indication of the mechanisms involved in the perpetuation and transmission of the parasite. The natural route(s) of *Ichthyophonus* transmission in Pacific herring remain unresolved and laboratory studies have generally been unsuccessful at demonstrating transmission through host cohabitation, immersion in parasite isolates, or feeding with infected tissues or isolates (Gregg *et al.* 2012). A leading hypothesis accounting for the transmission of *Ichthyophonus* to herring includes the possible involvement of an intermediate host, where the parasite likely develops into a stage that becomes more infectious to herring. This hypothesis is further supported by extreme plasticity in *Ichthyophonus* morphology that can be induced by manipulating various host and culture conditions. If an intermediate host (or hosts) exists, then the results from this study indicate that its geographic range must be very expansive throughout the NE Pacific.

Decreases in infection prevalence during spring surveys, such as those observed in Lower Cook Inlet and among the largest size cohorts in Sitka Sound, were likely the result of mortality among the infected cohorts. Laboratory exposure studies provide no indication that, once infected, herring are capable of

completely clearing *Ichthyophonus* infections; rather, infected individuals experience either acute mortality (Kocan *et al.* 1999) or survival with persistent infections (Hershberger 2012). Elevated mortality of infected cohorts could occur from selective predation on *Ichthyophonus*-infected cohorts if infected individuals with decreased swimming performance (Kocan *et al.* 2006) are more easily captured by predators. This predator selection hypothesis is supported by field observations during an *Ichthyophonus* epizootic, when 60-80% of Atlantic cod stomachs contained Atlantic herring that were heavily-infected with *Ichthyophonus* (Kramer-Schadt *et al.* 2010).

Although recurring *Ichthyophonus* epizootics, fish kills, and associated host population declines have been reported since 1913 (reviewed in McVicar 2011), major information gaps continue to exist regarding the natural history of the parasite. Most importantly, a paucity of information exists regarding the *Ichthyophonus* life cycle and the involvement of herring in completion of this cycle. It is recommended that future research efforts are committed to investigating possible intermediate hosts which, if identified, could offer a predictive tool for forecasting the emergence of new *Ichthyophonus* epizootics in clupeids. As a result of current EVOS TC support, the tools required to begin searching for alternate *Ichthyophonus* hosts have now been developed, including conventional PCR, quantitative PCR, and chromogenic in situ hybridization (CISH). By utilizing these tools, ongoing studies are underway to identify the natural transmission route(s) of *Ichthyophonus* to herring, including the possible involvement of alternate intermediate hosts.

Viral hemorrhagic septicemia (VHS) is another disease that is endemic in herring populations throughout the eastern North Pacific, where epizootics occur periodically. Although VHS virus infection prevalence data continue to be provisioned into the ASA model, results from these EVOS TC-funded projects indicate that a different modelling approach is required for documenting the full impact of this disease to herring populations. For example, unlike *Ichthyophonus*, where the kinetics of the chronic disease can be quite slow and infected individuals never completely clear the infection, VHS is a much more acute disease that can run a complete course from host exposure to host mortality in a couple of weeks. Further, herring that become infected with VHS virus either die quickly from the disease, or recover and completely clear the infection. Therefore, provision of VHS virus prevalence data, based on a single sample of pre-spawn herring, is likely to under-report the mortality impacts from the disease, as exposure and mortality can occur throughout the remainder of the year. The only conceivable way to justify the incorporation of VHS prevalence data into an ASA-type model would be to perform monthly disease sampling on the PWS herring population. Unfortunately, this expanded disease sampling effort would be extremely costly, as the adult and juvenile herring populations subscribe to a highly migratory life history.

As a result of these epidemiological principles of VHS, new disease forecasting tools are being developed based on the concept of herd immunity. Briefly, herring that have never been exposed to VHS virus are highly susceptible to mortality from the resulting disease; conversely, individuals that survived prior exposure to VHS virus develop adaptive immunity that renders them refractory to the disease (and disease-related mortality) for the remainder of their lives. Therefore, as a result of EVOS TC-funded projects, high-throughput serological assays are being developed that will be capable of determining

whether individual herring have survived prior exposure. When scaled up to the population level, these assays will indicate whether a herring population has a high potential for future VHS epizootics (i.e. lacks herd immunity) or a low potential for future VHS epizootics (i.e. has survived prior exposure to VHS virus and now demonstrates herd immunity). We are in the final stages of validating and optimizing several of these immunological assays, including a plaque neutralization test, and two enzyme-linked immunosorbent assays (ELISA's). Upon completion and validation of these assays, it is expected that their outputs will be used to engineer new models that are capable of integrating VHS potential into an annual herring abundance forecast.

Viral erythrocytic necrosis (VEN) is a common disease in herring populations, especially among juvenile cohorts. Unfortunately, the disease is easily overlooked, as diagnosis requires relatively unique necropsy procedures involving the collection of blood films. Citizens and researchers who periodically encounter sick or dying herring in the field are typically not trained to collect samples for pathogens. Most specimens collected during these epizootics are typically stored in a freezer, thereby negating our ability to test for VEN using traditional blood flim techniques. As a result of the EVOS TC-funded projects, we have developed two new molecular tools (a conventional and a quantitative PCR) that are capable of diagnosing VEN from either fresh or frozen samples. Methods for the cPCR are published (Emmenegger et al 2014), and the final validation for the qPCR is expected in December, 2014.

Estimating recruitment

The ages3-4 year classes can make up a large portion of the herring biomass in PWS. One of the difficulties with predicting changes in biomass is having good knowledge of new recruits to the spawning biomass. In PWS the age-3 herring are the youngest fish generally captured in the spawning population and the youngest age class incorporated in the ASA model. There is not a strong relationship between the number of spawners and the subsequent recruitment (Zheng 1996). Small spawning events can lead to large recruit classes and vice versa. For this reason, in the updated ASA model each year's recruitment is estimated independently, and there is no assumption of a built in stock-recruit relationship. The initial estimate of the incoming number of age-3 fish is based on an assessment of the accuracy of the previous year class or mean or median recruitment for two to ten previous years. This approach is unable to account for the two orders of magnitude difference in recruitment seen in Figure 2. Improving on this approach requires estimates of brood year strength before recruitment. This is a challenging task and we are trying multiple approaches to provide an index of incoming year-class strength.

The spawning biomass survey has the advantage of having all the fish aggregated in a limited number of areas. Estimating the incoming year class requires quantifying fish in the nursery grounds. We do not have a good understanding of where the age-2 and age-3 fish are. Based on evidence from Stokesbury et al. (2000) the current hypothesis regarding the distribution of juvenile herring is that the youngest fish tend to be at the head of nursery bays and tend to be higher in the water column. The older the fish the further down the bay and deeper in the water column. Aerial surveys suggest that the age-2 and

age-3 fish may occur outside of the nursery bays during the summer. At some point a portion of the age-3 fish join the spawning stock, but we are unsure what proportion joins the adults as we have caught age-3 fish in the nursery grounds just prior to the start of spawn. This leaves us with age-0 and age-1 fish to try and survey to provide an index. Efforts to catch age-0 fish in the fall suggest that they tend to be fully moved into to the nursery areas by November. Observations from aerial surveys indicate that the age-1 fish remain in the bays through June and transition to deeper water in July. The best opportunity for observing a cohort prior to recruitment to the spawning stock appears to be when young fish are aggregated in the nursery grounds between November and June. Age-0 fish can be observed in the fall and that same cohort as age-1 through early summer.

Hydroacoustic and aerial surveys have been used to provide an index of juvenile herring abundance in PWS during this time period. Acoustic surveys have been conducted in five to ten bays for the past seven years. In November 2012 the single-beam 70 kHz system was replaced by a 120 kHz split beam system. The sample design also changed slightly in 2012 that included an increase in survey effort. The validation of the acoustic signal shifted from gill nets to a mid-water trawl in 2013.

The results from the acoustic surveys conducted from 2007 to 2012 are reported in Thorne and Buckhorn (2013). They divided the acoustic signal by distance from the head of the bay and whether it is above or below 15m. The assumption being that the age-0 herring tend to be in the upper water column near the head of the bay. Unfortunately they did not report the interannual differences in abundance by location. They did report the interannual differences in total estimated biomass, but it cannot be used as an index of age-0 herring abundance since it is a mix of all fish. Results since the fall of 2012 are only available as qualitative observations. In November 2012 and 2013 the acoustic surveys did not observe many fish believed to be age-0 herring (Buckhorn personal communication).

A second measure of juvenile abundance may be obtained from aerial surveys. Dr. Evelyn Brown conducted aerial surveys for forage fish, including herring, as part of the Sound Ecosystem Assessment and Apex Predator Experiments (Brown and Moreland 2000). She also conducted surveys from 2010 to 2012. Surveys occurred in June, July, and August. At the end of her project she provided protocols for local pilots to continue the aerial surveys. In June 2013 a reduced version of her survey was conducted, whereby the school sizes were recorded in three size categories and locations were recorded by general area instead of by GPS location. In 2014 a GPS was again used to record school locations. Surveys each year flew the entire coastline of PWS and schools of forage fish were recorded by species and for herring as either age-1 or age-2 and older. Schools were identified by their location, size, color, and shape. In 2013 and 2014 the aerial surveys worked in conjunction with the Gulf Watch Alaska forage fish sampling project to provide validation of the aerial identifications, but there is not yet enough information to determine the accuracy of the observations.

A simple index of juvenile abundance is the number of schools of age-1 herring observed during the June survey. June was selected because there are no age-0 herring to confound the observations. From 2010 to 2014 the number of age-1 herring schools observed was 579, 75, 279, 2544, and 180 respectively. The 2011 survey did not reach all areas so the count should be considered minimal. These age-1 fish are

expected to recruit to the spawning biomass in 2012-2016. The estimated number of age-3 herring from the ASA model was 125.5 million in 2012 and 2.1 million in 2013. There were few age-3 herring observed in the spawning stock in 2014 suggesting it also was a small cohort, consistent with the number of schools observed by the aerial survey.

Based on the aerial surveys, the age-3 class to be observed in 2015 is expected to be large. It should be noted that the observations by the aerial survey are in conflict with those reported by the acoustic surveys, which reported observing few areas with what were believed to be age-0 herring. Given the conflict between the two sets of observations, are there other observations that may be used to predict the size of the expected 2015 age-3 recruit class? The 2013 pink salmon return to PWS was a record return. These fish entered the ocean in the summer of 2012. The age-0 pollock bycatch in salmon smolt surveys was the highest since 1999. Since 1984, five of six of the largest herring classes by percentage of the age composition match large recruit classes of pollock observed in Shelikof Strait (Figure 20). The 2013 Shelikof Strait pollock survey found the second largest number of age-0 pollock observed (Dorn et al. 2013). The November 2012 cruise was the only one in seven years in which over 25 juvenile herring were caught in all bays sampled. These are all anecdotal evidence that 2012 may have been a very good year for young fish in PWS and are consistent with the aerial observations.

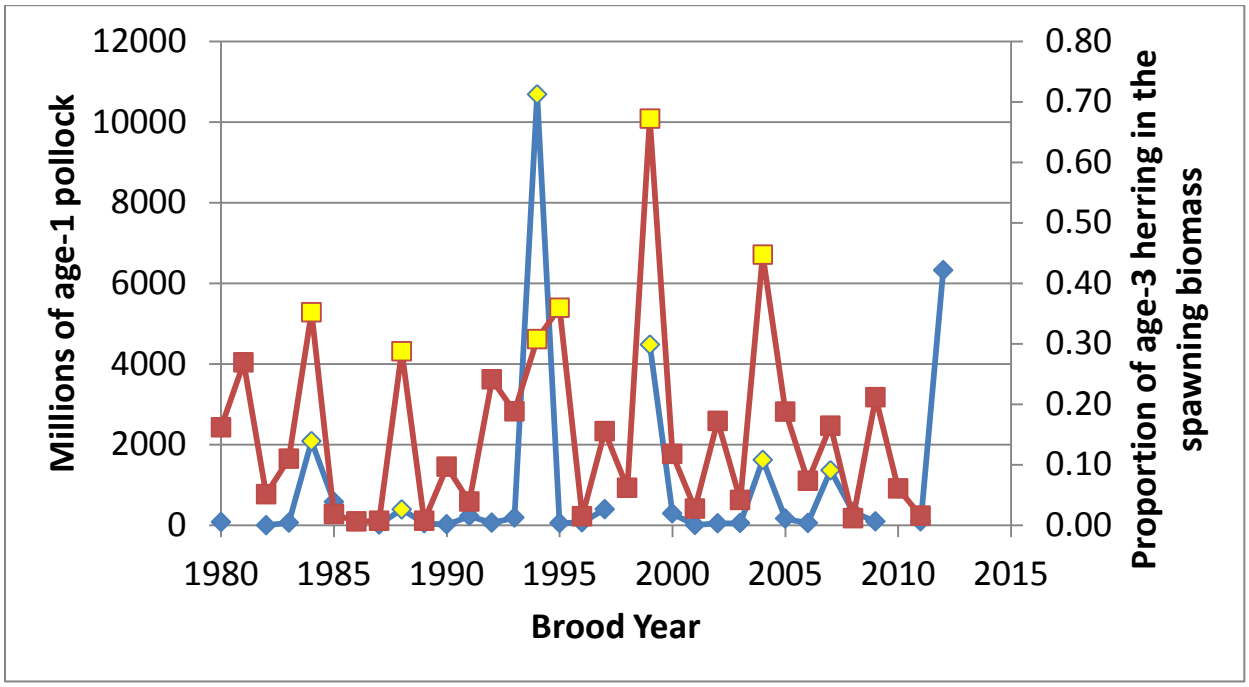

Figure 20. The estimated number of age-1 pollock in Shelikof Strait (blue diamond) and the proportion of age-3 herring observed in the spawning stock (red square) is presented. The top six years prior to 2010 in each data is marked by the yellow symbols.

Movements and habitat

Several studies have been conducted to better understand the movement and habitat use of herring. In estimating survival of overwintering juvenile herring it is assumed that the population estimate from the acoustics is accurate and that there is no immigration or emigration within the nursery area. An acoustic intensive was conducted between October 2013 and April 2014 to examine if the population juvenile herring population estimate was constant between days and weeks.

A tagging study examined the movement of adult herring. While the project was designed as a pilot study to confirm that wild herring could be tagged using acoustic tags, the study was able to provide interesting insights to the movement of the adult fish.

Age-0 movement

Hydroacoustic surveys of juvenile herring nursery areas in Prince William Sound have been conducted during November and March for the last several years. The number of locations surveyed have varied from five to nine, including the four Sound Ecosystem Assessment (SEA) bays. However, each seasonal effort included only a single night survey in each of location. Thorne (2010) examined seasonal changes from fall 2006 to spring 2009. He showed that apparent overwinter mortality of age-0 herring appeared to be greatest in Simpson Bay and least in Whale Bay. However, he also pointed out that the differences over winter could also be the result of migration between bays. Not only might age-0 herring move among bays during the winter, but movement into and out of bays may be progressive during a season. It is possible the overwintering component of age-0 herring may not be fully recruited into a bay at the time a single fall survey, or spring movement may have begun out of bays prior to any given late-winter survey. Another potential source of variability in the population estimate could be the stage of the moon.

Ambient light is known to affect fish distributions. On many occasions, age-0 concentrations were readily identified by their distinct distribution: a diffuse layer near surface, near shore and near the heads of bay. On other occasions, this distinctive distribution was absent even though age-0 herring were present. The change might have been the result of different ambient light regimes.

Four, three-night hydroacoustic surveys were conducted between October and December of 2013 and another four, three-night surveys were conducted between February and April 2014 in Simpson and Windy bays. The purpose of the surveys was to determine the level of consistency in the estimated population of age-0 herring on both a daily and fortnightly scale. The analysis of the acoustic data is currently underway, but the general observations were the acoustic surveys were highly variable between each survey for each bay.

During October there was a large increase in the fish observed in Simpson Bay by the acoustics and in the trawl surveys during the final set of surveys in the month (Figure 21). The age-0 catch per kilometer was nearly two orders of magnitude greater during the last set of surveys in October compared to the previous two series of surveys. The catch per kilometer decreased in December to approximately the same as early October. Differences in survey locations may account for some of the observed changes in

the catch, but the much higher catch levels in the last week of October were consistent with the acoustic observations during the cruise.

While differences in catch between days within a cruise might be related to the location of the trawls, there was one occasion with a significant increase in catch per kilometer. That increase occurred on the last day of the April surveys when an ice sheet left Simpson Bay and the catch again increased nearly two orders of magnitude.

The cause of the observed variability across surveys is not understood. The variability in the fall may have resulted from a migration of the herring towards a nursery ground at the head of the bay. It could also be a result of different phases of the moon causing changes in behavior. The decrease observed in early December may have been a result of the fish moving into areas not covered by the acoustic survey. In the spring it is clear that large numbers of fish were under the ice that was present and could not be surveyed using the acoustics.

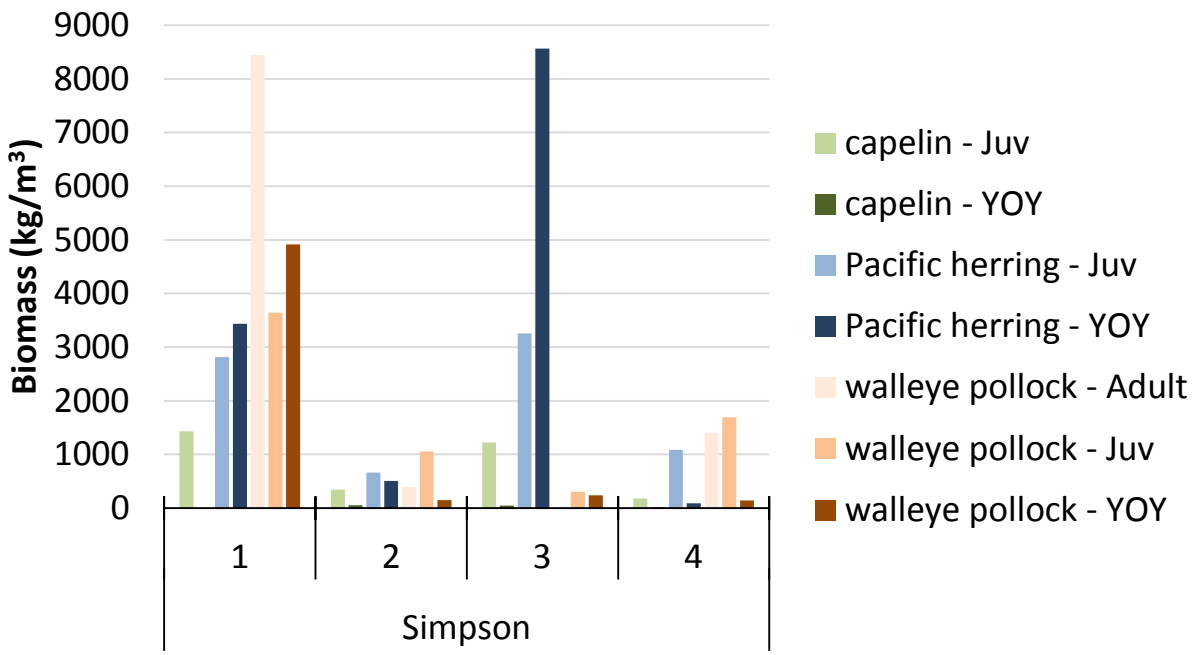

Figure 21. The biomass observed within the trawl regions during the acoustic intensive surveys in Simpson Bay. The survey numbers correspond to October 1-4, 16-19, 28-31, and December 3-6, 2013.

Ice shelves as overwintering habitat

An observation made during the PWS Herring Survey program was that the age-0 herring seemed to be associated with ice shelves during the winter. These shelves form as freshwater mixes into the surface waters under freezing conditions and are a common occurrence within PWS bays. The ice does not form all years or at all locations. An objective of the non-lethal sampling project was to determine if the juvenile herring could be identified under the ice using acoustic and optical sensors on a remotely operated vehicle. Additionally an ice sheet formed in Simpson Bay and was present for most of the late

winter sampling during the acoustics intensive project. The ice sheet broke out of the bay on the final day of sampling, which provided an opportunity to examine the herring that had been under the ice.

During a three-day cruise in March 2014 the non-lethal sampling project was able to survey under the sheet ice in Simpson and Beartrap bays. A remotely operated vehicle (ROV) carrying an imaging sonar and camera was used to survey for juvenile herring under the ice sheets present in those bays. The dual frequency identification sonar (DIDSON; SoundMetrics) uses a series of high frequency transducers firing in sequence to create video quality data of the ensonified volume (Figure 22). Data collected with the DIDSON can allow for estimates of fish density and size distributions of ensonified herring schools. An HD video camera with tilt and zoom capabilities and separate lights allowed for the identification of fish seen by the DIDSON.

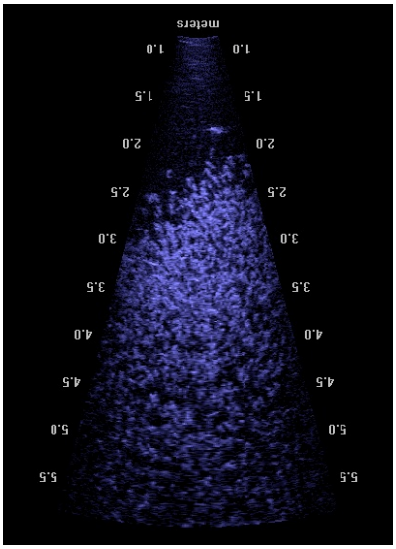

Figure 22. A DIDSON stillshot showing a large, dense school of herring.

The ROV was deployed at each site at least in the morning and at night, encompassing crepuscular periods thought to be important in structuring herring schools. Because this was a pilot project to determine the utility of the approach the surveys were mostly exploratory and unequal search effort was expended towards school detections in each bay. Upon detecting a school in either the ROV camera or DIDSON, attempts were made to steady the ROV to enhance the quality and accuracy of the coupled video-DIDSON data to derive density and length distributions. Several schools were observed under the ice at both locations.

There were differences in school densities as a function of time of day and location. Herring densities in Beartrap Bay ranged from 1.172 fish/m^3 in the afternoon, dropping to 0.4067 fish/m^3 at night, and 0.4147 fish/m^3 in the morning. Whereas in Simpson Bay the densities ranged from 2.566 fish/m^3 in the night survey, to 3.495 fish/m^3 in the morning survey (Table 2). There was also a behavioral change

observed. The fish avoided the ROV during daylight hours, but at night they were attracted to the lights of the camera.

