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

Modeling the Population Dynamics of Prince William Sound Herring

Exxon Valdez Oil Spill Trustee Council Project 16120111-Q
Final Report

Trevor A. Branch

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Study History: This five-year project ran from 1 February 2012 to 31 January 2017, with four prior annual reports filed with the *Exxon Valdez* Oil Spill Trustee Council. Full details of the Bayesian age-structured model have recently been published (Muradian et al. 2017).

Abstract: A stock age-structured assessment model of Prince William Sound Pacific herring (*Clupea pallasii*) was implemented in a Bayesian framework, to complement the current age-structured assessment model used by the Alaska Department of Fish and Game. The Bayesian model, implemented in AD Model Builder, allows for fast and efficient estimation of uncertainty around key model parameters such as spawning biomass over time, while retaining the same structure as the current model. The model estimated that this herring population remains at low levels, below the management targets for reopening the fishery. The Bayesian model was used to assess the cost-effectiveness of past data in estimating biomass trends in Prince William Sound herring, finding that the relatively cheap disease survey provided the best trade-off between survey cost and precision, followed by the egg-deposition diver survey, which provides an absolute estimate of biomass to anchor the assessment. Meta-analysis of all herring populations worldwide collated time series of catches (53), spawning biomass (50) and recruitment (37), and highlighted that it is highly unusual for any herring population to have remained at low levels for as long as herring in Prince William Sound. Ongoing analyses are using the model to test alternative hypotheses for the decline and lack of recovery in this population.

Key words: Bayesian, *Clupea pallasii,* management, meta-analysis, modeling, Pacific herring, Prince William Sound, uncertainty

Project Data:
Description of data: Source code, executable files, and input files for the Bayesian age-structured assessment model. Time series collated for the meta-analysis of herring catches, spawning biomass, and recruitment.

Data format: Excel, AD Model Builder, R code.

Data archive and custodians:
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https://portal.aoos.org/gulf-of-alaska.php#metadata/4aaecfe2-de4b-4b6b-ba8e-bb715d26c6f1/project.

There are no limitations on the use of the data, however, it is requested that the authors be cited for any subsequent publications that reference this dataset. It is strongly recommended that careful attention be paid to the contents of the metadata file associated with these data to evaluate data set limitations or intended use.

<u>Citation:</u>

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EXECUTIVE SUMMARY

Four major projects were completed as part of the modeling component of the Prince William Sound (PWS) herring program: (1) The first implementation of a Bayesian stock assessment model of PWS herring. (2) An examination of the value of past survey data collected in reducing the uncertainty in the stock assessment model for PWS herring. (3) A meta-analysis of trends in catches, biomass, and recruitment for all populations of herring worldwide, to place the decline and lack of recovery of PWS herring into context. (4) An examination of the relative strength of different hypotheses for the decline and lack of recovery of Prince William Sound herring. Each project is outlined in more detail below.

BASA, Bayesian age-structured assessment model:

The core of the modeling project was converting the existing assessment model into a Bayesian framework. The existing age-structured assessment model (the ASA Model) used by the Alaska Department of Fish and Game (ADF&G) for assessing PWS herring for many years is based on minimizing sums of squares in an Excel-based framework. This model was converted to a Bayesian framework to run in AD Model Builder (ADMB, Fournier et al. 2012), which is much faster and more efficient than Excel. In addition, the Bayesian framework allows for consistent statistical weighting of different data sources and allows uncertainty to be automatically calculated from the Bayesian posteriors. This model now allows fisheries managers, should they choose to do so, to choose management rules that directly include uncertainty in deciding on how and whether to open the PWS herring fishery in the future.

The Bayesian model provides good fits to the time series of data. In the most recent Bayesian assessment (2015), the estimated biomass in early 2014 was 17,000 metric tonnes, just below the threshold for opening the fishery (19,958 mt). There was a wide 95% posterior probability interval (10,300-41,700 mt), with an 80% probability that spawning biomass was below the management threshold. The last year of medium recruitment was in 2002, but since then recruitment has been poor, ranging from 9 to 103 million fish compared to 117-1234 million fish in every year from 1980 to 1988. Taken as a whole, the Bayesian model confirmed the conclusions from the ADF&G assessment model that the fishery should not be reopened, and that biomass and recruitment have been low since the mid- to late-1990s.