The average length of the fish in Beartrap Bay was slight smaller than in Simpson Bay. The average herring length under the ice in Beartrap Bay was approximately 11 cm, which is consistent with the fish being age-0 herring. The length of herring observed under the ice in Simpson Bay herring lengths was slightly over 12 cm. These fish were likely to be age-1 herring based on the size distribution of herring caught in the trawl during the acoustics intensive study being conducted at the same time (Figure 23).

Table 2. The average lengths (N = 30 per site) and densities of fish schools encountered in each of the bay surveys.

	Average length (cm)	Average density (fish/m^3)	School Events
Beartrap Bay Afternoon	11.4 ± 2.3	1.172	2
Beartrap Bay Night	10.4 ± 1.5	0.4067	20
Beartrap Bay Morning	11.5 ± 1.8	0.4147	23
Simpson Bay Night	12.2 ± 1.5	2.566	3
Simpson Bay Morning	12.3 ± 1.9	3.495	10

The length of the fish observed under the ice edge in Simpson Bay is also consistent with the length of fish caught near the ice edge using the trawl (Figure 24).

Additional evidence of juvenile herring using the sheet ice as habit comes from the trawl sampling of fish associated with the acoustics intensive survey. An ice edge was present during all trawls conducted in February and March and two of three sampling nights in April (Number of trawls = 24) and no ice was present from October through December and one night in April (Number of trawls = 25). Size structure was investigated by categorizing all catch data as either from “ice” or “open” periods and generating length frequency histograms. During open periods age-0 herring were captured in the highest proportion, fewer juvenile fish were captured, and adults were captured infrequently (Figure 24). Catches from periods with ice cover were dominated by age-1 herring, while age-0 herring were present in lower proportions (Figure 24).

During the final sampling period (April 2- 6), ice was present the first two nights of sampling but retreated during the final night of sampling. As a result, the April sampling period included six tows conducted while ice was present and three when the bay was open. This allowed for a comparison of size distribution based on ice cover with data from the same time period. During the two sampling nights with ice, catches were dominated by herring age-1 and older herring and contained a low proportion of age-0 herring. However, during the final sampling night without ice, catches contained

only age-0 herring. Finally, the size distribution of herring caught during the open, no-ice sampling night in April 2014 was found to be similar to that of the fish caught in October 2013 when no ice was present.

The number of age-0 herring per trawl with or without ice present was also examined. During April, the catch rates of age-0 herring during ice and open water periods were drastically different. A maximum of 103 age-0 herring were captured per km tow during periods with ice, while the maximum during open periods was 12,423. The location of the trawls during the open water period in April was closer to the head of the bay and in shallower water. The trawl location may represent a confounding factor. However, the location where the greatest number of age-0 fish was caught was well over a kilometer inside of the previous ice sheet, which suggests that the age-0 herring were under the ice far from the edge.

Since a spring population estimate is necessary to calculate overwintering survival, and it appears that the age-0 herring are present under the ice, it is important that any survey be conducted after the ice has left the area. This has not occurred in the past because the sampling occurred at the time when the age-0 herring were expected to be at their minimum condition.

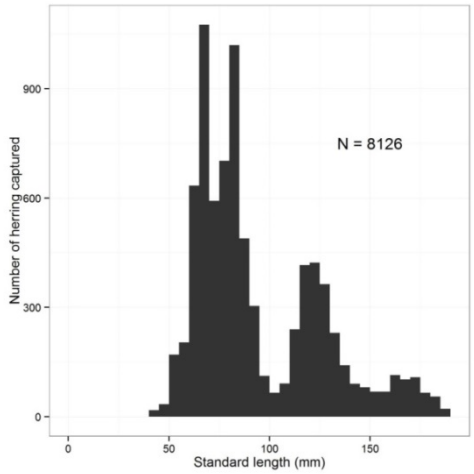

Figure 23 - Length frequency histogram in 5-mm bins of all herring caught by trawling in Simpson Bay between October 2013 and April 2014. The first broad peak represents the size of age-0 herring, the second is age-1 and the third is older fish.

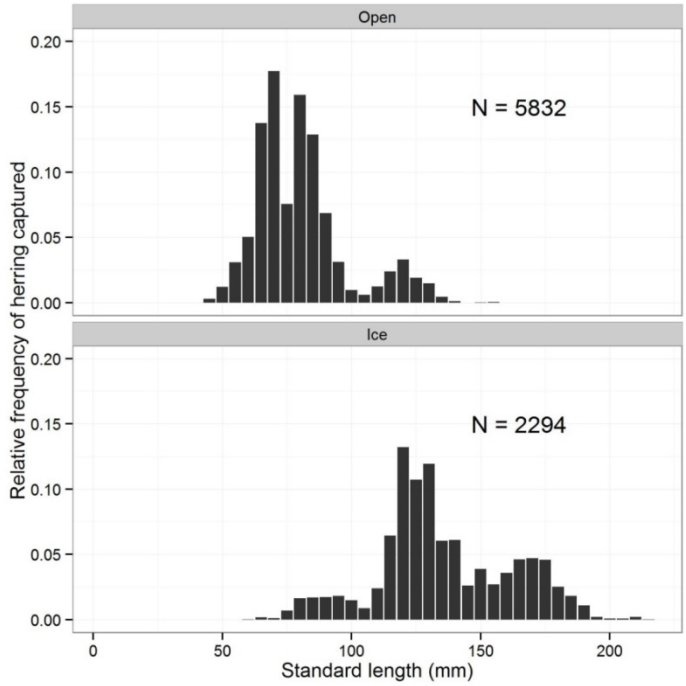

Figure 24- Length frequency histograms with 5-mm bins of herring caught in Simpson Bay from October 2013 through April 2014 separated by the presence of ice.

Adult herring movement

The movement of adult herring was examined by a pilot project designed to examine if herring could successfully be implanted with acoustic tags, and to determine if their movements could be detected by an acoustic array. In 2012 twenty five fish were tagged and in 2013 sixty nine fish were tagged in Port Gravina during the spring herring spawn there. The Ocean Tracking Network (OTN) arrays were installed in the spring of 2013 so most of the tracking information available is from the 2013 release. In 2013, 43 of the 69 tagged fish were detected at one or more of the OTN arrays (Figure 25). Departure from Port Gravina was concentrated during two time periods: 6-10 Apr and 22-26 Apr (Figure 26), and coincided with spawning activity in the area. Based on the number of days since herring were released or last detected at Port Gravina, migration time was 6.5 $\pm$ 4.3 d (n = 13; range = 2, 15d) to Hinchinbrook Entrance (~50 km from the Port Gravina array) and 19.04 $\pm$ 21.9 d (n = 25; range = 3, 80) to Montague Strait (~115 km), and 50.2 $\pm$ 39.4 d (n = 5, range = 13, 107) to the Southwest Passages (130+ km).

Phenology of herring use at Hinchinbrook Entrance and Montague Strait was similar from April through August. Detection numbers peaked in early May and remained relatively high throughout the month. At both sites, detections were much lower in June. Notably, no tagged fish were recorded at Hinchinbrook Entrance between 9 July and 15 October, nor at Montague Strait between 24 July and 6 September (Figure 27). The average length of stay, defined as first day detected to last day detected was shorter at Hinchinbrook Entrance (x = 17.6 $\pm$ 15.1 d) compared to Montague Strait (x = 29.5 $\pm$ 29.9 d) although the difference was not significant. We did observe movements between Hinchinbrook

Entrance and Montague Strait. Six herring that initially arrived at Hinchinbrook Entrance were later detected at Montague Strait, while only one herring was first detected at the Strait and then later at Hinchinbrook Entrance. Of the six herring moving from Hinchinbrook Entrance to Montague Strait, four arrived at the Strait between 18-20 May, suggesting they may have been part of the same fish school.

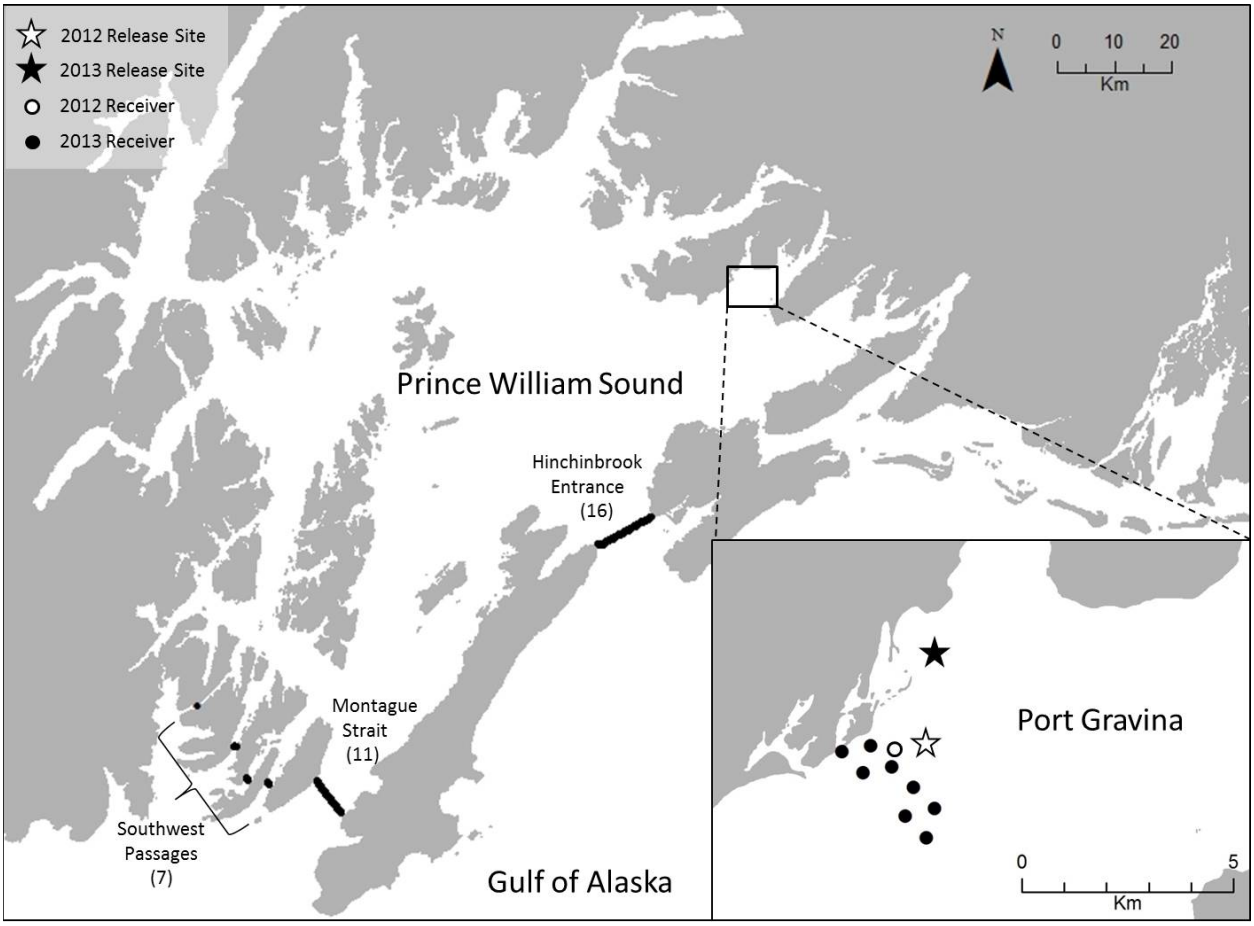

Figure 25. Location of herring tagging and acoustic monitoring areas in Prince William Sound. Numbers in parentheses indicate total number of acoustic receivers.

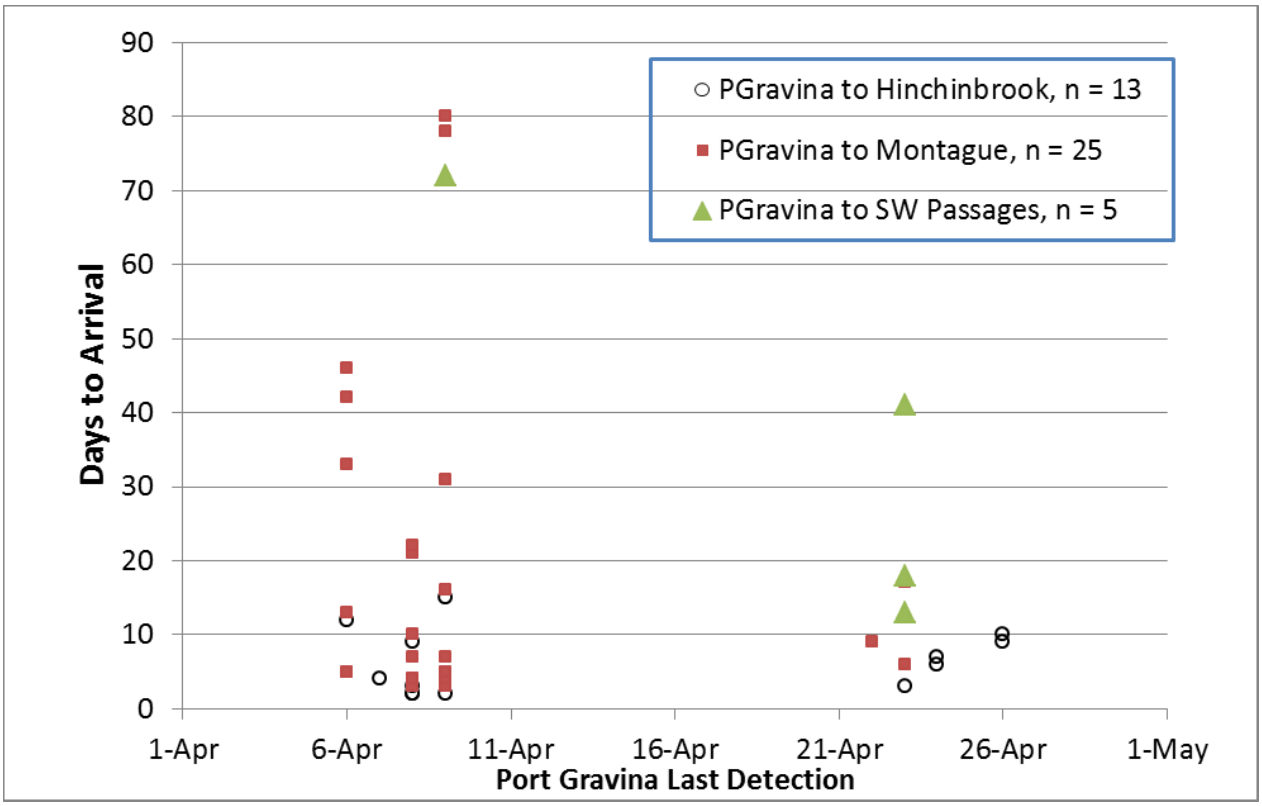

Figure 26. Number of days from release date (n = 8) or final detection at Port Gravina array (n = 35) to first detection at Ocean Tracking Network arrays. Herring tagged at Port Gravina on 6 and 7 Apr 2013. Not shown is one herring that arrived at the Southwest Passages 107 d after its final detection at Port Gravina.

A total of 16 herring were detected between September and early January, when tag batteries expired. First fall detections for 14 of the 16 herring occurred at Montague Strait, with fish pulsing through between 7 September and 21 October (Figure 28). During this four month period only one tagged herring was detected on one day (16 October) at Hinchinbrook Entrance. Two of the 15 fish detected at Montague Strait were also detected on one day only, suggesting these fish, as well as the one fish at Hinchinbrook Entrance were returning from the Gulf of Alaska.

Most herring detected during fall were detected multiple days, and during at least two of the four months. The intermittent detections of individual fish over multiple months in fall suggest that residency in wintering areas is not stable, but rather that fish schools are highly mobile. At the same time, the use of Montague Strait and the Southwest Passages during November and December suggest that some schools may be wintering in this area. Brown et al. (2002) interviewed crab fisherman that fished in the northern Gulf of Alaska during winter. One of those fishers believed that herring spent winter between Wessels Reef, Cape Cleare and Middleton Island, and enter the Sound in spring via Hinchinbrook Entrance. If this is the case, it may explain why >60% of the herring detected at the entrance arrays during spring and early summer were not detected again.

Because the arrays are a single line across the entrances, it is not possible to determine if the herring continued to travel into the Gulf of Alaska or returned to PWS after spending time in the entrances. Based on the final detections of individual herring in spring, followed by their subsequent reappearance in fall, it appears that some schools of herring are moving out into the Gulf of Alaska immediately after spawn, with peak departures occurring mid to late May.

The length of time the herring were observed in Montague Strait suggests that oceanographic conditions may be favorable for foraging in that region. Willettte et al. (1999) examined diets of herring collected between late April and July over a three year period and found that large calanoid copepods (primarily *Neocalanus plumchrus* and *Neocalanus flemingeri)* composed a significantly greater proportion of herring diets during May, with a June shift in diet to alternative prey (e.g. euphausiids, amphipods, pteropods and fish) coinciding with the decline of the bloom. Similarly during this study, *Neocalanus* numbers peaked during May 2013 at both Hinchinbrook Entrance and Montague Strait, disappeared by June 2013 samples at Hinchinbrook and decreased by 80% at Montague Strait that same month (R. Campbell, PWS Science Center, unpubl. data).

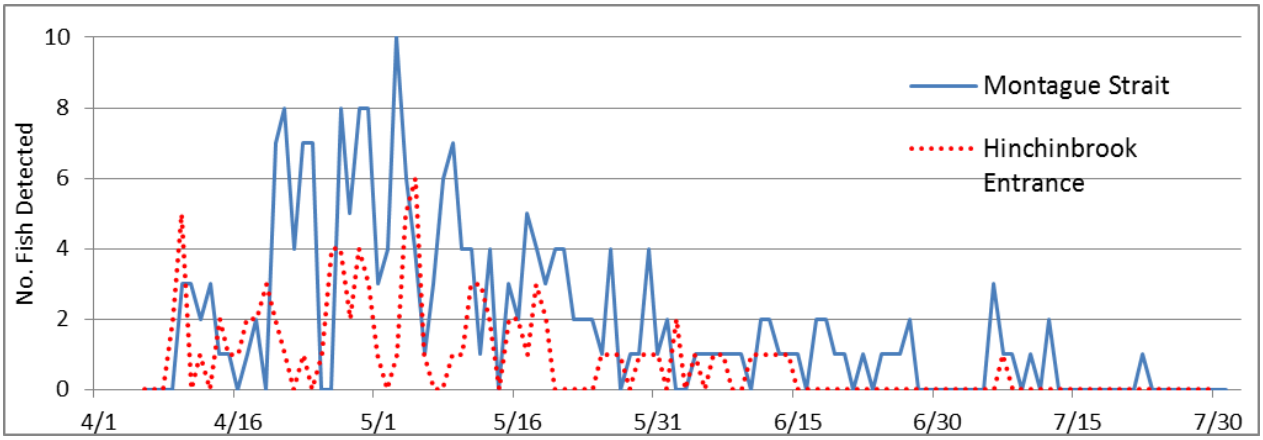

Figure 27 Number of acoustic tagged Pacific herring detected by date at Hinchinbrook Entrance and Montague Strait arrays. April 1 – July 30, 2013.

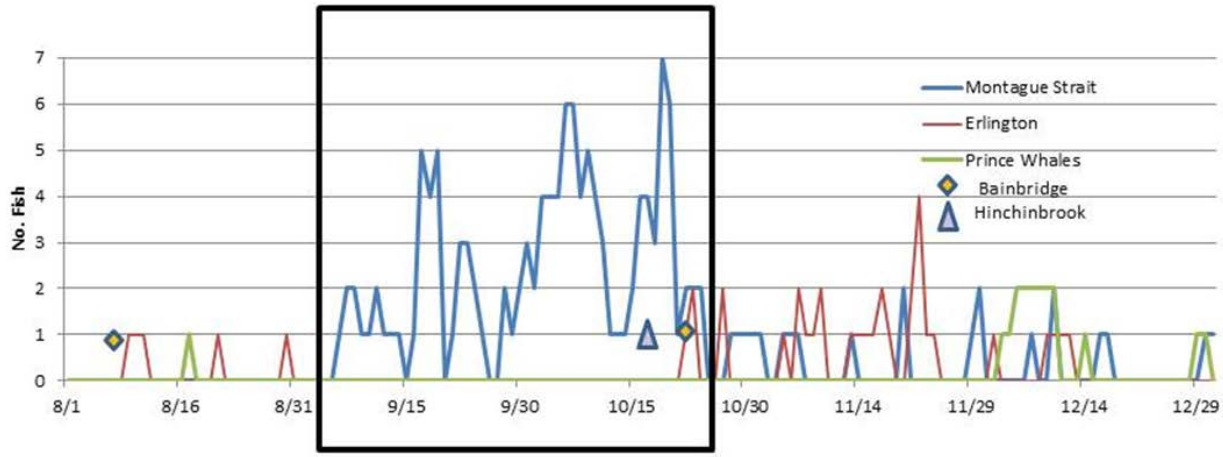

Figure 28. Number of acoustic tagged Pacific herring detected by date and array, August 1, 2013 - January 2, 2014. No detections occurred at LaTouche Passage. Box added to emphasize the predominance of fish at the Montague Strait array throughout September and October 2013.

This pilot project has demonstrated the ability to tag herring with acoustic tags and detect them for several months after their release. Additional information about the releases is provided in Appendix 4.

Predation

Recent work on herring predation in PWS has focused on that by Humpback whales. Results from that research are reported in the synthesis provided by the Gulf Watch Alaska program. As reported by Pegau (2013) there are several papers in review and press discussing herring predation by marine birds (Bishop et al. in press), fish (Watson et al. in review, Bishop and Powers 2013), and marine mammals (Moran et al. in review). In the overview paper being prepared by Ron Heintz there is a table describing the known herring predators. That table is provided in Appendix 5.

Future research recommendations

One of the strengths of the existing HRM program is the goal to improve predictive models of herring stocks through research and monitoring. This provides a strong tie between the research being conducted and ADF&G, the management organization. Research should be applicable to the fishing community as well as the managers. Therefore, we recommend that the goal remain the same in the future.

We recommend a program that uses a model to continue to identify important inputs to the population models and guide future research directions. Monitoring should provide necessary inputs to the population model. Research should address assumptions in the existing model, provide connection to the environmental data being collected, and lay the groundwork for future research.

The program should be built around a population model that can incorporate more life stages and environmental relationships and can simulate the value of additional inputs and investigate alternative management rules, such as changes to the fisheries threshold. The updated ASA model structure can be expanded to allow for the inputs associated with fish younger than age-3 to test the value of different recruitment predictors and environmental factors associated with juvenile herring. It can also be expanded to estimate natural mortality. By using the model to simulate different inputs we can guide future research directions.

The existing modeling efforts demonstrate the importance of ensuring high quality hydroacoustic estimates of the spawning biomass and the program should continue to include hydroacoustic monitoring. A large knowledge gap is being able to predict the incoming year class in order to estimate the spawning population. We recommend continuing efforts to estimate new recruitment levels using aerial or hydroacoustic surveys. Potential changes in spawning locations needs to be considered. Expanded aerial surveys to reach areas not covered by ADF&G are likely to be more cost effective in identifying changes than boat based surveys. The hydroacoustic surveys could occur once the timing and location of other spawning aggregations are identified.

We recognize the importance of disease in determining the population levels. Considerable discussion has occurred about how to best use the prevalence information being collected. We recommend continuing to collect the disease prevalence information while working on better measures of the impact of disease and better interpretations of how to use the existing data. Additionally, an understanding of the basic epidemiological principles governing the common herring diseases in PWS is providing important new insights that are important for the model input parameters. It is recommended that these avenues of research continue.

An important gap in the existing research is the economic impacts of fisheries decisions. We are not recommending focusing on this topic, but it should be considered as a component that can provide connections between the research and local communities.

Developing connections between herring and environmental factors, both bottom up and top down, require an understanding of the time and space they occupy at different life stages. It is a bit surprising how little we understand regarding where the fish are distributed during their different life stages. We observe the adults during the spawning event and the tagging results show that they move to the entrances, but we cannot determine if they leave PWS for the Gulf of Alaska. Reports from fishermen and results of forage fish sampling show that a portion of the adult population remains in PWS. What portion of the total population remains in PWS is unknown. There is very limited information about where the adults go between when they are seen in the entrances in the fall and when they gather prior to spawn. Even less is known about juvenile herring. Age 2 and 3 juvenile fish are occasionally observed in PWS. Even though we know a portion of the age-3 fish are recruited to the spawning stock, we also have observed a portion in nursery grounds at the same time. We don't know when and where new fish recruit to the spawning biomass, which makes determining the maturation function difficult as we don't know what portion of the population we are sampling. There are still gaps in our knowledge of the

locations of even younger herring. Recent research has focused on overwintering age-0 herring and our knowledge of their abundance and locations before and after overwintering remains limited.

Much of the research conducted during the past five years is well suited for developing connections between age-0 herring and environmental conditions. One issue that needs to be resolved is the temporal and spatial scales appropriate for connecting the age-0 herring to their environment. We have a good understanding about where the fish overwinter and overwintering factors, but the preliminary work presented here indicates that age-0 herring growth may be more dependent on conditions during larval through recruitment to nursery bays life stages when we have less knowledge of their locations.

To address questions regarding how environmental conditions and predation affect the herring population, it is important to understand where the fish reside throughout their life. It is also important that population surveys be of adequate accuracy to determine survival to provide a more direct tie to the environmental conditions. If we are to examine how herring interact with other species, such as salmon, we need to know where to look for overlaps between the species. With the Ocean Tracking Network in place we have the opportunity to leverage their efforts to better understand the movement of adult herring. We also have the capabilities to examine the movement of larval and recently metamorphosed fish to examine how environmental conditions determine their growth. Multi-frequency acoustics and other technologies can help improve our identification and population level estimates of different life stages that are necessary to provide a measure of survival. Given the need to understand the various life stages of herring, the capabilities to conduct the work, and the opportunities available for tracking herring we recommend focusing on projects that help identify seasonal distribution of herring and their connection to environmental conditions.

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Appendix 1 ADF&G PWS ASA model equations and inputs

Equations

1) Number of herring of a particular age in a particular year.

$$N_{a+1,t+1} = \left[\left(\left(N_{a,t} - \left(C_t^s \Theta_{a,t}^s + C_{a,t}^g + P_k C_{a,t}^P\right)\right) S_{a,t}^{\frac{1}{2}}\right) - C_{a,t}^{\frac{f}{b}}\right] S_{a,t+1}^{1/2}$$

2) Half year survival $S_{a,t}^{1/2} = e^{-M_{a,t}/2}$

3) Mortality $M_{a,t} = M_0 + \sum_i \beta_i x_{i,t}$

4) Conversion to pre-fishery spawning biomass $PB_{a,t} = w_{a,t} mat_{a,t} N_{a,t}$

5) Abundance of spawning population $SN_{a,t} = mat_{a,t}(N_{a,t} - \left(C_t^s \Theta_{a,t}^s + C_{a,t}^g + P_k C_{a,t}^P\right))$

6) Spawning biomass $SB_t = \sum_a w_{a,t}\ SN_{a,t}$

7) Computed seine age composition $\widehat{\Theta}_{a,t}^s = \frac{V_a N_{a,t}}{\sum_a V_a N_{a,t}}$

8) Computed spawning age composition $\widehat{\Theta}_{a,t}^{SP} = \frac{SN_{a,t}}{\sum_a SN_{a,t}}$

9) Computed mile-days of milt $\hat{L}_t = \frac{(1-\%F_t)SB_t}{\psi}$

10) Computed egg deposition $\hat{E}_t = \%F_t \sum_a f_{a,t} SN_{a,t}$

11) Computed hydroacoustic biomass $\hat{H}_t = B_t e^{\gamma}$

12) Prefishery estimated biomass $B_t = \sum_a w_{a,t}\ N_{a,t}$

13) Computed Ricker spawner-recruit $\hat{R}_t = \alpha e^{-\tau SB_t + \varepsilon_t}$

14) Residual sum of squares of age composition $RSS_i = \sum_t \sum_a (\Theta_{a,t}^i - \widehat{\Theta}_{a,t}^i)^2$

15) Residual sum of squares of L, E, H, and R $RSS_i = \sum_t (\ln O_t^i - \ln \hat{O}_t^i)^2$

16) Objective function $RSS_{tot} = \sum_i \lambda_i RSS_i$

Notation

Observed quantities

$C_{a,t}^{i}$ Catch in the ith fishery at age a in year t

$w_{a,t}$ Weight-at-age in year t

$\Theta_{a,t}^{i}$ Age composition of the ith dataset at age a in year t

$f_{a,t}$ Fecundity at age a in year t

$x_{i,t}$ Disease prevalence variables

H_t Hydroacoustic biomass in year t

E_t Egg deposition in year t

L_t Mile-days of milt in year t

$\%F_t$ Percentage of females present

Estimated quantities used as inputs

$N_{3,t}$ Age 3 recruits in year t

$N_{a,1980}$ Initial abundances for all ages

V_a Gear vulnerability of age a

$mat_{a,t}$ Maturity at age a in year t

$M_{a,t}$ Mortality with disease parameter β

M_0 Background mortality

$S_{a,t}$ Survival of age a in year t (calculated from $M_{a,t}$)

P_k Proportion of impounded fish killed.

λ_i Weighting function applied to residual sum of squares

Model derived quantities

$N_{a,t}$ Total abundance at age a in year t

$PB_{a,t}$ Pre-fishery spawning biomass at age a in year t

$SN_{a,t}$ Natural spawning population after spring fisheries at age a in year t

SB_t Total spawning biomass in year t after spring fisheries

B_t Pre-fishery biomass

β Disease scaling parameter

$\widehat{\Theta}_{a,t}$ Estimated age composition

$\hat{E}_t$ Estimated egg deposition in year t

$\hat{L}_t$ Estimated mile-days of milt in year t with parameter ψ

$\widehat{H}_t$ Estimated hydroacoustic biomass in year t with parameter γ

$\hat{R}_t$ Ricker estimates of recruits in year t with parameters α and τ

Estimated quantities used as inputs

$N_{a,t}$ Initial estimated abundances

INITIAL COHORT SIZES (millions of fish)			
	AGE		
YEAR	3	4	5
1980	231.0	528.9	81.9
1981	127.0		
1982	129.2		
1983	439.7		
1984	365.9		
1985	108.1		
1986	83.1		
1987	1104.7		
1988	84.0		
1989	22.8		
1990	46.6		
1991	1004.4		
1992	51.5		
1993	131.3		
1994	47.0		
1995	125.1		
1996	92.5		
1997	164.3		
1998	83.9		
1999	2.1		
2000	22.0		
2001	1.0		
2002	142.1		
2003	13.8		
2004	2.9		
2005	10.5		
2006	1.5		
2007	1.1		
2008	13.4		
2009	12.7		
2010	6.8		
2011	0.6		
2012	2.8		
2013	2.1		

V_a Seine gear vulnerability of age a

AGE						
3	4	5	6	7	8	9
0.14	0.76	0.98	1.00	1.00	1.00	1.00

$mat_{a,t}$ Maturity at age (proportion of mature fish at each age)

	Age 3	Age 4	Age 5 +
1980 - 1996	0.19	0.82	1.00
1997 - 2006	0.47	0.77	1.00

Disease prevalence numbers used in the calculation of mortality. The red numbers represent where a shift in observation methods occurred. The new Ichthyophonus prevalence numbers are not currently being used and prevalence is set to 2004 values. Values in 1993 are assumed to provide a mortality consistent with the observed decline in adult population.

	ages 3-4		ages 5-8	
Year	VHSV	Ichthy	VHSV	Ichthy
1993	1.0000	0.0000	0.0000	0.3282
1994	1.04%			7.47%
1995	0.14%			11.98%
1996	0.00%			11.35%
1997	9.40%			10.24%
1998	0.60%			15.19%
1999	1.05%			11.22%
2000	0.00%			11.15%
2001	0.01%			20.00%
2002	0.14%			15.79%
2003	0.01%			30.30%
2004	0.05%			16.42%
2005	0.05%			16.42%
2006	0.05%			16.42%
2007	0.00%			16.42%
2008	0.00%			16.42%
2009	0.00%			16.42%

2010	1.67%		16.42%
2011	0.00%		16.42%
2012	0.00%		16.42%
2013	0.00%		16.42%

M_0 Background mortality M_0 =0.25 for age 5-8.

Survival of age 9+ fish prior to 1993 is 0.25 and from 1993 on is .567 times that of age5-8.

P_k Proportion of impounded fish killed P_k = 0.75

Weighting functions λ_i

Egg surveys	0.25
Mile-days of milt	1.00
Seine age composition	0.25
Spawn age composition	1.00
Acoustics Surveys	0.25
Ricker spawner-recruit	0.03

Appendix 2 UW ASA model equations and inputs

Table 2.1 *Data types. The first column lists the data type index number used in the text, the second column lists the data type, n_y refers to number of years that data type was collected, and final column reports the first and last year of collection.*

Index	Data type	Symbol	n_y	Years
2.1.1	Gillnet catch age-composition	$C_{2,y,a}$	15	(1980, 1998)
2.1.2	Pound utilization catch age-composition	$C_{3,y,a}$	16	(1980, 1999)
2.1.3	Food/bait catch age-composition	$C_{4,y,a}$	17	(1980, 1998)
2.1.4	Disease index of VHSV mortality, ages 3, 4	$d_{1,y}$	19	(1994, 2012)
2.1.5	Disease index of *I. hoferi* mortality, ages 5–8	$d_{2,y}$	19	(1994, 2012)
2.1.6	Fecundity-at-age, number of eggs per female	$f_{y,a}$	7	(1984, 1993)
2.1.7	Weight-at-age of spawning herring, mt/million fish	$w_{y,a}$	33	(1980, 2012)
2.1.8	Purse-seine age-composition	$\Theta_{1,y,a}$	13	(1980, 1998)
2.1.9	Spawner survey age-composition	$\Theta_{Sp,y,a}$	31	(1982, 2012)
2.1.10	Proportion of female spawners	$\rho_{f,y}$	33	(1980, 2012)
2.1.11	Total purse-seine yield, mt	$\Omega_{1,y}$	13	(1980, 1998)
2.1.12	Eggs deposited, trillions	E_y	10	(1984, 1997)
2.1.13	C.V. for eggs deposited	$\sigma_{E,A,y}$	10	(1984, 1997)
2.1.14	ADF&G spring hydroacoustic survey biomass, mt	$H_{1,y}$	5	(2005, 2009)
2.1.15	PWSSC spring hydroacoustic survey biomass, mt	$H_{2,y}$	20	(1993, 2012)
2.1.16	C.V. for PWSSC hydroacoustic biomass	$\sigma_{H_{2,A,y}}$	20	(1993, 2012)
2.1.17	Milt, mile/days	T_y	33	(1980, 2012)

Table 2.2 *Key model parameter estimates (medians and 95% intervals).*

Index	Parameters	Symbols	Parameter values Median and 95% CI		Prior
2.2.1	Natural mortality, 1980–91, ages 3–8	$m_{a\in(3,\ldots,8)}$	0.25	–	Not estimated
2.2.2	Natural mortality, 1980–91, age 9^{+}	$m_{9^+} = \mu_{9^+}$	0.90	(0.58, 1.27)	$U\sim(0.301, 1.386)$
2.2.3	VHSV disease scalar, ages 3-4	β_1	84.08	(11.45, 157.31)	$U\sim(0, 1000)$
2.2.4	*I. hoferi* scalar, ages 5-8, 1994–2006	$\beta_{2,1}$	0.99	(0.37, 1.71)	$U\sim(0, 25)$
2.2.6	*I. hoferi* scalar, ages 5-8, 2007–12	$\beta_{2,2}$	0.51	(0.02, 1.31)	$U\sim(0, 25)$
2.2.7	Disease mortality in 1993, VHSV	$m_{1,1993,a} = \mu_{1,1993}$	0.73	(0.22, 1.2)	$U\sim(0, 5)$
2.2.8	Disease mortality in 1993, *I. hoferi*	$m_{2,1993,a} = \mu_{2,1993}$	0.69	(0.28, 1.12)	$U\sim(0, 5)$
2.2.9	Purse-seine gear selectivity	α_V	3.81	(3.52, 4.13)	$U\sim(3, 5)$
2.2.10	Purse-seine gear selectivity	β_v	2.23	(1.54, 3.13)	$U\sim(1, 7)$
2.2.11	ADF&G acoustic scalar, log-link	q_1	-0.34	(-0.72, 0.03)	$U\sim(-5, 5)$
2.2.12	ADF&G acoustic biomass CV	σ_{H_1}	0.27	(0.15, 0.39)	$U\sim(0, 0.4)$
2.2.13	PWSSC acoustic scalar, log-link	q_2	-0.30	(-0.58, 0)	$U\sim(-5, 5)$
2.2.14	PWSSC acoustic biomass add'l error	$\sigma_{H_2,B}$	0.32	(0.22, 0.4)	$U\sim(0, 0.4)$
2.2.15	Egg deposition additional error	$\sigma_{E,B}$	0.30	–	Not estimated
2.2.16	Milt scalar, log-link	q_T	311.24	(247.83, 399.39)	$U\sim(2.3, 7)$
2.2.17	Milt CV	σ_T	0.33	(0.25, 0.39)	$U\sim(0, .04)$
2.2.18	Proportion mature at age 3, 1980–96	$\nu_3;\ \rho_{M,1,3} = \nu_3\rho_{M,1,4}$	0.39	(0.28, 0.53)	$U\sim(0, 0.75)$
2.2.19	Proportion mature at age 4, 1980–96	$\rho_{M,1,4}$	0.79	(0.61, 0.97)	$U\sim(0, 1)$
2.2.20	Proportion mature at age 3, 1997–2012	$\rho_{M,2,3}$	0.46	(0.35, 0.62)	$U\sim(0.1, 1)$
2.2.21	Proportion mature at age 4, 1997–2012	$\rho_{M,2,4}$	0.99	–	Not estimated
2.2.22	Age-3 abundance (millions), log-link	$N_{y,3} = e^{\eta_{y,3}}$	Table 2.3	–	$U\sim(0, 8.007)$
2.2.23	Age-4 abundance in 1980, log-link	$N_{1980,4} = e^{\eta_{1980,4}}$	540.68	(445.47, 670.48)	$U\sim(0, 8.007)$
2.2.24	Age-5 abundance in 1980, log-link	$N_{1980,5} = e^{\eta_{1980,5^+}}$	70.65	(45.99, 105.38)	$U\sim(0, 8.007)$

Table 2.3 *Posterior medians for recruitment (in millions of age-3 fish), exploitation rate, biomass (median and 95% intervals), the probability that biomass is smaller than 20,000 mt, total mortality for age 3-4 fish, and total mortality for age 5+ fish.*

Year	Rec. median	Rec. 95% CI	Median biomass	Biomass 95% CI	Prob. B<20K	Exploit. Rate	Age 3-4 total mortality	Age 5-8 total mortality
1980	215.86	(158.45, 288.11)	54.67	(41.1, 71.12)	0	0.13	0.25	0.25
1981	114.33	(77.36, 166.71)	64.00	(52.13, 79.44)	0	0.22	0.25	0.25
1982	154.99	(110.45, 212.24)	55.30	(43.5, 71.38)	0	0.15	0.25	0.25
1983	427.09	(332.66, 549.41)	64.03	(49.57, 83.5)	0	0.05	0.25	0.25
1984	358.77	(277.88, 463.57)	75.54	(58.85, 96.84)	0	0.09	0.25	0.25
1985	116.1	(79.88, 169.79)	91.64	(71.82, 115.36)	0	0.09	0.25	0.25
1986	137.12	(95.47, 200.18)	80.94	(64.78, 100.71)	0	0.14	0.25	0.25
1987	1209.67	(984.97, 1499.57)	91.61	(72.68, 113.37)	0	0.07	0.25	0.25
1988	136.08	(94.25, 199.87)	117.08	(91.6, 146.63)	0	0.09	0.25	0.25
1989	28.78	(19.46, 53.11)	120.38	(99.87, 148.6)	0	0	0.25	0.25
1990	30.04	(12.63, 68.17)	104.43	(86.33, 128.81)	0	0.1	0.25	0.25
1991	876.84	(599.45, 1319.79)	93.56	(75.31, 117.35)	0	0.18	0.25	0.25
1992	67.01	(24.24, 155.71)	93.53	(71.92, 125.34)	0	0.22	0.98	0.94
1993	136.94	(66.53, 283.34)	38.01	(29.91, 47.79)	0	0.07	0.98	0.94
1994	17.87	(6.52, 44.51)	19.82	(14.97, 26.16)	0.528	–	1.12	0.32
1995	93.33	(64.64, 132.46)	18.15	(14.24, 23.78)	0.767	–	0.37	0.37
1996	78.02	(48.77, 119.38)	19.83	(15.66, 25.61)	0.535	0.03	0.25	0.36
1997	145.08	(82.55, 242.96)	26.80	(21.5, 34.39)	0.006	0.18	0.33	0.35
1998	71.19	(39.26, 122.2)	20.86	(16.19, 27.45)	0.365	0.2	0.75	0.4
1999	5.9	(1.58, 16.82)	14.36	(10.41, 20.19)	0.972	0	0.26	0.36
2000	21.24	(10.86, 40.33)	13.18	(9.55, 17.93)	0.993	–	0.25	0.36
2001	10.1	(3.79, 22.67)	11.52	(8.44, 15.71)	1	–	0.26	0.45
2002	206.97	(147.06, 287.51)	14.04	(10.45, 18.98)	0.988	–	0.37	0.41
2003	40.91	(25.65, 65.4)	18.25	(13.59, 24.32)	0.731	–	0.27	0.55
2004	18.91	(10.69, 30.65)	19.75	(14.38, 26.35)	0.54	–	0.27	0.41
2005	26.55	(16.02, 44.91)	15.47	(11.3, 20.86)	0.957	–	0.27	0.41
2006	16.69	(9.16, 29.04)	13.14	(9.49, 18.34)	0.994	–	0.27	0.41
2007	103.16	(71.64, 147.82)	14.77	(10.89, 20.68)	0.968	–	0.25	0.4
2008	98.3	(68.8, 146.47)	20.03	(15.02, 27.22)	0.497	–	0.25	0.34
2009	29.05	(13.37, 57.82)	19.50	(14.77, 26.64)	0.572	–	0.25	0.36
2010	54.42	(22.87, 113.93)	20.35	(15.37, 28.1)	0.451	–	0.28	0.31
2011	10.55	(1.33, 47.5)	17.78	(13.07, 24.9)	0.765	–	0.25	0.33
2012	83.35	(19.56, 227.57)	18.08	(12.5, 26.37)	0.707	–	0.25	0.37
2013	36.32	(25.1, 52.44)	19.08	(11.95, 30.65)	0.581	–	–	–

Table 2.4 *Description of model in words and equations, together with equation numbers for cross-referencing.*

Eq. No	Description	Equation
	Catch, millions of fish	
2.4.1	Estimated total purse-seine catch	$\hat{C}_{1,y} = \frac{\Omega_{1,y}}{\sum_{a\in A}(\hat{\theta}_{1,y,a} w_{y,a})}$
2.4.2	Spring removals, $\rho_k = 0.75$	$\hat{C}_{S,y,a} = \hat{\theta}_{1,y,a}\hat{C}_{1,y} + C_{2,y,a} + \rho_k C_{3,y,a}$
	Survival, rate	
2.4.4	Half-year survival, 1980–1991, all ages	$S^{.5}_{y,a} = e^{-.5m_a}$
2.4.5	Half-year survival, 1993–2006, ages 3–8, diseases VHSV, *I. hoferi* denoted by *x=1,2*	$S^{.5}_{y,a} = e^{-.5(m_a+\beta_{x,1}d_{x,y})}$
2.4.6	Half-year survival, 2007–2012, ages 3–8, diseases VHSV, *I. hoferi* denoted by *x=1,2*	$S^{.5}_{y,a} = e^{-.5(m_a+\beta_{x,2}d_{x,y})}$
2.4.7	Half-year survival, 1993–2012, plus group	$S^{.5}_{y,9^+} = S^{.5}_{y-1,9^+}\left(\frac{S^{.5}_{y,8}}{S^{.5}_{y-1,8}}\right)$
2.4.8	**Selectivity, logistic form** Purse-seine gear selectivity by age	$V_a = \frac{1}{1+e^{-\beta_v(a-\alpha_v)}}$
	Abundance, millions of fish	
2.4.9	Pre-fishery total abundance, ages 3–8	$N_{y+1,a+1} = \left[\left(\left(N_{y,a} - \hat{C}_{S,y,a}\right)S^{.5}_{y,a}\right) - C_{4,y,a}\right]S^{.5}_{y,a}$
2.4.10	Pre-fishery total abundance, ages 9^+	$N_{y+1,a+1} = \left[\left(\left(N_{y,a} - \hat{C}_{S,y,a}\right)S^{.5}_{y,a}\right) - C_{4,y,a}\right]S^{.5}_{y,a} + \left[\left(N_{y,a+1} - \hat{C}_{S,y,a+1}\right)S^{.5}_{y,a+1} - C_{4,y,a+1}\right]S^{.5}_{y,a+1}$
2.4.11	Post-fishery spawning abundance	$\tilde{N}_{y,a} = \rho_{M,a}\left[N_{y,a} - \left(\hat{\theta}_{1,y,a}\hat{C}_{1,y} + C_{2,y,a} + C_{3,y,a}\right)\right]$
	Biomass, mt	
2.4.12	Pre-fishery total biomass	$B_y = \sum_{a\in A}\left(N_{y,a} w_{y,a}\right)$
2.4.13	Pre-fishery spawning biomass	$\tilde{B}_y = \sum_{a\in A}\rho_{M,a} N_{y,a} w_{y,a}$
2.4.14	Post-fishery spawning biomass	$\tilde{B}_{post,y} = \sum_{a\in A}\tilde{N}_{y,a} w_{y,a}$
2.4.15	Estimated 2013 pre-fishery run biomass	$B_{2013} = B_{2013,3} + \sum_{a\in A_{-3}}\rho_{M,a} N_{2013,a}\overline{w}_a$
2.4.16	Average weight-at-age over the last 5 years	$\overline{w}_a = \frac{1}{5}\sum_{i=2008}^{2012} w_{i,a}$
2.4.17	Estimated 2013 age-3 biomass	$B_{2013,3} = \rho_{M,2,3}\overline{w}_3 \exp\left(\frac{1}{10}\sum_{i=2003}^{2012}\ln(\eta_i)\right)$
	Estimates used in the likelihood expressions	
2.4.18	Estimated ADF&G hydro-acoustic biomass, mt	$\hat{H}_{1,y} = B_y e^{q_1}$
2.4.19	Estimated PWSSC hydro-acoustic biomass, mt	$\hat{H}_{2,y} = B_y e^{q_2}$
2.4.20	Estimated purse-seine age composition	$\hat{\theta}_{1,y,a} = \frac{V_a N_{y,a}}{\sum_{a\in A}(V_a N_{y,a})}$
2.4.21	Estimated spawning age composition	$\hat{\theta}_{Sp,y,a} = \frac{\rho_{M,a} N_{y,a}}{\sum_{a\in A}(\rho_{M,a} N_{y,a})}$