Value of past survey data:

The Bayesian model was used to assess which surveys in the past were the most valuable additions in terms of obtaining more precise estimates of spawning biomass. To test this, multiple iterations were created, each simulating an alternative set of realistic data, and then the Bayesian model was fit to the data. In the base scenario, all data were included in the assessment, while for the other scenarios, data from a particular survey or method of data collection were omitted. The degradation in the precision of model estimates of spawning biomass, when one type of data is omitted, provides a measure of the usefulness of that source of data. The trade-off between survey cost vs. measures of precision and bias revealed that the disease survey (which is relatively cheap and collects an index of additional mortality due to disease) and the egg-deposition diver survey (which is relatively expensive and provides an absolute index of abundance) were the most valuable sampling programs in the past.

Meta-analysis of herring populations:

The previous sections of the project confirm that PWS herring collapsed a few years after the *Exxon Valdez* oil spill, and have yet to recover to pre-collapse levels. We conducted a meta-analysis of all herring populations globally, to put into perspective this collapse and subsequent failure to recover. For the meta-analysis, we collated time series for multiple populations: 53 catch time series, 50 spawning biomass time series, and 37 recruitment time series. These data show that it is highly unusual for any herring population to have remained at low levels for as long as PWS herring has. The meta-analysis also demonstrates that post-collapse PWS herring have the lowest recruits per spawner of all herring populations worldwide. An attempt was made to find variables that could explain why some herring populations collapse while others do not, and why some herring populations recover after collapse while others do not recover. However, an array of different methods tested on a variety of environmental variables found no significant predictors of collapse or recovery.

Hypotheses to explain low recent PWS herring recruitment and survival:
The Bayesian model was altered to allow a variety of hypotheses (external drivers) to affect recruitment and survival in the model. These hypotheses included the oil spill, pink salmon hatchery production, increased predator numbers, freshwater discharge into PWS, winter mean sea level height, primary production, summer upwelling, and disease. Results are still preliminary but indicate that pink salmon production, freshwater discharge, sea level height and a variety of other factors including disease, may all play a role in the lack of recovery of PWS herring.

INTRODUCTION

More than 30% of global fisheries catches come from small pelagic fish species such as sardine and herring (Smith et al. 2011), and these fish species play key roles in ocean ecosystems both as predators and as food in turn for other predators such as larger fish, birds, and marine mammals (e.g. Cury et al. 2011, Atkinson et al. 2014). Prince William Sound (PWS) is no different: Pacific herring (*Clupea pallasii*) here play as outsize role as predators and prey, or at least they did throughout most of the 1980s when they were abundant. In the historical past, such as the 1930s, catches exceeded 40,000 metric tonnes (mt) in PWS, and even in the early 1990s, more than 20,000 mt was caught in PWS in a single year (Fig. 1). Not only are PWS herring an important ecosystem player, but they are also a key player in the local fishing economy.

In 1989, PWS was the scene of the *Exxon Valdez* oil spill, but herring biomass remained high until their collapse in 1993, when the fishery was closed. Although limited herring fisheries opened in 1996-1998, no fisheries have been conducted since 1999 and the population has remained at low levels. In addition to likely injury from the oil spill, other factors have been suggested as possible hypotheses for their decline, including disease, predation especially from humpback whales, competition from pink salmon hatchery production, and environmental regime shifts (e.g. Deriso et al. 2008, Hilborn & Eggers 2000, Hulson et al. 2008, Marty et al. 2010, Pearson et al. 2012, Teerlink et al. 2014).