2.4.22	Estimated naturally spawned eggs, trillions	$\hat{E}_y = 10^{-6}\rho_{f,y}\sum_{a\in A}\left(\tilde{N}_{y,a}f_{y,a}\right) \quad \forall\, y \in Y$
2.4.23	Estimated milt, mile-days	$\hat{T}_y = \frac{(1-\rho_{f,y})\tilde{B}_{post,y}}{e^{q_T}}$

Table 2.5 *Negative log-likelihoods for the different components of the model fit to data for the updated Bayesian ASA model.*

	Likelihood Components	
2.5.1	Complete expression	$L = \sum_{i=1}^{6} L_i$
2.5.2	Purse-seine age-composition	$L_1 = -\sum_{y=1980,\ldots}^{\sim 1998} Z_{1,y}\sum_{a\in A}\Theta_{1,y,a}\ln\left(\frac{\hat{\Theta}_{1,y,a}}{\Theta_{1,y,a}}\right)$
2.5.3	Spawner survey age-composition	$L_2 = -\sum_{y=1982}^{2012} Z_{Sp,y}\sum_{a\in A}\Theta_{Sp,y,a}\ln\left(\frac{\hat{\Theta}_{Sp,y,a}}{\Theta_{Sp,y,a}}\right)$
2.5.4	Number of eggs deposited	$L_3 = 10\ln\sigma_E + \frac{1}{2\sigma_{E,y}^2}\sum_{y\in Y_E}\left(\ln\left(\hat{E}_y\right) - \ln\left(E_y\right)\right)^2$
2.5.5	Total variance for L_3	$\sigma_{E,y}^2 = \sigma_{E,A,y}^2 + \sigma_{E,B}^2$
2.5.6	ADF&G hydroacoustic biomass	$L_4 = 5\ln\sigma_{H_1} + \frac{1}{2\sigma_{H_1}^2}\sum_{y\in Y_H}\left(\ln\left(\hat{H}_{1,y}\right) - \ln\left(H_{1,y}\right)\right)^2$
2.5.7	PWSSC hydroacoustic biomass	$L_5 = 20\ln\sigma_{H_2} + \frac{1}{2\sigma_{H_2,y}^2}\sum_{y\in Y_H}\left(\ln\left(\hat{H}_{2,y}\right) - \ln\left(H_{2,y}\right)\right)^2$
2.5.8	Total variance for L_5	$\sigma_{H_2,y}^2 = \sigma_{H_2,A,y}^2 + \sigma_{H_2,B}^2$
2.5.9	Milt mile-days	$L_6 = 33\ln\sigma_T + \frac{1}{2\sigma_T^2}\sum_{y\in Y}\left(\ln\left(\hat{T}_y\right) - \ln\left(T_y\right)\right)^2$

Appendix 3 Synthesis of *Ichthyophonus*

The parasite *Ichthyophonus sp*. in Pacific herring from the coastal NE Pacific

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Abstract

The protistan parasite *Ichthyophonus* occurred in populations of Pacific herring *Clupea pallasii* throughout coastal areas of the NE Pacific, ranging from Puget Sound, WA north to the Gulf of Alaska, AK. Infection prevalence in local Pacific herring stocks varied seasonally and annually, and a general pattern of increasing prevalence with host size and/or age persisted throughout the NE Pacific. An exception to this zoographic pattern occurred among a group of juvenile, age 1+ year Pacific herring from Cordova Harbor, AK in June 2010, which demonstrated an unusually high infection prevalence of 35%. Reasons for this anomaly were hypothesized to involve anthropogenic influences that resulted in locally elevated infection pressures. Inter-annual declines in infection prevalence from some populations (e.g. Lower Cook Inlet, AK; from 20-32% in 2007 to 0-3% during 2009-2013) or from the largest size cohorts of other populations (e.g. Sitka Sound, AK; from 62.5% in 2007 to 19.6% in 2013) was likely a reflection of selective mortality among the infected cohorts. All available information for *Ichthyophonus* in the NE Pacific, including broad geographic range, low host specificity, and presence in archived Pacific herring tissue samples dating to the 1980's, indicate a long-standing host-pathogen relationship.

Key Words: Ichthyophonus, Pacific herring

Introduction

Common throughout the North Pacific Ocean, Pacific herring (*Clupea pallasii*) are members of a species assemblage that is collectively referred to as forage fish. By occupying an ecological niche in the middle of the food web, the forage fish assemblage is often characterized in the 'Wasp Waist Hypothesis' as the critical determinant of energy flow and productivity in some coastal marine systems (Rice 1995 and Currey *et al.* 2000). Contrary to systems controlled by top-down or bottom-up forces, where limits on ecosystem productivity are exerted at the level of primary production or at the level of highest order predators, respectively; the Wasp Waist Hypothesis asserts that forage fish exert top-down control on all lower trophic levels and bottom-up control on all upper trophic levels (Fauchald *et al.* 2011). As such, sudden changes in forage fish abundances, demographics, and assemblages cascade throughout multiple trophic levels in the ecosystem. For example, a sudden mass mortality of pilchards in south Australia (Griffin *et al.* 1997; Jones *et al.* 1997; Ward *et al.* 2001), presumably caused by disease from an introduced herpesvirus (Hyatt *et al.* 1977; Gaughan *et al.* 2000; Whittington *et al.* 2008), was followed by diet shift, breeding failure, and starvation of closely-associated seabirds (Bunce & Norman 2000; Dann *et al.* 2000). Large oscillations in abundance are common in forage fish populations (Schwartzlose & Alheit 1999), yet ecological drivers of these population changes remain poorly understood. Determining the causes of population oscillations in highly migratory marine fishes is particularly difficult, owing largely to observational difficulties; however, cyclic declines in red grouse populations from Britain can be initiated by host / parasite interactions (Hudson *et al.* 1998, Redpath *et al.* 2006). We hypothesize that analogous ecological mechanisms can influence populations of wild marine fishes.

Ichthyophonus hoferi is a parasite that causes systemic infections primarily in marine fishes. Taxonomic and phylogenetic uncertainties have accompanied *I. hoferi* since its original description (reviewed McVicar 2011); however, the organism is currently considered a member of the Mesomycetozoea a monophyletic class of organisms that arose near the time when animals diverged from fungi (Mendoza *et al.* 2002). A lack of distinguishing characteristics provided in the original species description (von Hofer 1893), combined with a high degree of morphological plasticity in life history stages (Okamoto *et al.* 1985), likely resulted in the grouping of several closely-related organisms into a species assemblage that is collectively referred to as *I. hoferi* (reviewed in McVicar 2001). Phenotypic (Rand 1994; Hershberger *et al.* 2008) and genotypic (Criscione *et al.* 2002; Halos *et al.* 2005; Rand *et al.* 2000; Rasmussen *et al.* 2010; Hershberger *et al.* 2010; Gregg *et al*. *In Preparation*) differences in *I. hoferi* isolates from fishes provide preliminary evidence for apparent speciation within the genus. Consequently, several attempts at species designations have been made, including *I. hoferi*, *I. irregularis*, *I. gasterophilum*, *I. lotae*, *I. intestinalis* (reviewed in Rand 1990; Rand *et al.* 2000); however, the species descriptions are often incomplete, duplicative, and based on subjective criteria. To avoid further perpetuation of confusion surrounding the *Ichthyophonus spp.* complex, the organism(s) will hereafter be referred to generically.

Ichthyophonus is perhaps the most ecologically and economically significant pathogen of wild marine fishes throughout the world, based on its low host specificity, broad geographic range, and recurring association with epizootics that result in massive fish kills and population-level impacts (reviewed in Burge *et al.* 2014). The parasite has been reported in more than 35 species of marine fishes, and more than 80 species are reported as susceptible to infection (reviewed in McVicar 2011). Additionally, recurring epizootics have been reported in Atlantic herring (*Clupea harengus*) populations throughout the coastal regions of the Atlantic Ocean, Chinook salmon in the Yukon River (Alaska and Canada), yellowtail flounder in the western North Atlantic, and American shad in the Columbia River (Washington and Oregon) (reviewed in Burge *et al.* 2014). *Ichthyophonus* is also endemic in some populations of Pacific herring (Hershberger *et al.* 2002; Jones & Dawe 2002), where mortality from the resulting disease remains a leading hypothesis accounting for the population decline and failed recovery in Prince William Sound (Marty *et al.* 2003 & 2010). Details regarding the epizootiology of *Ichthyophonus* in Pacific herring remain largely uninvestigated, including its geographic range, seasonal and interannual persistence, and differences in infection prevalence within and between genetically distinct host metapopulations. The objective of this study was to examine these information gaps using the results from *Ichthyophonus* prevalence surveys in populations of Pacific herring that were performed throughout the Northeast Pacific Ocean over a recent 11 year period.

Methods

The prevalence of *Ichthyophonus* was assessed in populations of Pacific herring from California to Alaska during 2003 – 2013 (Table 1). Throughout this range, Pacific herring were collected by trawl, gill net, purse seine, cast net, beach seine, or hook-and-line. *Ichthyophonus* prevalence at each location was determined by tissue explant culture. The heart from each fish was aseptically removed and immersed in *Ichthyophonus* growth medium (>1:5 W:V), consisting of tris-buffered Eagle's Minimum Essential

Medium supplemented with 5% fetal bovine serum, 100 IU ml^{-1} penicillin, 100 µg ml^{-1} streptomycin, and 100 µg ml^{-1} gentamycin (MEM). Explant cultures were examined microscopically (40X magnification) for the presence of *Ichthyophonus* after 7d and 14d; any cultures without detectable *Ichthyophonus* schizonts or hyphae after 14d were considered negative. Fork length or standard length, sex, and age (from scales) were recorded from a portion of the sampled fish. *Ichthyophonus* prevalences were compared by Chi Square (χ^2), with statistical significance assigned to comparisons with $P < 0.05$.

The historical presence of *Ichthyophonus* in Puget Sound was evaluated from formalin-fixed Pacific herring specimens archived at the University of Washington Fish Collection. Hearts were removed from archived specimens and embedded in paraffin blocks, following standard histological procedures. Thin sections (2-3µm) of the hearts were stained with periodic acid-Schiff (PAS) and examined microscopically for the presence of PAS-positive *Ichthyophonus* schizonts and hyphae.

Results

Ichthyophonus occurred in Pacific herring populations throughout the eastern North Pacific Ocean, ranging from Puget Sound, WA north to the Gulf of Alaska (Table 1); the parasite was not detected in any Pacific herring samples as far south as San Francisco Bay, CA (n=141). On an annual basis, the prevalence of *Ichthyophonus* infection was not consistent in Pacific herring stocks throughout this range; for example, infection prevalence in adults during 2008 ranged from 5% in Lynn Canal, AK to 48% in Holmes Harbor (Puget Sound), WA. This disparate prevalence pattern also occurred on smaller geographic scales, with the infection prevalence in adult Pacific herring throughout Puget Sound, WA ranging from 5% in Case Inlet to 50% in Holmes Harbor during 2006. Similarly, infection prevalence differed among Pacific herring collected throughout British Columbia during 2011 (Table 1), with higher prevalence occurring in pre-spawn populations that overwintered in nearshore locations than those that overwintered in offshore locations (Figure 1). Inter-annual changes also occurred in the infection prevalence from specific sampling locations; for example, the infection prevalence in adult Pacific herring from Cook Inlet, AK declined from 38-55% in 2005 to 2-3% in 2009.

Among samples of pre-spawn Pacific herring collected in the spring, the prevalence of *Ichthyophonus* generally increased with host size and age (Figures 2-5). For example, the annual spring infection prevalence in Prince William Sound increased with size class from 15-60% in 2008, 16-80% in 2009, 13-33% in 2010, 13-47% in 2011, and 4-50% in 2013; the trend was less apparent in 2012, where data from the smallest size classes were likely confounded by small sample sizes (Figure 3A). Among Pacific herring collected in the spring, *Ichthyophonus* prevalence in each age class followed an analogous pattern as size; for example the infection prevalence in Lower Cook Inlet increased from 0% in age 2-3 yr cohorts to 50% in age 8+ yr cohorts during 2006, and from 7% among age 2-3 yr cohorts to 67% in age 8+ yr cohorts during 2007 (Figure 4B). The infection prevalence in Lower Cook Inlet dropped dramatically after 2007, after which the parasite was detected only in low percentages among the largest size classes / oldest age cohorts (Figures 4A&B). This increased prevalence with size / age was also generally reflected in lower infection prevalence among collections of juveniles than of adults (Table 1). However, a single exception to this pattern occurred with the detection of an unusually high

Ichthyophonus prevalence (35%) in juvenile cohorts from Cordova Harbor (Prince William Sound, AK) during June, 2010. The infection prevalence of Pacific herring collected in the spring (Figure 3A) did not necessarily correspond with that of samples collected in the fall of the same year (Figure 3B).

A consistent pattern between *Ichthyophonus* prevalence and Pacific herring sex did not occur (Table 2), as the infection prevalence was not significantly ($P = 0.97$) different between males and females that were combined from all locations and years (25.2% and 25.1%; respectively). Similarly, inter-annual infection prevalence was not significantly different ($P \geq 0.09$) between males and females from general geographic locations including Puget Sound (33.2% and 30.0%; respectively), Cook Inlet (11.2 and 8.8%; respectively), Prince William Sound (30.8% and 31.0%), and Lynn Canal (25.2% and 25.1%). Statistical significance ($P \leq 0.03$) appeared to occur in some intra-annual comparisons between males and females from some locations, including Puget Sound in 2003 (64.0% and 29.7%; respectively) and 2010 (19.7% and 2.7%; respectively), Prince William Sound in 2010 (27.0% and 6.8%; respectively), Sitka Sound in 2011 (11.8% and 28.8%; respectively), and Lynn Canal (8.1% and 34.8%; respectively). However, these apparent patterns were likely reflective of a Type 1 Error, as the *Ichthyophonus*-dominant sex was inconsistent among these groups, with males having a higher prevalence in three groups and females having a higher prevalence in two groups.

Analysis of archived samples indicated that *Ichthyophonus* occurred in Pacific herring populations since at least 1986 (Table 3). Histological sections of Pacific herring hearts with PAS-positive *Ichthyophonus*-schizonts were identified in archived samples that were collected from Puget Sound on October 21, 1986 (6/9 samples), August 18, 1987 (3/8 samples), October 13, 1987 (3/11 samples), and October 14, 1987 (1/9 samples).

Discussion

The widespread distribution of *Ichthyophonus* in Pacific herring throughout the west coast of North America provides some indication of the mechanisms involved in the perpetuation and transmission of the parasite. The natural route(s) of *Ichthyophonus* transmission in Pacific herring remain unresolved and laboratory studies have generally been unsuccessful at demonstrating transmission by host cohabitation, immersion in parasite isolates, or feeding with infected tissues or isolates (Gregg *et al.* 2012). A leading hypothesis accounting for the transmission of *Ichthyophonus* to Pacific herring includes the possible involvement of an intermediate host, where the parasite likely develops into a stage that becomes more infectious to Pacific herring. This hypothesis is further supported by extreme plasticity in *Ichthyophonus* morphology that can be induced by manipulating various host and culture conditions. If an intermediate host (or hosts) exists, then the results from this study indicate that its geographic range must be very expansive throughout the NE Pacific. Further, patchiness or seasonality of this proposed intermediate host may partially explain the differences in infection prevalence that we detected over relatively small geographic distances within Puget Sound (Table 1) and between Pacific herring populations in British Columbia that overwinter in nearshore vs offshore locations (Figure 1). Similar spatial differences in *Ichthyophonus* prevalence also occur in populations of Atlantic herring, which have

been hypothesized to result from exposure differences resulting from host seasonal migration patterns (Kramer-Schadt *et al.* 2010).

Lack of detections in Pacific herring from San Francisco Bay, CA suggests that the southern extreme of *Ichthyophonus* range in Pacific herring may end north of this latitude (Table 1), and the northern extreme of its range in Pacific herring ends south of the Bering Sea (Gregg *et al*. In Preparation and Kocan *et al*. 2004). An expansive area exists between the two southern-most sampling locations in this study (Puget Sound and San Francisco Bay) and Pacific herring populations throughout this gap tend to be relatively small; however, it is likely that *Ichthyophonus* occurs in some of these stocks, as the parasite can occur in high prevalence among another clupeid, American shad (*Alosa pseudoharengus*), from the Oregon / Washington boarder (Hershberger *et al.* 2010). Although these results indicate that Pacific herring represent a dominant host species for *Ichthyophonus* in the NE Pacific, other species appear to maintain the parasite northward into the Bering Sea, where a paucity of infections in Pacific herring (Kocan *et al.* 2004, Gregg *et al.* In Preparation) are replaced by often-high prevalences in Chinook salmon and walleye pollock (White *et al.* 2014). The geographical extremes of the *Ichthyophonus* range in Pacific herring likely shift on an interannual basis in response to changing climatic conditions, ocean circulation patterns, water temperatures and invertebrate assemblages. For example, the prevalence of *Ichthyophonus* in Pacific herring from southern Cook Inlet, AK, near the current northern boundary of the *Ichthyophonus* range in Pacific herring, declined from 20-32% in 2007 to 2-3% in 2009. We hypothesize that this recent decrease in infection prevalence at the northern extreme of the parasite range in Pacific herring reflects a wandering northern boundary that is influenced by ocean and climatic conditions.

Reason(s) for the increased *Ichthyophonus* prevalence with Pacific herring size and age (Figures 2-5) remain unknown; however, this pattern is consistent over broad spatial-temporal scales in populations of Pacific (Hershberger *et al.* 2002; Marty *et al.* 2003) and Atlantic herring (Kramer-Schadt *et al.* 2010). This zoographic pattern is consistent with that of a chronic infection that accumulates in a population via recurring exposures throughout the lifetime of the host. The timing, location, and route of *Ichthyophonus* exposures to Pacific herring remain unknown; however, this accumulation hypothesis suggests that the clearance or elimination of the parasite from infected host tissues must be a rare event. It is important to consider this *Ichthyophonus* pattern with Pacific herring age / size when surveying wild populations. For example, a standard 60 fish sample from a population may contain a biased age / size distribution due to sampling gear / techniques; this size bias is subsequently reflected in the reported *Ichthyophonus* infection prevalence for the population (Holst 1996). Therefore, it is recommended that *Ichthyophonus* prevalence in Pacific herring populations be reported by age / size class (i.e. Figures 1-3) rather than as a single prevalence from a geographic stock / location (i.e. Table 1).

A clear exception to this direct relationship between Pacific herring age / size and *Ichthyophonus* prevalence occurred in a sample from Cordova Harbor (June 2010), where juveniles (mean length 85mm, age 1 yr) had an unusually high prevalence of 35% (Table 1). Interestingly, these juvenile Pacific herring were also experiencing an epizootic of viral erythrocytic necrosis (71% infection with 92% of the infections scored as moderate-to-high intensity; data not shown) and heavy infestations with sea lice

(predominantly *Caligus clemensi*). The aggregation of juvenile Pacific herring around boat harbors is not unusual; however juvenile cohorts sampled from boat harbors in Puget Sound typically demonstrate low prevalence of *Ichthyophonus* infection (Hershberger unpublished data). Although additional studies are needed for confirmation, it is possible that these abnormal fish health conditions were a reflection of activities associated with a fish processing plant located adjacent to Cordova Harbor. Raw offal from this processing plant is discharged directly into the water and it is likely that exposure to infected offal increased the infection pressures to nearby juvenile Pacific herring. Follow-up efforts later in the summer were unsuccessful, as the age 1+ yr cohorts disappeared from the harbor and were replaced by newly-metamorphosed, age 0 yr cohorts; none of which tested positive for *Ichthyophonus* (Table 1).

Although *Ichthyophonus* appears to typically persist in Pacific herring at chronic levels that accumulate in populations over time, several lines of evidence indicate that the parasite may periodically contribute to negative impacts on Pacific herring population dynamics. Laboratory exposures indicate that *Ichthyophonus* can be highly pathogenic to Pacific herring, with intraperitoneal injections resulting in host mortality with a mean day-to-death of 36d (Kocan *et al.* 1999). Subsequent studies have indicated that this post-exposure mortality can be reproduced most commonly in younger (age 0 yr) age cohorts (Hershberger personal observation), likely as a result of factors involving dose per fish size (Okamoto *et al.* 1987). Regardless, massive epizootics and associated fish kills periodically occur in populations of adult Atlantic herring, often culminating in population-level impacts (reviewed in Burge *et al.* 2014). Causes of these periodic epizootics remain undetermined, but a leading hypothesis asserts that they result from episodic and punctuated exposures to high levels of the parasite. This hypothesis infers that increases in infection prevalence / intensity and epizootics may result from situations where Pacific herring feeding aggregations become sympatric with zooplankton aggregations that serve as intermediate hosts for the parasite (Kramer-Schadt *et al.* 2010); however, additional research efforts are needed to determine whether an intermediate host exists. Additionally, *Ichthyophonus* may impact Pacific herring demographic patterns in Puget Sound, WA, where increased infection prevalence with host size and age (Hershberger *et al.* 2002) occurred concomitantly with a loss of older age cohorts and a resulting decreased median age of the populations (Bryant &Landis 2010). Similarly, the prevalence of *Ichthyophonus* decreased from 62.5% (5/8) to 19.6% (22/112) in the largest size class (>240mm) from Sitka Sound during 2007-2013 (Figure 2). It is likely that this size-specific decrease in *Ichthyophonus* prevalence resulted from selective mortality among the infected cohorts, as the heaviest infection intensities observed throughout this 7 year survey (2007-2013) occurred in Sitka Sound during 2012 (Figure 6). Analogous demographics changes occurred in populations of Atlantic herring after ichthyophoniasis epizootics (Tibbo & Graham 1963).

Seasonal, geographic, and demographic patterns in *Ichthyophonus* prevalence are difficult to interpret, largely because of the highly migratory nature of Pacific herring throughout the region. For example, novel acoustic tagging results indicate that many Pacific herring in northeast PWS migrate to the southern PWS, and presumably into the Gulf of Alaska, shortly after spawning (Bishop personal communication). Therefore, it is difficult to directly compare the spring and fall infection prevalences from a particular location (Figures 3A&B), as samples may have consisted of different groups of Pacific

herring with inconsistent exposure histories. However, inter-annual differences in spring infection prevalence are easier to compare, as Pacific herring typically demonstrate general fidelity to broad geographic spawning regions. Decreases in infection prevalence, such as those observed in Lower Cook Inlet (Figure 4 A/B) and among the largest size cohorts in Sitka Sound (Figure 2), were likely the result of proximate or ultimate mortality among the infected cohorts. Laboratory exposure studies provide no indication that, once infected, Pacific herring are capable of completely clearing *Ichthyophonus* infections; rather, infected individuals experience either acute mortality (Kocan *et al.* 1999) or survival with persistent infections (Hershberger 2012). Elevated mortality of infected cohorts could occur from selective predation on *Ichthyophonus*-infected cohorts if infected individuals with decreased swimming performance (Kocan *et al.* 2006) are more easily captured by predators. This predator selection hypothesis is supported by field observations during an *Ichthyophonus* epizootic, when 60-80% of Atlantic cod stomachs contained heavily-infected Atlantic herring (Kramer-Schadt *et al.* 2010).

All available information indicates a long-standing host / pathogen relationship between Pacific herring and *Ichthyophonus* rather than a recent introduction in the NE Pacific. Although few archived samples of Pacific herring were available for *Ichthyophonus* assessment, the parasite was detected in formalin-fixed Pacific herring samples from Puget Sound dating back to 1986 (Table 3). Inability to detect *Ichthyophonus* in any of the earlier samples should not be interpreted as absence of the parasite in the years prior to this year, as only a limited number of samples were processed (n=16 from 1888 – 1980). Further, although histological assessment of PAS-stained slides is effective at identifying high-intensity *Ichthyophonus* infections, the technique demonstrates low sensitivity for low-intensity infections (Kocan *et al.* 2011); therefore, low-intensity cases were likely mis-diagnosed as false-negatives. A long-standing host-pathogen relationship was further supported by the ubiquity of *Ichthyophonus* in Pacific herring populations throughout coastal waters of the NE Pacific, ranging from Washington State north to the Gulf of Alaska.

Although recurring *Ichthyophonus* epizootics, fish kills, and associated host population declines have been reported since 1913 (reviewed in McVicar 2011), major information gaps continue to exist regarding the natural history of the parasite. Most importantly, a paucity of information exists regarding the *Ichthyophonus* life cycle and the involvement of Pacific herring in completion of this cycle. It is recommended that future research efforts are committed to investigating possible intermediate hosts which, if identified, could offer a predictive tool for forecasting the emergence of new *Ichthyophonus* epizootics in clupeids.

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Hay (DFO – Canada_. Access to archived Pacific herring at the University of Washington Fish Collection was provided by Drs. T. Pietch and K. Pearson Maslenikov The use of trade, firm, or corporation names in this publication is for the information and convenience of the reader. Such use does not constitute an official endorsement or approval by the U.S. Department of Interior or the U.S. Geological Survey of any product or service to the exclusion of others that may be suitable.

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Table 1. Prevalence of *Ichthyophonus* in Pacific herring populations.

Year	Stock	Site	Collection Date	Gear Type	Adult / Juvenile (A/J)	Mean Fork Length mm (SD)	*Ichthyophonus* Prevalence
2003	Puget Sound	Pt Orchard / Madison	Feb 5	Trawl	A	176 (19)	31% (28/120)
		Skagit Bay	Feb 11	Trawl	A	161 (10)	42% (25/60)
		Port Susan	Feb 12	Trawl	A	171 (14)	47% (28/60)
		Port Gamble	Feb 25	Trawl	J	122 (24)	25% (15/60)
2004	Puget Sound	Cherry Point	May 4	Trawl	A	218 (17)	53% (37/70)
		Cherry Point	May 23	Gill Net	A	202 (21)	40% (24/60)
2005	Puget Sound, WA	Port Gamble Bay	Feb 2	Trawl	A	181 (15)	53% (32/60)
		Port Townsend Bay	Feb 2	Trawl	J	115 (15)	13% (8/60)
		Port Gamble Bay	March 3	Gill Net	A	214 (9)	68% (41/60)
		Port Gamble Bay	March 9	Gill Net	A	191 (17)	48% (57/120)
		Kilisut Harbor	March 17	Gill Net	A	226 (11)	50% (26/52)
		Hood Canal	April 28	Trawl	A	191 (17)	69% (35/51)
		Cherry Point	May 2	Trawl	A	178 (11)	27% (16/60)
		Cherry Point	May 3	Gill Net	A	213 (22)	47% (28/60)
		Cherry Point	May 11	Gill Net	A	216 (23)	53% (32/60)
		Cherry Point	May 26	Gill Net	A	228 (28)	52% (32/62)
		Hood Canal	June 7	Trawl	A	179 (11)	73% (44/60)
	Cook Inlet, AK	Kamishak Bay	May 16	Purse Seine	A	ND	38% (20/53)
		Kamishak Bay	May 16	Purse Seine	A	ND	55% (24/44)
2006	Puget Sound, WA	Case Inlet	Jan 17	Trawl	A	170 (13)	5% (3/59)
		Quartermaster Harbor	Jan 17	Trawl	A	168 (11)	18% (11/60)
		Pt Orchard / Madison	Feb 2	Trawl	A	177 (20)	14% (8/59)
		Skagit Bay	Feb 2	Trawl	A	174 (10)	34% (20/59)
		Holmes Harbor	March 30	Gill Net	A	193 (13)	50% (30/60)
	Cook Inlet (AK)	Kamishak Bay	May 18	Purse Seine	A	ND[1]	18% (11/60)
		Kamishak Bay	May 21	Purse Seine	A	ND[1]	17% (10/60
		Kamishak Bay	May 22	Purse Seine	A	ND[1]	10% (10/60)

Year	Stock	Site	Collection Date	Gear Type	Adult / Juvenile (A/J)	Mean Fork Length mm (SD)	*Ichthyophonus* Prevalence
2007	Puget Sound, WA[1]	Johnson Point	Jan 18	Trawl	A	181 (8)	7% (4/59)
		Pt Orchard / Madison	Feb 1	Trawl	A	181 (11)	17% (10/60)
		Skagit Bay	Feb 8	Trawl	A	184 (11)	37% (22/60)
		Cherry Point	April 30	Trawl	A	184 (13)	25% (15/60)
	Cook Inlet, AK	Kamishak Bay	May 16	Purse Seine	A	ND[1]	32% (19/60)
		Kamishak Bay	May 27	Purse Seine	A	ND[1]	20% (12/59)
		Kamishak Bay	May 27	Purse Seine	A	ND[1]	28% (17/60)
	Prince William Sound, AK	St. Matthews Bay	April 5	Cast Net	A	224 (17)	42% (25/60)
		Simpson Bay	April 19	Purse Seine	J	86 (6)	15% (9/60)
		Sawmill Bay	Nov. 30	Purse Seine	A	215 (21)	25% (15/60)
		Simpson Bay	Dec. 2	Purse Seine	A	187 (13)	37% (22/60)
	Sitka Sound, AK	S. Cannon Island	April 9	Cast Net	A	215 (18)	28.3% (17/60)
	Lynn Canal, AK	Benjamin Island	Nov. 10	Trawl	A	199	11% (7/61)
2008	Puget Sound, WA	Drayton Pass	Jan 15	Trawl	A	144 (7)	2% (1/60)
		Pt Orchard / Madison	Feb. 5	Trawl	A	154 (16)	7% (4/60)
		Skagit Bay	Feb 2	Trawl	A	176 (17)	23% (14/60)
		Holmes Harbor	Mar 13	Trawl	A	193 (8)	48% (29/60)
	Prince William Sound, AK	Fish Bay	Mar 19	Purse Seine	A	236 (27)	33% (19/58)
		unknown	Mar 17	Purse Seine	J	141 (11)	20% (12/59)
		Whale Bay	Mar 24	Purse Seine	J	149 (22)	15% (9/60)
		Port Gravina	Nov 8-12	Purse Seine	A	197 (23)	24% (19/80)
		Simpson Bay	Nov 8-12	Purse Seine	J	65 (7)	0% (0/78)
	Sitka Sound, AK	Beli Rock	Mar 5	Purse Seine	A	262 (14)	30% (18/60)
		N. Middle Island	March 26	Purse Seine	A	249 (14)	28% (17/60)
	Lynn Canal, AK	Breadline	Feb 23	Trawl	A	ND	5% (3/61)
		Cohen Island	April 12	Trawl	A	ND	5% (3/61)
		Aaron Island	May 10	Trawl	A	ND	19% (11/59)

Year	Stock	Site	Collection Date	Gear Type	Adult / Juvenile (A/J)	Mean Fork Length mm (SD)	*Ichthyophonus* Prevalence
2009	Puget Sound, WA	Pt Orchard / Madison	Feb 2	Trawl	A	170 (9)	3% (2/60)
		Skagit Bay	Feb 2	Trawl	A	166 (23)	18% (11/60)
		Port Gamble	Feb 12	Trawl	A	169 (12)	27% (16/60)
		Holmes Harbor	March 18	Trawl	A	193 (20)	22% (13/60)
	Cook Inlet, WA	Kamishak Bay	May 8	Purse Seine	A	ND[1]	3% (2/60)
		Kamishak Bay	May 21	Purse Seine	A	ND[1]	2% (1/60)
	Prince William Sound, AK	Port Gravina	Mar 20	Purse Seine	A	199 (15)	43% (26/60)
		Port Gravina	Mar 20	Purse Seine	J	168 (11)	25% (15/60)
		Simpson Bay	Mar 22	Purse Seine	J	94 (8)	13% (8/60)
		Snug Corner Cove	April 13	Cast Net	A	217(27)	26% (16/62)
		Port Gravina	April 4-9	Gill Net	A	222 (24)	45% (27/60)
		Port Gravina	Nov 15	Purse Seine	A	179 (17)	12% (7/60)
		Elrington Pass	Nov 17	Purse Seine	A	216 (19)	17% (10/60)
		Simpson Bay	Nov 19	Purse Seine	J	87 (14)	5% (3/60)
		Eaglek Bay	Nov 14	Purse Seine	J	98 (4)	3% (1/29)
		Lwr. Herring Bay	Nov 16	Purse Seine	J	99 (4)	0% (0/14)
		Simpson Bay	Nov 19	Purse Seine	J	70 (12)	5% (1/20)
	Sitka Sound, AK	Guide Island	Feb 15-16	Trawl	A	256 (15)	40% (32/80)
		unknown	Mar 24	Purse Seine	A	270 (19)	46% (20/44)
		St. John Babtist Bay	Mar 26	Purse Seine	A	248 (23)	31% (21/67)
		unknown	Mar 27	Purse Seine	J	175 (7)	4% (3/69)
	Lynn Canal, AK	Amalga Trench	Feb 11-12	Trawl	A	203 (15)	7% (3/44)
		Fritz Cove	Mar 18-19	Trawl	A	ND	13% (8/60)
		Benj. Isl. Trench	Nov 24	Gill Net	A	210 (14)	18% (11/60)
		Benj. Isl. Trench	Dec. 7	Gill Net	A	198 (23)	8% (5/60)
	San Francisco Bay, CA	Pt. Chauncey	Feb 11	Gill Net	A	155 (15)	0% (0/81)
		Pt Chauncey	Feb 25	Gill Net	A	149 (18)	0% (0/60)

Year	Stock	Site	Collection Date	Gear Type	Adult / Juvenile (A/J)	Mean Fork Length mm (SD)	*Ichthyophonus* Prevalence
2010	Puget Sound, WA	Squaxin Pass	Jan 28	Trawl	A	140 (12)	3% (2/60)
		Holmes Harbor[2]	March 23	Trawl	A	171 (15)	28% (17/60)
	Cook Inlet, AK	Kamishak Bay	May 4	Purse Seine	A	ND[1]	2% (1/60)
		Kamishak Bay	May 18	Purse Seine	A	ND[1]	3% (2/60)
	Prince William Sound, AK	Port Gravina	Mar 16	Purse Seine	A	213 (14)	18% (11/60)
		Port Fidalgo	Mar 19	Purse Seine	A	200 (15)	23% (14/60)
		Simpson Bay	Mar 20	Purse Seine	J	109 (23)	13% (8/60)
		Cordova Harbor	June 2-13	Cast Net	J	85 (12)	35% (17/49)
		Cordova Harbor	Aug 18	Cast Net	J	44 (2.8)	0% (0/18)
		Cordova Harbor	Sept 28 -Oct 7	Cast Net	J	50 (5.9)	0% (0/22)
		Simpson Bay	Nov. 2	Purse Seine	J	73 (6.8)	0% (0/38)
		Port Fidalgo	Nov. 4	Purse Seine	J	77 (3.7)	0% (0/22)
		Eaglik	Nov. 5	Purse Seine	J	90 (8.7)	0% (0/34)
		Whale Bay	Nov 10-11	Purse Seine	J	95 (33)	3% (2/58)
	Sitka Sound, AK	Indian River	Mar 22	Purse Seine	A	242 (22)	27% (16/60)
		Boarder / Sitka Rocks	Mar 23	Purse Seine	A	209 (28)	15% (9/60)
		Kruzof Island	Mar 24	Purse Seine	A	241 (25)	37% (22/60)
	Lynn Canal, AK	Shelter Island	Mar 15-16	Gill Net	A	202 (20)	5% (3/56)
		Bridget Cove	April 26	Cast Net	A	212 (11)	13% (5/40)

Year	Stock	Site	Collection Date	Gear Type	Adult / Juvenile (A/J)	Mean Fork Length mm (SD)	*Ichthyophonus* Prevalence
2011	Cook Inlet, AK	Kamishak Bay	May 4	Purse Seine	A	ND[1]	0% (0/60)
		Kamishak Bay	May 13	Purse Seine	A	ND[1]	2% (1/60)
	Prince William Sound, AK	Lower Herring Bay	March 11	Cast Net	J	95 (3.9)	2% (1/60)
		Eaglik Bay	March 15	Cast Net	J	113 (22)	5% (3/60)
		Port Fidalgo	March 16	Cast Net	J	76 (5.8)	10% (6/60)
		Port Gravina	April 4	Cast Net	A	219 (20)	27% (16/60)
		Port Gravina	April 6	Purse Seine	A	253 (13)	47% (28/60)
		Port Gravina	Nov 21	Purse Seine	A	205 (20)	63% (19/30)
		Port Gravina	Nov 22	Purse Seine	J	157 (12)	13% (4/30)
		Simpson Bay	Nov 15	Cast Net	J	60 (6.1)	0% (0/57)
		Whale Bay	Nov 20	Cast Net	J	83 (8.2)	0% (0/60)
		Simpson Bay	Dec. 13	Cast Net	J	60 (5.0)	0% (0/60)
	Sitka Sound, AK	Bear Cove	March 24	Cast Net	J	108 (11)	2% (1/60)
		Long Island	March 22	Purse Seine	A	232 (16)	18% (11/60)
		Salsberry Island	April 6	Cast Net	A	228(20)	20% (12/60)
	Lynn Canal, AK	Halibut Cove	Jan 12	Gill Net	A	ND	2% (1/60)
		Amalga Trench	Jan 28	Trawl	A	ND	10% (6/60)
		Amalga Trench	April 9	Gill Net	A	ND	18% (11/60)
		Auke Bay[3]	Apr 18, Jun 4	Beach Seine	A	202 (15)	18% (11/60)
	British Columbia, Canada	Little Qualicum	March 1	Purse Seine	A	180 (16)	23% (14/60)
		Sydney Inlet	March 17	Purse Seine	A	189 (14)	8% (5/60)
		Prince Rupert,	March 23	Purse Seine	A	183 (16)	20% (12/60)
		Kwakshua Inlet	March 23	Purse Seine	A	167 (18)	22% (13/60)
		Prince Rupert	March 24	Purse Seine	A	194 (16)	27% (16/60)
		Haid Gwaii	March 26	Purse Seine	A	191 (12)	8% (5/60)
		Haid Gwaii	March 30	Purse Seine	A	192 (13)	5% (3/60)

Year	Stock	Site	Collection Date	Gear Type	Adult / Juvenile (A/J)	Mean Fork Length mm (SD)	*Ichthyophonus* Prevalence
2012	Cook Inlet, AK	Kamishak Bay	May 7	Purse Seine	A	ND[1]	2% (1/60)
	Prince William Sound, AK	Simpson Bay	Jan 11	Cast Net	J	57 (2.8)	0% (0/60)
		Simpson Bay	April	Cast Net	J	ND	3% (1/30)
		Port Gravina	March 28	Purse Seine	A	218 (16)	42% (25/60)
		Port Gravina	March 31	Purse Seine	A	215 (21)	40% (24/60)
		Fidalgo Bay	April 2	Purse Seine	A	231 (19)	35% (21/60)
		Port Gravina	Nov. 15	Purse Seine	A	159 (14)	3% (2/60)
	Sitka Sound, AK	N. Kasiana Isl.	April 3	Cast Net	A	232 (23)	20% (12/60)
		St. John Bay	April 4	Purse Seine	A	214 (24)	32% (19/60)
		Sitka breakwall	April 4	Cast Net	A	225 (22)	10% (6/60)
	Lynn Canal, AK	Tee Harbor	June 8	Hook-and-Line	A	176 (13)	0% (0/60)
2013	Puget Sound, WA	Hood Canal[4]	May 19	Trawl	A	171 (18)	57% (25/44)
	Cook Inlet, AK	Kamishak Bay	May 20	Purse Seine	A	ND[1]	2% (1/60)
	Prince William Sound, AK	Port Gravina	March 27	Purse Seine	J	147 (16)	3% (2/60)
		Port Gravina	March 31	Purse Seine	A	232 (20)	34% (20/59)
		Port Gravina	April 1	Purse Seine	A	225 (23)	32% (19/60)
	Sitka Sound, AK	Apple Islands	March 29	Cast Net	A	246 (28)	18% (11/60)
		Silver Bay	March 30	Purse Seine	A	251 (16)	18% (11/60)
		Unknown	March 30	Purse Seine	A	226 (26)	18% (11/60)
	Craig, AK	Diamond Point	Feb 20	Cast Net	A	214 (23)	22% (13/60)

[1]ND: Herring lengths in Cook Inlet from 2006-2013 were recorded as standard length, not fork length.
[2]Biased population sample: largest fish were removed from this sample for other purposes prior to determination of *Ichthyophonus* prevalence.
[3]Herring from Lynn Canal on April 18 and June 4, 2011 were transported to a tank at the NOAA Ted Stevens Marine Science Laboratories prior to sampling for *Ichthyophonus*. Tank confinement likely had little impact on the reported prevalence, as *Ichthyophonus* is not easily transferred between Pacific herring through cohabitation (Gregg et al. 2012).
[4]Sample consisted of post-spawn herring.

Table 2. Comparison of *Ichthyophonus* prevalence between male and female Pacific herring.

	% infected males (n)	% infected females (n)	P value (χ^2)
Puget Sound			
2003	64.0% (86)	29.7% (138)	1.0×10^{-7}
2004	48.2% (56)	45.1% (71)	0.86
2005	52.9% (121)	55.8% (120)	0.89
2006	24.3% (152)	22.9% (140)	0.87
2007	20.3% (143)	22.6% (93)	0.94
2008	29.2% (96)	27.1% (59)	0.93
2009	20.8% (101)	16.5% (91)	0.56
2010	19.7% (76)	2.7% (37)	0.03
total	33.2% (831)	30.0% (749)	0.19
Cook Inlet			
2006	15.7% (89)	14.4% (90)	0.97
2007	27.4% (113)	25.4% (67)	0.90
2009	2.9% (69)	0% (51)	0.61
2010	5.3% (57)	1.6% (63)	0.54
2011	1.3% (76)	2.3% (43)	0.74
2012	2.8% (36)	0% (24)	0.84
2013	0% (23)	2.7% (37)	0.81
total	11.2% (463)	8.8% (375)	0.30
Prince William Sound			
2007	28.9% (45)	27.9% (68)	0.92

2008	32.6% (43)	21.4% (42)	0.36
2009	28.3% (152)	28.9% (142)	0.99
2010	27.0% (37)	6.8% (44)	0.03
2011	39.1% (87)	42.3% (78)	0.79
2012	29.9% (107)	40.4% (89)	0.16
2013	29.7% (64)	35.1% (57)	0.66
total	30.8% (535)	31.0% (520)	0.98
Sitka Sound			
2007	27.8% (36)	30.4% (23)	0.94
2008	31.0% (29)	29.0% (31)	0.91
2009	30.2% (63)	45.8% (48)	0.13
2010	24.1% (83)	28.1% (96)	0.66
2011	11.8% (68)	28.8% (96)	0.03
2012	21.1% (123)	20.4% (49)	0.92
2013	18.7% (91)	18.0% (89)	0.94
total	22.1% (493)	27.3% (338)	0.09
Lynn Canal			
2009	9.55% (42)	19.0% (58)	0.31
2010	15.2% (33)	4.8% (63)	0.17
2011	8.1% (37)	34.8% (23)	0.02
total	10.7% (112)	15.2% (144)	0.38
Total (all locations, all years)	25.2% (2,434)	25.1% (2,176)	0.97

Table 3. *Ichthyophonus* in historical specimens of Pacific herring from Puget Sound; archived at the University of Washington Fish Collection. *Ichthyophonus* status was determined by microscopic evaluation of PAS-stained histological sections of heart tissues.