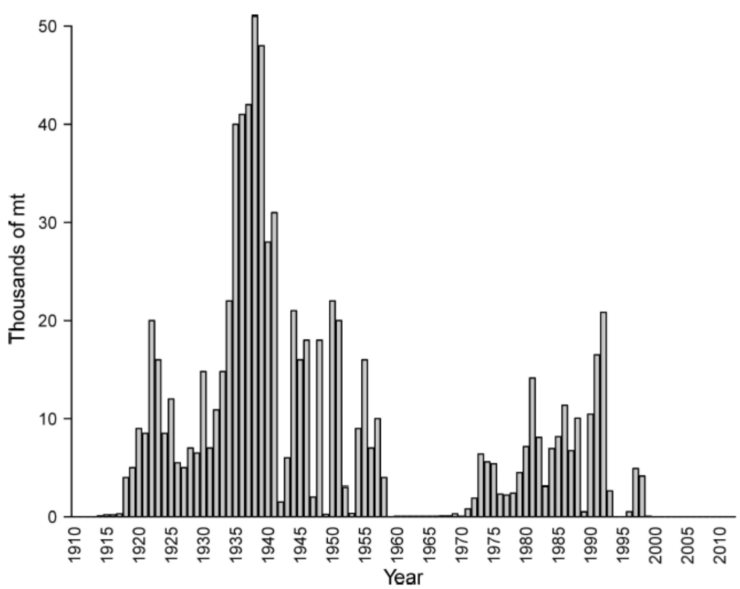

Figure 1. Total catches of herring in Prince William Sound from 1914 to 2012 (Muradian et al. 2017).

Current management of PWS herring is based on an age-structured assessment model (the ASA model) developed by the Alaska Department of Fish and Game (ADF&G). If the model estimates biomass to fall below 19,958 mt, then the fishery remains closed; if biomass is between this lower regulatory threshold and an upper regulatory threshold of 38,555 mt then a harvest rate of 0.0-0.2 yr^{-1} may be set; and if biomass is above the upper threshold then a harvest rate of 0.2 yr^{-1} is set. Thus the ASA model plays an important role in determining whether the fishery is opened, and the level of allowable catch. The ASA model is an age-structured model that is fitted to catch-at-age data, catches, and a variety of surveys, notably the aerial milt surveys, hydroacoustic surveys, a diver egg deposition survey in 1987-1991 that is used as an absolute biomass estimate. In addition, the model incorporates biological data about age at maturity, natural mortality, disease prevalence, and individual growth rates, as well as assumptions about the spawner-recruit relationship. A series of publications have detailed the ASA model (e.g. Hulson et al. 2008, Marty et al. 2003) as described in Muradian et al. (2017).

The ASA model is Excel-based, and relies in minimizing sum-of-squares model fits to the data using Solver. In this project, we translated the model into a Bayesian framework in AD Model Builder (Fournier et al. 2012), which is a much more efficient framework with a more sound statistical basis for estimating uncertainty. We use this Bayesian age-structured assessment model (the BASA model) to test the value of different types of data, use it to assess the relative validity of different hypotheses about the decline of PWS herring. In addition, we place PWS herring trends into context by comparing this population with all other herring populations worldwide.

OBJECTIVES

The original objectives of the approved proposal were as follows:

1) Determine which datasets provide the most informative information for the ASA model.

2) Predict levels of future recruitment, and autocorrelation in recruitment, using information from other herring populations and other species of clupeids.

3) Synthesize the data collected from the monitoring program into a holistic model of herring dynamics, to determine which life stages the observational program should focus on.

During the process of this work, these original three objectives were more precisely codified and expanded into the following four objectives:

a) Develop a Bayesian version of the ASA model that models herring dynamics (expands on original objective 3). This was necessary to form as a basis for the other objectives, as the existing ASA model was not otherwise modifiable enough or fast enough.

b) Determine which datasets provide the most informative information for the BASA model (original objective 1).

c) Meta-analysis of other herring populations to predict recruitment and the factors leading to biomass and recruitment declines, as well as putting PWS herring into context (expanded from original objective 2).

d) Use the BASA model to assess the evidence for different hypothesis for the decline and failure to recover of PWS herring (new objective expanded from original objective 3)

METHODS

This modeling study was based on Pacific herring occupying the entirety of PWS. At present, although there are distinct spawning sites within PWS, all herring are assumed to belong to a single population for management and assessment purposes.