UW Archive Number	Collection Location	Collection Date	Fork Length (mm)	*Ichthyophonus* status
UW 428	Elliot Bay	Nov 10, 1888	215	
			224	
UW 426	Puget Sound	Pre-1929	206	
			193	
No Data	Dabob Bay	Jan 16, 1979	214	
			206	
UW 42796	Nisqually River delta	Jan 17, 1980	219	
			240	
			239	
UW 45151	Dabob Bay	Jul 26, 1980	174	
			198	
			182	
			184	
			197	
			203	
			194	
UW 045319	Dabob Bay	Oct 21, 1986	210	Positive
			183	Positive
			201	Positive

			183	Positive
			185	Positive
			191	
			206	
			202	Positive
			179	
UW 045266	Dabob Bay	May 5, 1987	163	
			185	
			181	
			198	
UW 045192	Dabob Bay	Aug 18, 1987	181	
			174	
			165	Positive
			168	Positive
			179	
			151	
			168	
			159	Positive

UW 45227	Dabob Bay	Oct 14, 1987	198	
			178	
			176	Positive
			162	
			157	
			169	
			187	
			176	
			192	
UW 045248	Dabob Bay	Oct 14, 1987	221	
			204	
			179	
			178	
			182	
			157	
			161	
			183	
UW 045099	Dabob Bay	Oct 13, 1987	216	Positive
			192	
			213	
			191	Positive
			174	
			198	Positive
			179	
			176	

			176
			194
			166
UW 045192	Mouth of Nisqually River	Jan 17, 1989	210
			211
			205

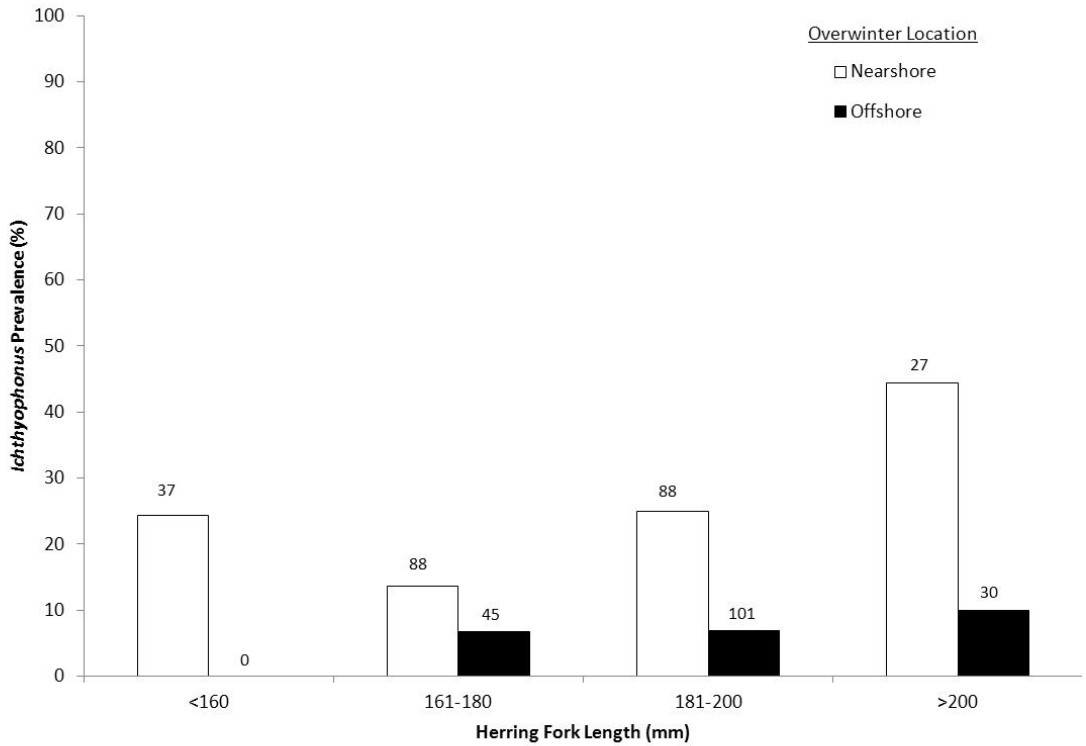


Figure 1. *Ichthyophonus* infection prevalence in each size class of Pacific herring collected during the spring of 2011 from British Columbia. Nearshore samples included herring from Little Qualicum, Prince Rupert, and Kwakshua Inlet; offshore samples included those from Sydney Inlet and Haid Gwaii (Table 1). Numerals above the bars indicate sample size (n).

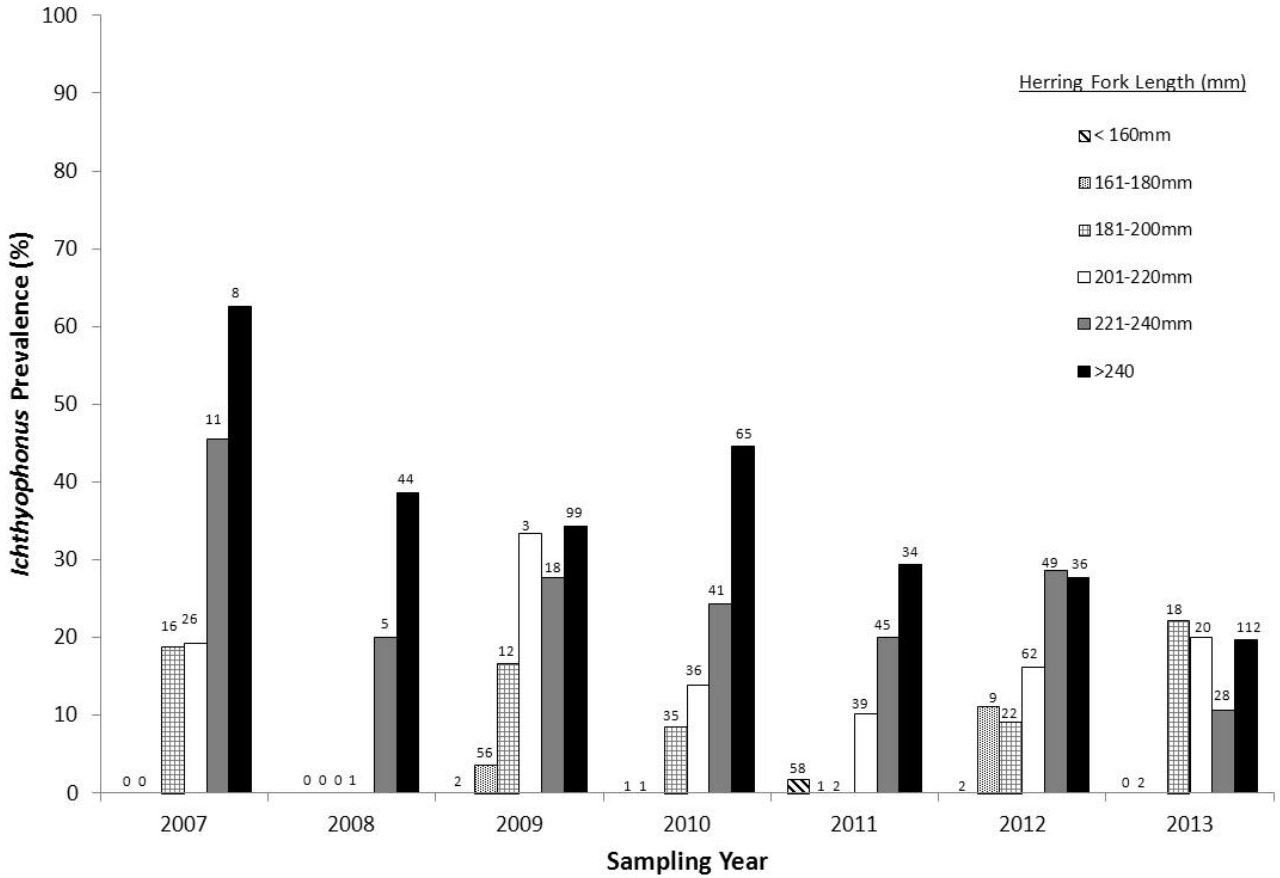
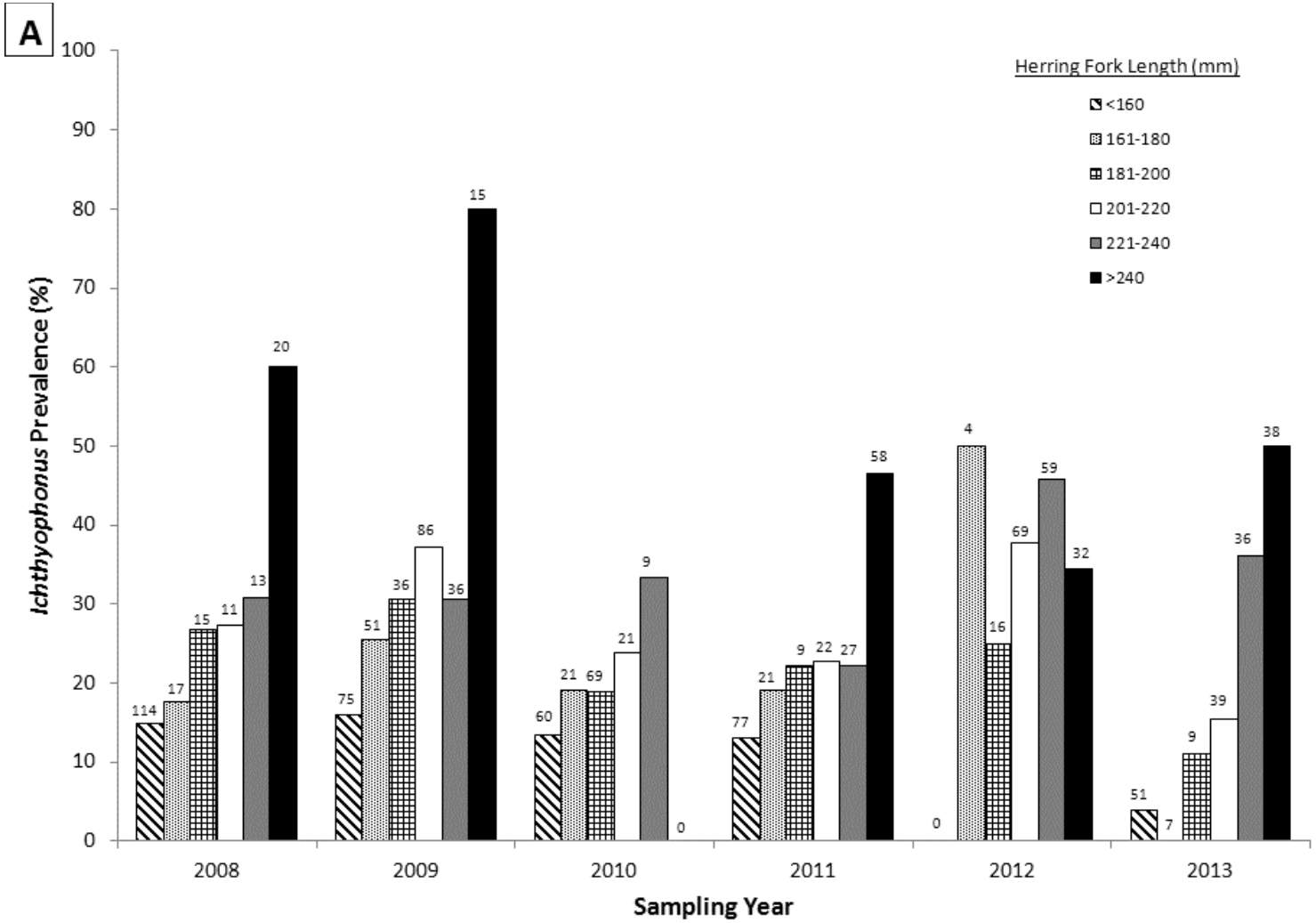


Figure 2. *Ichthyophonus* infection prevalence in each size class in spring samples of Pacific herring from Sitka Sound, AK during the spring. Numerals above the bars indicate sample size (n).


A
Herring Fork Length (mm)
<160
161-180
181-200
201-220
221-240
>240
Ichthyophonus Prevalence (%)
Sampling Year
2008
2009
2010
2011
2012
2013
0
10
20
30
40
50
60
70
80
90
100
114
17
15
11
13
20
75
51
36
86
36
15
60
21
69
21
9
0
77
21
9
22
27
58
0
4
16
69
59
32
51
7
9
39
36
38

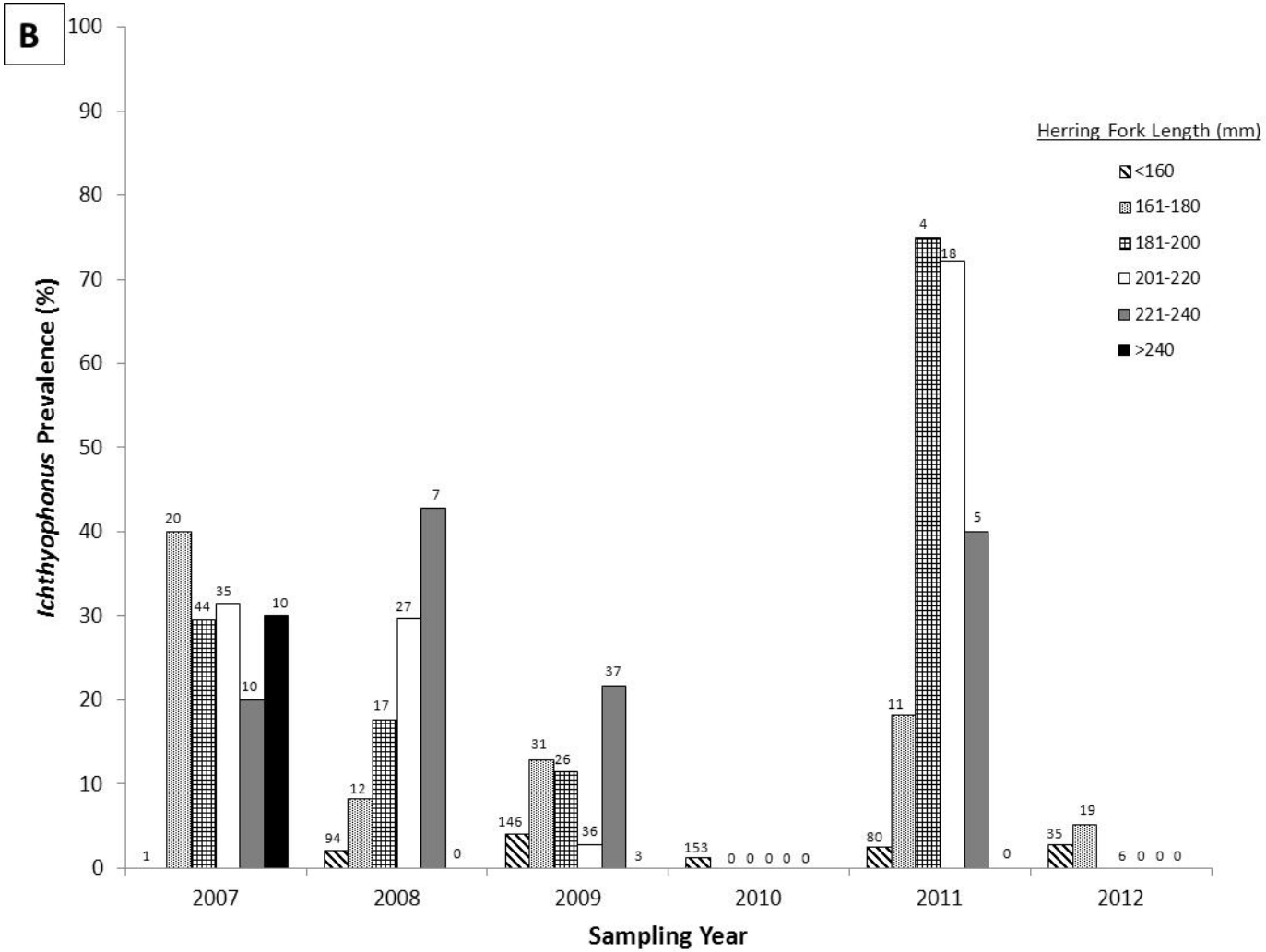
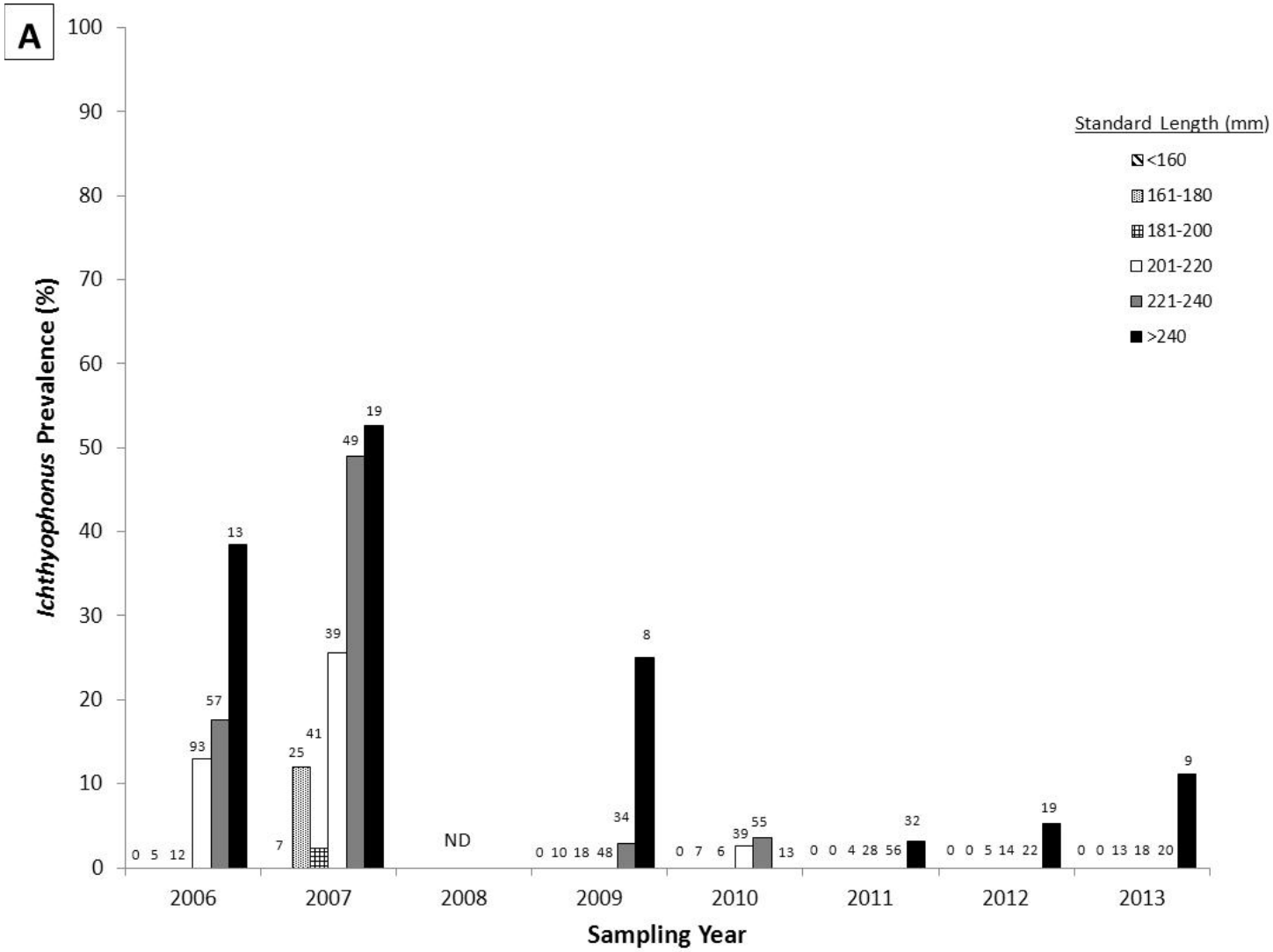


Figure 3. *Ichthyophonus* infection prevalence in each size class of Pacific herring collected from Prince William Sound, AK during the spring (A) and fall (B). Numerals above the bars indicate sample size (n). Note that the spring / fall sampling years are offset on the respective horizontal axes.


A
Ichthyophonus Prevalence (%)
100
90
80
70
60
50
40
30
20
10
0
Standard Length (mm)
<160
161-180
181-200
201-220
221-240
>240
0 5 12 93 57 13
7 25 41 39 49 19
ND
0 10 18 48 34 8
0 7 6 39 55 13
0 0 4 28 56 32
0 0 5 14 22 19
0 0 13 18 20 9
2006
2007
2008
2009
2010
2011
2012
2013
Sampling Year

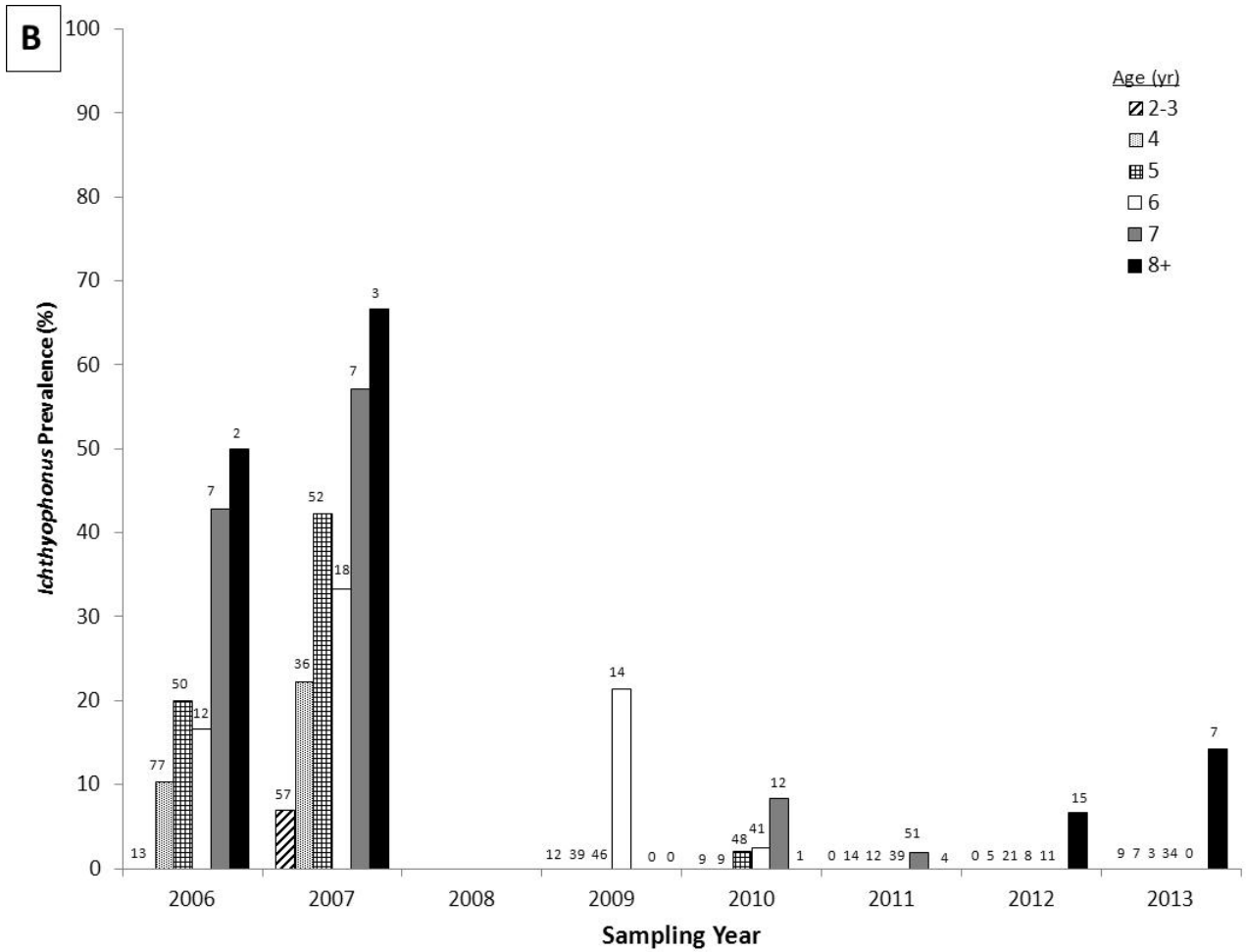


Figure 4. *Ichthyophonus* infection prevalence in each size (A) and age (B) class of Pacific herring collected from Cook Inlet, AK during the spring. Numerals above the bars indicate sample size (n).

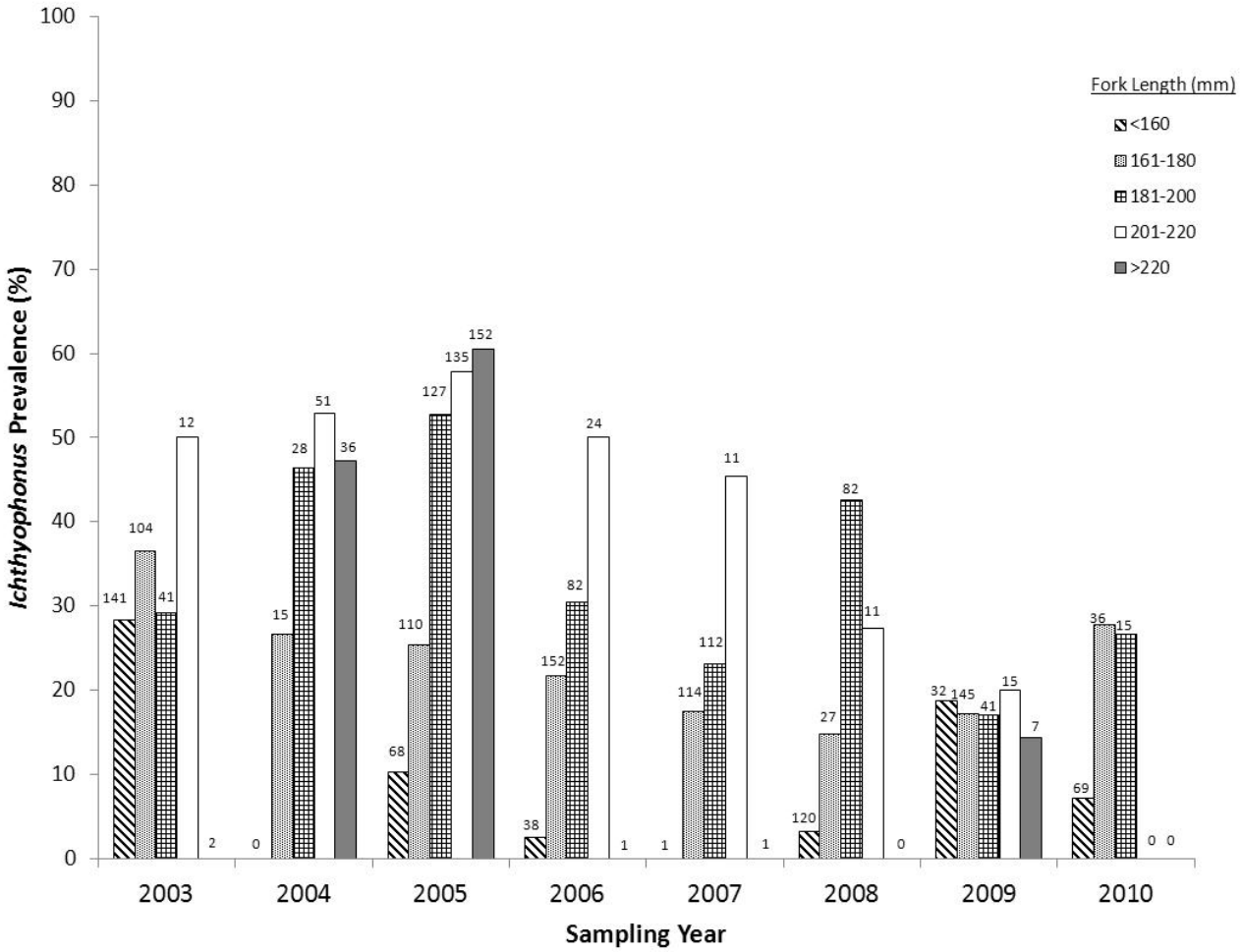


Figure 5. *Ichthyophonus* infection prevalence in each class of Pacific herring collected from Puget Sound, WA during the spring. Numerals above the bars indicate sample size (n).

Figure 6. Gross signs of heavy ichthyophoniasis in the heart of a Pacific herring collected from Sitka Sound, AK during 2012. The heart and pericardium were nearly completely displaced by whitish colored parasitic material. Note: With the exception of Sitka Sound in 2012, high-intensity *Ichthyophonus* infections such as this were rare.

Appendix 4 Acoustic tagging of Pacific herring

Post-spawning Movements of Acoustic-tagged Pacific Herring in PWS

Principal Investigator: Mary Anne Bishop, Prince William Sound Science Center
Collaborator: John Eiler, National Marine Fisheries Service, Alaska Fisheries Science Center

One of the important knowledge gaps for the Pacific herring population in Prince William Sound (PWS) is where adult herring disperse after spawning. Conservation concerns about this recovering population make it increasingly important to document migration patterns to inform our understanding of PWS adult herring survival. Elsewhere, it is common for large herring populations to migrate from nearshore spawning areas to coastal shelf areas for summer feeding habitat (Hay and McCarter 1997, Hay et al. 2008). In PWS, fishers have reported herring moving into PWS through Montague Strait prior to the fall bait fishery while others reported herring moving into PWS in spring through Hinchinbrook Entrance, Montague Strait and the southwest passages of Erlington and LaTouche (Brown et al. 2002). These observations suggest that PWS herring are regularly migrating out of PWS and onto the shelf. Here we describe our efforts to 1) develop a method to acoustic-tag wild herring, and 2) demonstrate our ability to detect movements by tagged adults both at the tagging site as well as at the entrances to Prince William Sound, ranging from 50 to more than 115 km from the initial tagging site.

Developing methodology to acoustic-tag wild herring

Prior to this pilot study, only one study successfully acoustic-tagged wild herring. In that study, eight, pre-spawning Atlantic herring (*Clupea harengus*) were individually gill netted , acoustic-tagged, released and actively tracked for 1-27 h in the St. Lawrence estuary (Lacoste et al.2001). More recently, Seitz et al. (2010) acoustic-tagged captive herring and monitored their survival over a 135 d period.

For this study we jigged fish from prespawning aggregations in Port Gravina (Fig. 1). Jigged herring were first transferred to a 40 gallon holding tank, later removed individually in a plastic container and anesthetized with MS222, and then surgically implanted with an acoustic tag (Vemco model V9-2L/2 H, 69 kHz, 9 mm x 21 mm, 2.9 g in water) within the peritoneal cavity. Our post-surgery holding tank included non-tagged herring that served as control “buddies”. Acoustic-tagged and controls (untagged) herring were released simultaneously and near a herring school.

In 2012 we tagged 25 herring on 11 April and in 2013 we tagged 69 herring between 6 and 7 April. Mean SL (± sd) of tagged herring were similar both years (2012: 226.6 ± 11.8 mm, range 194,255; 2013: 230.1 ± 11.3 mm, range 197,250). Based on Alaska Department of Fish and Game age-length-weight data (S. Moffitt, ADF&G, unpubl. data), we estimated that 22/25 of fish tagged in 2012 and 62/69 of fish tagged in 2013 were 7 years or older (>216 mm).

In 2012, 23 of 25 (92%) tagged individuals were detected by a Vemco VR2W acoustic receiver in Port Gravina multiple times on one or more days (≤ 5d) post release with final detections coinciding with cessation of spawning in the immediate area. Only 1 of the 25 herring was never detected, and one fish exhibited signs of post-tagging mortality (a significantly high number of detections through May). In 2013, 64 (93%) of the 69 tagged individuals were detected at the Port Gravina array (n = 8 receivers) or subsequently at one of the Ocean Tracking Network arrays (Fig. 1). Post release, five herring were never detected.

In conclusion, we have developed an effective method for acoustic tagging wild Pacific Herring that minimizes mortality. We suggest that our success is due to 1) minimal handling, 2) a tagging cradle with a built-in pump that insures the opercular cavity is constantly irrigated with ambient seawater; 3)

holding pre- and post-tagged fish in small schools that include control, untagged "buddies" ; and, 4) releasing fish as a school.

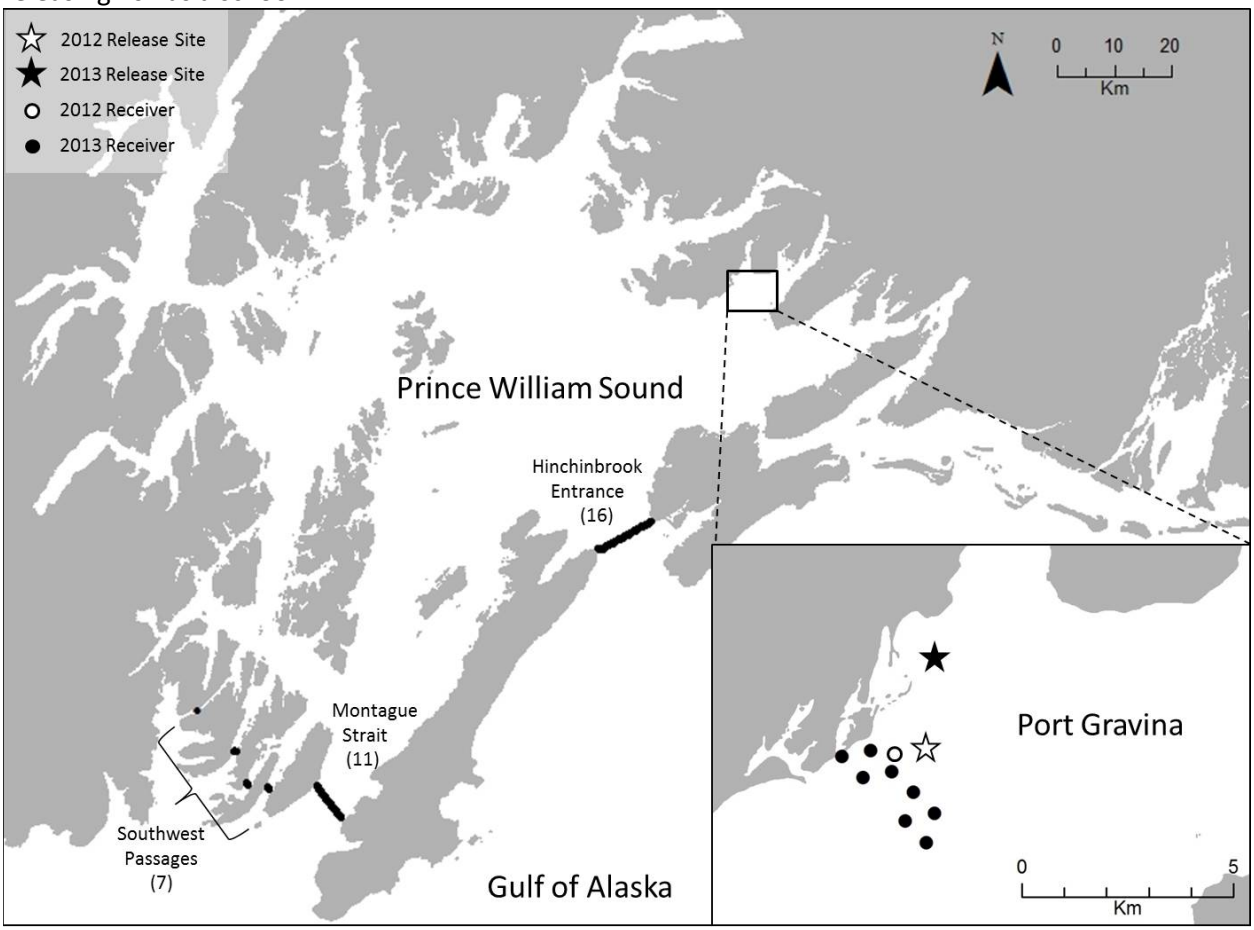


Fig. 1. Location of herring tagging and acoustic monitoring areas in Prince William Sound. Prespawning herring were tagged during early April 2012 and 2013 in Port Gravina. The Ocean Tracking Network arrays at Hinchinbrook Entrance, Montague Strait, and Southwest Passages were deployed in March 2013. Numbers in parentheses indicate total number of acoustic receivers.

Post-spawning movements to Gulf of Alaska Entrances

The March 2013 installation of the Ocean Tracking Network arrays across the entrances to the Gulf of Alaska provided the first opportunity to detect movements from the spawning grounds to the Gulf of Alaska entrances. In addition, the estimated 263d battery life of the acoustic tags meant that fish tagged 6-7 April could potentially be detected through the end of December 2013.

Sixty-two percent (43/69) of the herring tagged in Port Gravina in April 2013, were detected at one or more of the Ocean Tracking Network arrays (Table 1). Departure from Port Gravina was concentrated during two time periods: 6-10 Apr and 22-26 Apr (Fig. 2), and coincided with spawning activity in the area. Based on the number of days since herring were released or last detected at Prt Gravina, migration time was 6.5 $\pm$ 4.3 d (n = 13; range = 2, 15d) to Hinchinbrook Entrance (~50 km from the Port Gravina array) and 19.04 $\pm$ 21.9 d (n = 25; range = 3, 80) to Montague Strait (~115 km), and 50.2 $\pm$ 39.4 d (n = 5, range = 13, 107) to the Southwest Passages (130+ km).

Table 1. Detections of acoustic-tagged herring by array location.

N=69 Fish	Port Gravina	Hinchinbrook Entrance	Montague Strait	Southwest Passages (East to West)			
				LaTouche	Erlington	Prince of Whales	Bainbridge
# Detected	56	14	35	3	16	14	2
% of tagged	81%	20%	51%	4%	23%	20%	3%
First detection	7 Apr	10 Apr	11 Apr	9 May	6May	9 May	17 Jul
Last detection	21 May*	16 Oct	2 Jan	20 Jun	13-Dec	31 Dec	21 Oct

* Port Gravina array removed 21 May.

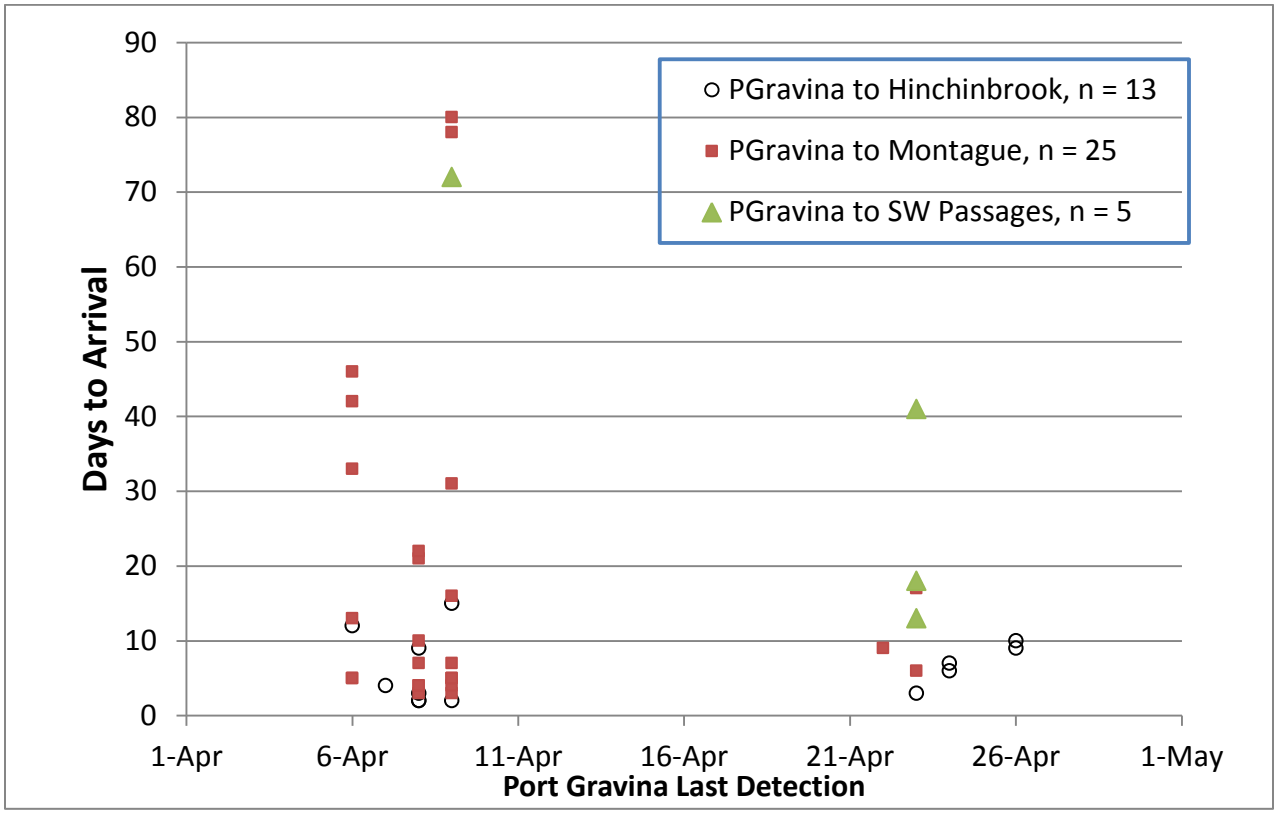


Fig. 2. Number of days from release date (n = 8) or final detection at Port Gravina array (n = 35) to first detection at Ocean Tracking Network arrays. Herring tagged at Port Gravina on 6 and 7 Apr 2013. Not shown is one herring that arrived at the Southwest Passages 107 d after its final detection at Port Gravina.

Movement to Gulf of Alaska entrances was often rapid with herring recorded at Hinchinbrook Entrance within 2 (n = 3) and 3 d (n = 2) and at Montague Strait within 3 (n = 2) and 4 d (n = 3; Fig. 2) of departure from Port Gravina. Nevertheless, even for the most rapid migration recorded (Table 2), estimated migration speed was < 0.5 m/s, the combined mean speed reported for schools of migrating and non-migrating Atlantic herring (*Clupea harengus;* Kvamme et al. 2003).

Table 2. Speed of migration (m/sec) for herring with fastest times between last detection at Port Gravina and first detection at Hinchinbrook Entrance and Montague Strait. April 2013.

From Gravina to:	Distance (~km)	Fastest time	Speed of Migration
Hinchinbrook Entrance, W side	50.4	46 h 32 min	0.30 m/sec
Montague Strait, W. side	115.1	76h, 23 min	0.41 m/sec

Phenology and Length of Stay at Entrances

April through August. Phenology of herring use at Hinchinbrook Entrance and Montague Strait was similar from April through August. Detection numbers peaked in early May and remained relatively high throughout the month. At both sites, detections were much lower in June. Notably, no tagged fish were recorded at Hinchinbrook Entrance between 9 July and 15 October, nor at Montague Strait between 24 July and 6 September (Figs. 3, 4). The average length of stay, defined as first day detected to last day detected was shorter at Hinchinbrook Entrance ($x = 17.6 \pm 15.1$ d) compared to Montague Strait ($x = 29.5 \pm 29.9$ d) although the difference was not significant. We did observe movements between Hinchinbrook Entrance and Montague Strait. Six herring that initially arrived at Hinchinbrook Entrance were later detected at Montague Strait, while only one herring was first detected at the Strait and then later at Hinchinbrook Entrance. Of the six herring moving from Hinchinbrook Entrance to Montague Strait, four arrived at the Strait between 18-20 May, suggesting they may have been part of the same fish school

No herring were detected at the Southwest Passages in April , but similar to Hinchinbrook Entrance and Montague Strait, detections peaked in May, then declined in June. However, in contrast to detection patterns from both Hinchinbrook Entrance and Montague Strait, tagged fish at the Southwest Passages were detected through August, although in small numbers (Fig. 4).