Bayesian age-structured model

Full details of the Bayesian age-structured model have recently been published (Muradian et al. 2017), which includes all data inputs, equations, and a detailed description of the model workings. In short, fifteen data types are incorporated in the model, which starts in 1980 and the most recent version was run on data up to 2015. The model is developed in AD Model Builder, and uses an MCMC algorithm to sample posterior distributions for estimated and derived model parameters. Prior information about estimated model parameters is included in the model in the form of likelihood distributions. Posteriors are obtained from a single long, converged MCMC run, and used to obtain median and 95% intervals for key parameters of interest, such as annual estimates of spawning biomass and recruitment. In addition, the posteriors can be used to make probabilistic statements such as the probability that spawning biomass is below the lower regulatory threshold for opening the fishery.

Value of past information

Full methods for this section can be found in the Masters thesis of Melissa Muradian (Muradian 2015), and are ready for submission to ICES Journal of Marine Science. In brief, multiple plausible copies of the datasets were generated, the BASA model was fit to these, and then datasets were dropped from the full set of data, and the BASA model refit excluding one dataset at a time. The degradation in precision and bias of estimates in BASA provides a measure of the value of the dataset that was dropped.

Meta-analysis of global herring

Time series of herring catch, biomass, and recruitment were compiled from around the world, using a variety of database searching techniques, personal contacts and requests from agencies. Time series were fairly evenly split between Pacific herring and Atlantic herring (*Clupea harengus*) (Fig. 2). The time series were divided into regimes using the methods in Rodionov (2004, 2006), and characteristics of regimes were compared among populations to place the collapse of PWS herring into global context. Similar analyses were conducted to estimate recruits-per-spawners over time for each time series to compare trends among populations.

To test if covariates could be found that predicted changes in spawning biomass, recruitment or recruits-per-spawners, a variety of methods were employed, ranging from random forests to empirical dynamic modeling (Sugihara et al. 2012). Empirical dynamic modeling proved best suited to the system at hand since it does not assume linearity, and can identify drivers during collapse periods. Covariates tested included a wide range of environmental factors such as chlorophyll, temperature, freshwater discharge, and regional sea height anomalies.

Testing alternative hypotheses for PWS herring decline

The BASA model was modified so that a variety of alternative hypotheses could be tested. The general method was to allow recruitment or natural mortality to vary from year to year as a function of one or more covariates, such as disease prevalence, pink salmon abundance, humpback whale trends, and the oil spill. Hypothesis testing was on effects on annual recruitment (number of age-3 fish) and adult survival. Various environmental data representing bottom-up controls (freshwater discharge, temperatures, sea level, upwelling) and ecosystem components acting through predation (humpback whales, adult pink salmon) or competition (juvenile pink salmon) are incorporated into the model as covariates for which we determine the posteriors on their effects. These covariates are represented in individual models that are fit and further grouped into recruitment and mortality hypotheses. Model selection criteria (DIC) is used to determine the best fitting models within each subset of hypotheses.