Based on the final detections of individual herring in spring followed by their subsequent reappearance in fall, it appears that some schools of herring are moving out into the Gulf of Alaska immediately after spawn, with peak departures occurring mid to late May. We suggest that the high use of the entrances by herring during April and May followed by a sudden drop is related to the *Neocalanus* bloom and its subsequent decline as well as oceanographic conditions at the Gulf of Alaska entrances. Willettte et al. (1999) examined diets of herring collected between late April and July over a three year period and found that large calanoid copepods (primarily *Neocalanus plumchrus* and *Neocalanus flemingeri)* composed a significantly greater proportion of herring diets during May, with a June shift in diet to alternative prey (e.g. euphausiids, amphipods, pteropods and fish) coinciding with the decline of

the bloom (Fig. 5). Similarly during this study, *Neocalanus* numbers peaked during May 2013 at both Hinchinbrook Entrance and Montague Strait, disappeared by June 2013 samples at

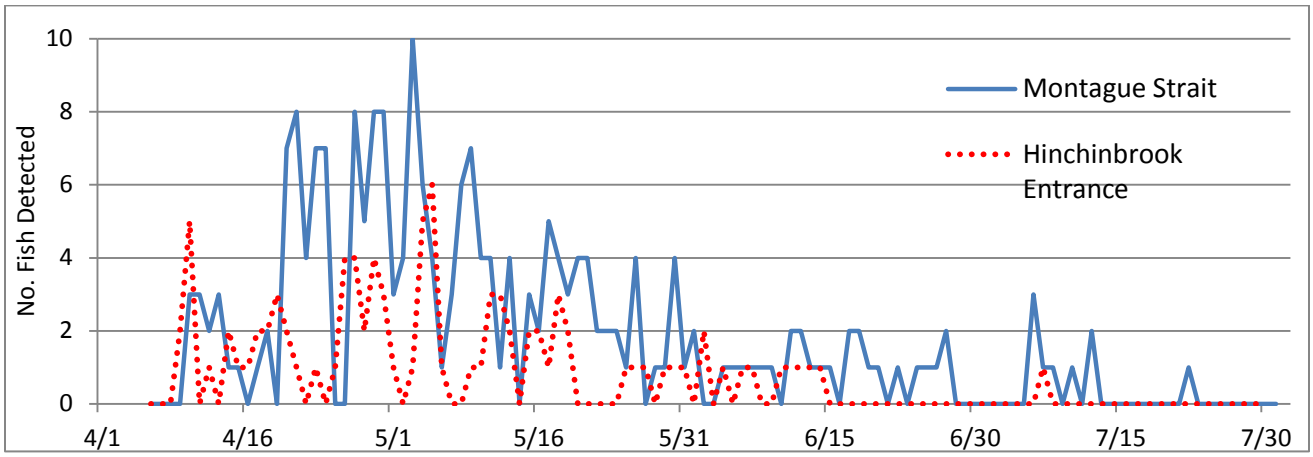


Fig.3. Number of acoustic tagged Pacific herring detected by date at Hinchinbrook Entrance and Montague Strait arrays. April 1 – July 30, 2013.

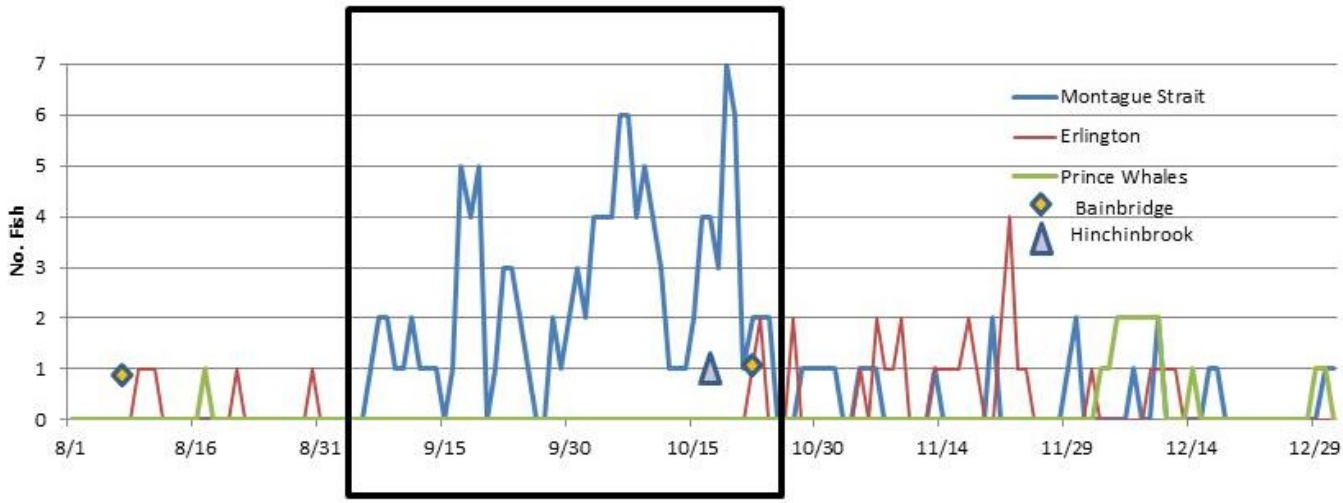


Fig. 4. Number of acoustic tagged Pacific herring detected by date and array, August 1, 2013 -January 2, 2014. No detections occurred at LaTouche Passage. Box added to emphasize the predominance of fish at the Montague Strait array throughout September and October 2013.

Hinchinbrook and decreased by 80% at Montague Strait that same month (R. Campbell, PWS Science Center, unpubl. data).

Oceanographic conditions in PWS during April, may also be conducive to retention of *Neocalanus* around the entrances. By early spring, freshwater runoff is low in PWS, the throughflow

from the Alaska Coastal Current (inflow via Hinchinbrook Entrance and outflow via Montague Strait) is weak, and seasonal northeast are also weak (Wang et al. 2001). The reduced throughflow conditions may be entraining *Neocalanus* that originate from both the shelf the PWS, resulting in predictable, high density patches during their spring bloom at Hinchinbrook Entrance and Montague Strait.

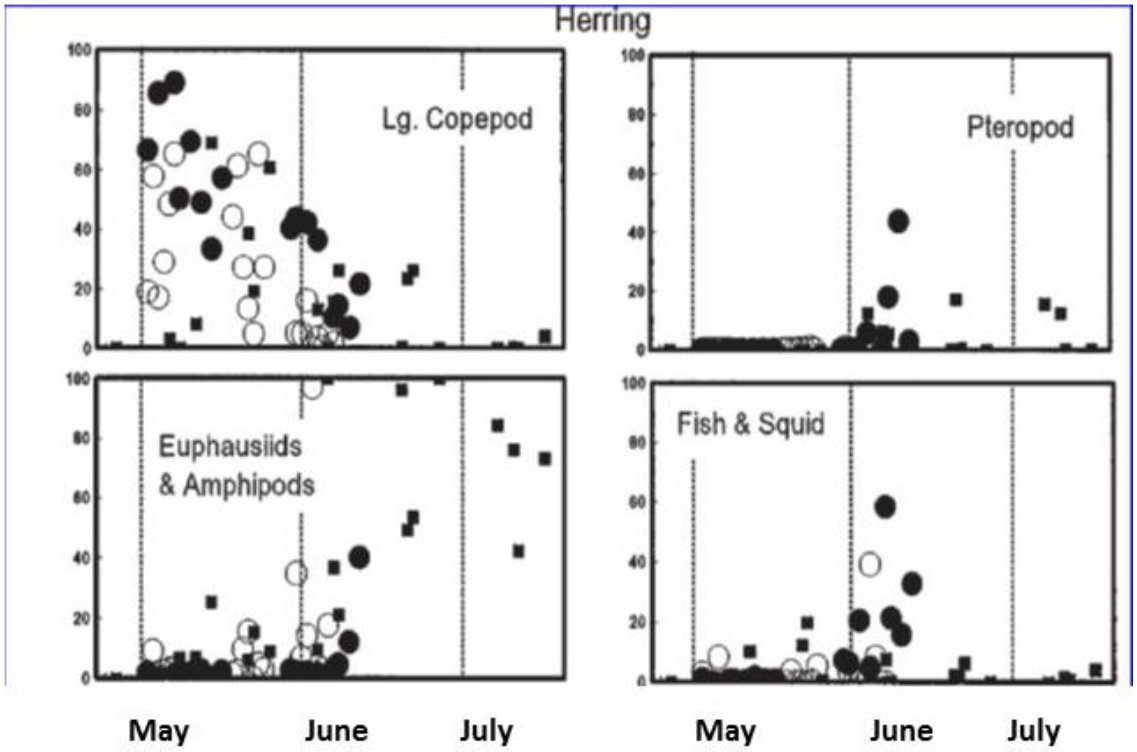


Fig. 5. Mean percentage of the diet composed of large copepods, pteropods, euphausiids and amphipods, and nekton (fish and squid) for Pacific herring in western Prince William Sound during 1994 (solid squares), 1995 (solid circles), and 1996 (open circles). From Willette et al. 1999.

The lack of herring at both Hinchinbrook Entrance and Montague Strait from mid to late July through early September while fish were still being detected in the southwest Passages is more difficult to interpret. Historically, July through late September was peak fishing for herring in PWS with most effort occurring in western PWS from Main Bay south to Montague Strait, including the southwest passages (Rousefell and Dahlgren 1932). More recently, acoustic surveys and validation seines have detected adult herring in July at LaTouche and Port Etches, sites close to the Montague and Hinchinbrook arrays, respectively. In addition, the acoustic surveys have documented adult herring in northern PWS at Point Freemantle, Glacier Island, as well as close to the spawning grounds at Knowles Head (M. Armitsu, USGS, pers. comm.). Future tagging efforts could elucidate the importance of PWS as summer habitat for adult herring.

September 2013 through early January 2014. A total of 16 herring were detected between September and early January, when tag batteries expired. First fall detections for 14 of the 16 herring occurred at Montague Strait, with fish pulsing through between 7 September and 21 October (Fig. 4). During this four month period only one tagged herring was detected on one day (16 October) at Hinchinbrook Entrance. Two of the 15 fish detected at Montague Strait were also detected on one day only, suggesting these fish, as well as the fish at Hinchinbrook Entrance were returning from the Gulf of Alaska.

Most herring detected during fall were detected multiple days, and during at least 2 of the 4 months. The intermittent detections of individual fish over multiple months in fall suggest that residency in wintering areas is not stable but rather that fish schools are highly mobile. At the same time, the use of Montague Strait and the Southwest Passages during November and December suggest that some schools may be wintering in this area. Brown et al. (2002) interviewed crab fisherman that fished in the northern Gulf of Alaska during winter. One of those fishers believed that herring spent winter between Wessels Reef, Cape Cleare and Middleton Island, and enter the Sound in spring via Hinchinbrook Entrance. If this is the case, it may explain why >60% of the herring detected at the entrance arrays during spring and early summer, were not detected again.

In summary, we documented post-spawn herring movements from Port Gravina to the Ocean Tracking Network arrays located at the entrances to the Gulf of Alaska. While some herring appeared to quickly move out into the Gulf, many remained in and around the entrances, most likely to feed on the *Neocalanus* bloom. Following the decline of the *Neocalanus* bloom, herring departed from Hinchinbrook Entrance and Montague Strait, with fish at Montague often shifting west and into to the Southwest Passages. Herring schools appeared to be actively moving throughout fall in and around Montague Strait and the Southwest Passages, although no equivalent movements were detected at Hinchinbrook Entrance. Arrays detected herring around Montague Strait and the Southwest Passages right up to when tags expired in January 2014, indicating that not all herring winter in northeast PWS and that some herring may be moving back and forth into the Gulf even during winter months.

In conclusion, the results of this pilot study demonstrate the exceptional opportunity to document migration patterns by PWS herring, and specifically the connectivity between the Gulf of Alaska and Prince William Sound. The Ocean Tracking Network is expected to last at least 5-6 more years. As currently configured, however, the Ocean Tracking Network arrays do not permit determination of movement direction by tagged fish. With a relatively small investment, this could be remedied. We found that most detections occurred at the outermost receivers, therefore placement of receivers just above and below the outermost receivers would allow for determination of the movement direction for a large proportion of the detections. In addition, by using acoustic tag programmed at low power only, battery life on acoustic tags would be increased to of ~400 d days. This would allow us to monitor acoustic-tagged herring from one spawning season to the next.

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Appendix 5. Known Pacific herring predators

Type	*Common Name*	*Scientific Name*	*Reference*	*Location*	*Prey*
Bird	Bald eagle	*Haliaeetus leucocephalus*	Willson et al. (2006)	SEAK	spawners
Bird	Barrow's goldeneye	*Bucephala islandica*	Willson et al. (2006)	BC	spawners
Bird	Black scoter	*Melanitta americana*	Willson et al. (2006)	BC	spawners
Bird	Black turnstone	*Arenaria melanocephala*	Bishop and Green (2001)	PWS	eggs, spawners
Bird	Black-legged kittiwake	*Rissa tridactyla*	Bishop, this volume	PWS	juveniles
Bird	Brandt's comorant	*Phalacrocorax penicillatus*	Willson et al. (2006)	BC	spawners
Bird	Brant	*Branta bernicla nigricans*	Willson et al. (2006)	BC	spawners
Bird	Bufflehead	*Bucephala albeola*	Willson et al. (2006)	BC	spawners
Bird	Canada goose	*Branta canadensis*	Willson et al. (2006)	BC	spawners
Bird	Common goldeneye	*Bucephala clangula*	Willson et al. (2006)	BC	spawners
Bird	Common loon	*Gavia immer*	Willson et al. (2006); Bishop, this volume	BC, PWS, SOG	spawners
Bird	Common merganser	*Mergus merganser*	Wood (1987); Bishop, this volume	BC, PWS	
Bird	Common murre	*Uria aalge*	Willson et al. (2006)	BC, SOG	spawners
Bird	Double-crested cormorant	*Phalacrocorax auritus*	Bishop, this volume	PWS	all
Bird	Glaucous wing gull	*Larus glaucescens*	Willson et al. 2006, bishop this volume, bishop and green 2001	BC, PWS	spawners
Bird	Greater scaup	*Aythya marila*	Willson et al. (2006)	BC	spawners
Bird	Harlequin duck	*Historonicus historonicus*	Rodway et al (2003); Willson et al. (2006)		spawners
Bird	Herring gull	*Larus smithsonianus*	Willson et al. (2006); Bishop, this volume	BC, PWS	spawners
Bird	Horned grebe	*Podiceps auritus*	Bishop, this volume	PWS	juveniles
Bird	Horned puffin	*Fratercula corniculata*	Furness and Furness (1985)	GOA	age-0
Bird	Long-tailed duck	*Clangula hyemalis*	Willson et al. (2006)	BC	spawners
Bird	Mallard	*Anas platyrhynchos*	Willson et al. (2006)	BC	spawners
Bird	Marbled murrelet	*Brachyramphus marmoratus*	Furness and Furness (1985)	PWS	age-0
Bird	Mew gull	*Larus canus*	Willson et al (2006); Bishop and Green (2001); Bishop, this volume	PWS	eggs, spawners

Type	*Common Name*	*Scientific Name*	*Reference*	*Location*	*Prey*
Bird	Northwestern crow	*Corvus caurinus*	Willson et al. (2006)	SEAK	spawners
Bird	Pacific loon	*Gavia pacifica*	Bishop, this volume	PWS	adults
Bird	Pelagic cormorant	*Phalacrocorax pelagicus*	Willson et al. (2006); Bishop, this volume	BC, PWS	spawners
Bird	Red-breasted merganser	*Mergus serrator*	Willson et al. (2006); Bishop, this volume	BC, PWS, SOG	spawners
Bird	Red-faced cormorant	*Phalacrocorax urile*	Bishop, this volume	PWS	all
Bird	Red-necked grebe	*Podiceps grisegena*	Bishop, this volume	PWS	juveniles
Bird	Red-throated loon	*Gavia stellata*	Bishop, this volume	PWS	adults
Bird	Rhinoceros auklet	*Cerorhinca monocerata*	Heintz, unpublished	Sitka	juveniles
Bird	Surf bird	*Aphriza virgata*	Bishop and Green (2001)	PWS	eggs
Bird	Surf scoter	*Melanitta perspicillata*	Willson et al. (2006), Bishop and Green (2001); Lok et al. (2008)	BC, PWS	eggs, spawners
Bird	Surfbird	*Aphriza virgata*	Willson et al. (2006)	PWS	spawners
Bird	Thayer's Gull	*Larus thayeri*	Willson et al. (2006)		spawners
Bird	Tufted puffin	*Fratercula cirrhata*	Furness and Furness (1985)	GOA	age-0
Bird	Western grebe	*Aechmophorus occidentalis*	Willson et al. (2006)	BC, SOG	spawners
Bird	White-winged scoter	*Melanitta deglandi*	Willson et al. (2006); Lok et al. (2008)	BC	spawners
Bird	Yellow-billed loon	*Gavia adamsii*	Bishop, this volume	PWS	mostly adult
Elasmobranch	Bering Skate		Bishop and Powers 2013	PWS	juveniles
Elasmobranch	Big skate	*Raja binoculata*	Bishop and Powers 2013	PWS	juveniles (winter)
Elasmobranch	Dogfish	*Squalus acanthias*	Tanasichuk et al. (1991)	BC	
Elasmobranch	Longnose skate	*Raja rhina*	Bishop and Powers (2013)	PWS	juveniles (winter)
Elasmobranch	Salmon shark	*Lamna ditropis*	Carlisle et al. (2011), Hulbert et al. 1995		adults
Elasmobranch	Spiny dogfish		Bishop and Powers (2013)	PWS	juveniles (winter)
Fish	Arrowtooth flounder	*Artheresthes stomias*	Brown and Norcross (2002); Boldt et al. (2010); Yang (2000); Yang (2003), Bishop and Powers (2013)	PWS, BC	juveniles
Fish	Chinook salmon	*Oncorhynchus tshawytscha*	Sturdevant et al. (2013); Scott and Crossman (1973); Reid (1961)	BC, PWS, SEAK	juveniles, adults
Fish	Coho salmon	*Oncorhynchus kisutch*	Beamish et al. (2001); Sturdevant et al. (2013); Scott and Crossman (1973)	BC, PWS, SEAK, SOG	

Type	*Common Name*	*Scientific Name*	*Reference*	*Location*	*Prey*
Fish	Dolly varden	*Salvelinus malma*	Rooper and Haldorson (1999)	PWS	Eggs
Fish	Flathead sole		Bishop and Powers (2013)	PWS	juveniles (winter)
Fish	Great sculpin	*Myoxocephalus polyacanthocephalus*	Bishop and Powers (2013)	PWS	juveniles winter
Fish	Greenlings	*Hexagrammus spp*	Brown and Norcross (2002)	PWS	juveniles
Fish	Halibut	*Hippoglossus stenolepis*	Best and St. Pierre (1986); Brown and Norcross (2002); Boldt et al. (2010); Yang (2000); Yang (2003)	BC, GOA, PWS	juveniles, adults
Fish	Kelp greenling	*Hexagrammos decagrammus*	Rooper and Haldorson (1999); Bishop and Powers (2013)	PWS	eggs, juveniles (winter)
Fish	Lingcod	*Ophiodon elongatus*	Boldt et al. (2010), Bishop and Powers	BC, PWS	adult? juveniles
Fish	Pacific cod	*Gadus macrocephalus*	Brown and Norcross (2002); Boldt et al. 2010; Yang 2000; Yang 2003, Bishop and Powers 2013,	BC, PWS	juveniles
Fish	Pacific hake	*Merluccius productus*	Tanasichuk et al. (1991)	BC	adults
Fish	Pacific halibut		Yang 2000, Bishop and Powers 2013	GOA, PWS	Adults, juveniles
Fish	Pacific herring	*Clupea pallasii*	Hourston and Haegele (1980)	BC	larvae
Fish	Pink salmon	*Onchorhynchus gorbuscha*	Hourston and Haegele (1980); Sturdevant et al. (2013); Sturdevant et al. (2012); Armstrong et al. (2005)	BC, PWS, SEAK, GOA	larvae, juveniles
Fish	Quillback rockfish	*Sebastes maliger*	Bishop and Powers (2013)	PWS	juveniles (winter)
Fish	Redstripe rockfish		Bishop and Powers (2013)	PWS	juveniles (winter)
Fish	River lamprey	*Lampetra ayresi*	Beamish and Neville (2001)	BC, SOG	juveniles
Fish	Rock greenling	*Hexagrammos lagocephalus*	Rooper and Haldorson (1999)	PWS	eggs
Fish	Rougheye rockfish	*Sebastes aleutianus*	Yang (2000)	Shelf	unknown
Fish	Sablefish	*Anopoploma fimbria*	Sturdevant (2009); Yang (2000); Bishop and Powers (2013)	GOA, PWS	adult, juveniles (winter)
Fish	Saffron cod	*Eleginus gracilis*	Bishop and Powers (2013)	PWS	juveniles (winter)
Fish	Searcher		Bishop and Powers (2013)	PWS	juveniles (winter)
Fish	Sturgeon poacher		Bishop and Powers (2013)	PWS	juveniles (winter)
Fish	Walleye pollock	*Theragra chalcogramma*	Brown and Norcross (2002); Yang (2000); Yang (2003); Bishop and Powers 20113.	PWS	juveniles, adults

Type	***Common Name***	***Scientific Name***	***Reference***	***Location***	***Prey***
Fish	Yellow fin sole	*Limanda aspera*	Bishop and Powers 2013	PWS	juveniles (winter)
Fish	Yelloweye rockfish		Bishop and Powers (2013)	PWS	juveniles (winter)
Invertebrate	Amphipod	*Traskorchestia spp*	Fox et al. (2014)	BC	eggs
Invertebrate	Chaetognath	*Sagitta spp*	Hourston and Haegele (1980)	BC	larvae
Invertebrate	Hydromedusae	*Sarsia tubulosa or Aequorea victoria*	Arai and Hay (1982); Purcell (1990)	BC	larvae
Invertebrate	Hyperiid amphipod	*Hyperoche medusarum*	Westerhagen and Rosenthal (1976)		larvae
Invertebrate	Squid	*????*	Stokesbury (2002)	PWS	juveniles
Mammal	Black bear	*Ursus americanus*	fox u victoria PhD thesis Pacific herring and salmon: ecological interactions across the land-sea interface	BC	eggs
Mammal	California sea lion	*Zalophus californianus*	Boldt et al. (2010)	BC	adult?
Mammal	Dall's porpoise	*Phocoenoides dalli*	Ohizumi (2003); Walker et al. (1997)	N. Pacific, BC	mostly myctophids
Mammal	Fin whale	*Balaenoptera physalus*	Thorne unpublished report (2008)	Kodiak Uganik	spawners
Mammal	Harbor porpoise	*Phocoena phocoena*	Walker et al. (1997)	BC	adults
Mammal	Harbor seal	*Phoca vitulina*	Thomas et al. (2011); Boldt et al. (2010)	BC, SOG	adults, juveniles
Mammal	Humpback whale	*Megaptera novaeangliae*	Boldt et al. (2010); Straley, this volume	BC, PWS, SEAK	adult?
Mammal	Minke whale	*Balaenoptera acutorostrata*			
Mammal	Northern fur seal	*Calorhinus ursinus*	Taylor (1971)	BC	adults?
Mammal	Orca whale	*Orcinus orca*	Saulitis et al. (2000)	BC	spawners
Mammal	River otter	*Lontra canadensis*	Ben-David et al. (2005)	PWS	spawners?
Mammal	Sea otter	*Enhydra lutris*	Lee et al. (2009)	PWS	eggs
Mammal	Steller sea lion	*Eumetopias jubatus*	Thorne, unpublished report (2008); Boldt et al.	BC, PWS	adults (winter)