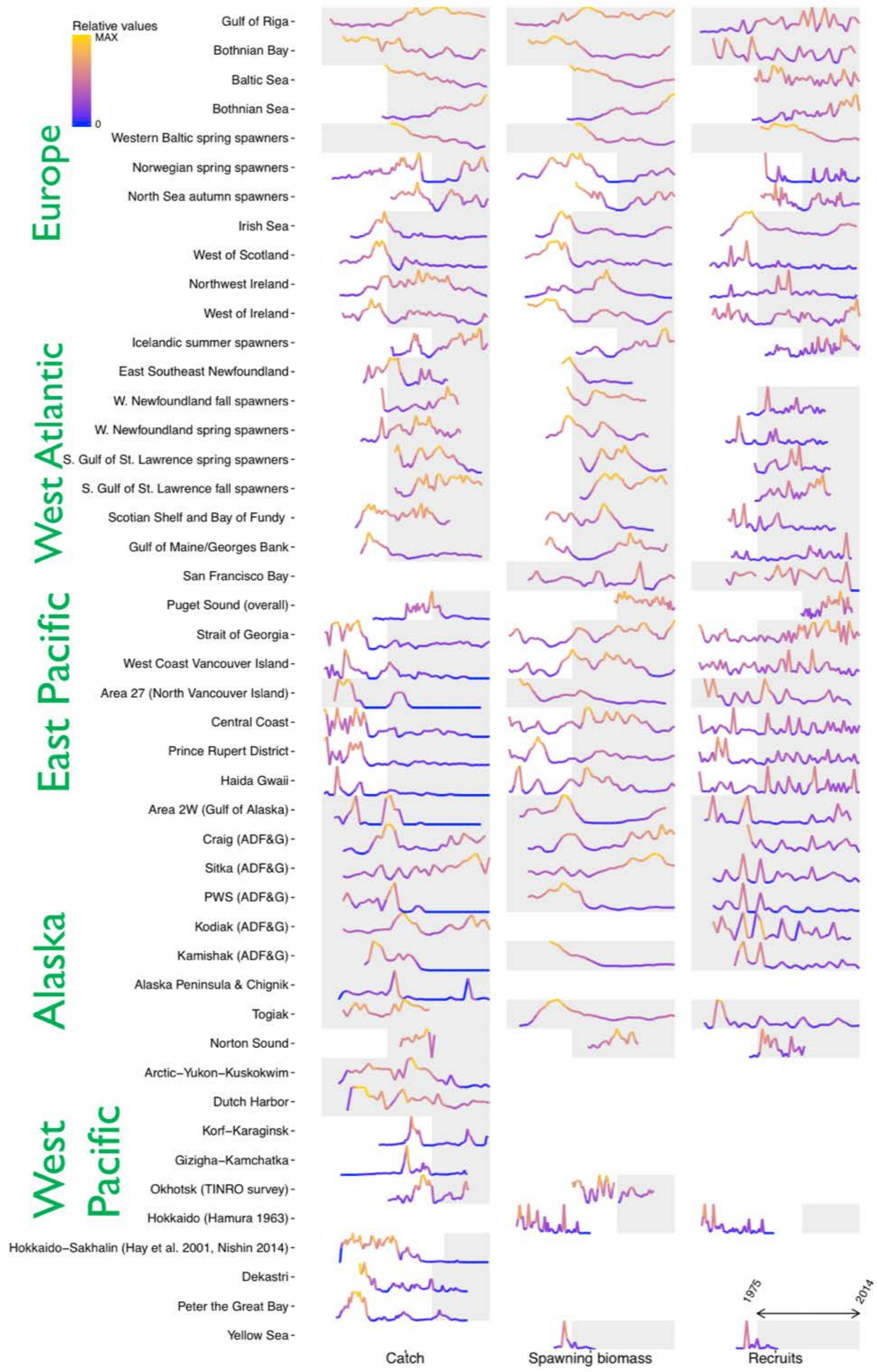

Figure 2. Compiled time series of catch (left), spawning biomass (center), and recruitment (right) for herring populations around the world. The duration of each series differs, as indicated by gray shading for the 1975-2014 period in each panel. This represents a sample of the total compilation.

RESULTS

Bayesian age-structured model

The BASA model provided good fits to the time series of biomass data (Fig. 3), showing the rapid decline in biomass starting in 1993 and the lack of recovery thereafter. In addition, the model demonstrated the high variance in recruitment evidenced in strong year classes visible in both the catch-at-age and survey numbers-at-age data (Fig. 4). The last dominant year class was in 1999, but since then a sequence of poor recruitments has been clear. Estimates of recruitment (Fig. 5A) show a sequence of good to excellent recruitment in the 1980s capped by the monster 1987 and 1991 year classes (two years after the oil spill), followed by below average recruitment in every year from 1992 onwards. Spawning biomass has been generally below the lower regulatory threshold since 1993, after a large downward shift from 1980-1992 to 1993-2013 (Fig. 5B). The probability obtained from the Bayesian posterior confirms this: there was a medium to high probability of being below the lower regulatory threshold in every year after 1993 except for 1997 when the fishery was briefly reopened (Fig. 5B). Estimated spawning biomass in 2013 was 19,400 mt with a wide 95% probability interval of 12,100-31,700 mt (Fig. 5C). PWS herring management aims to keep exploitation rates below 0.2 yr^{-1} and the model estimates that managers have been successful in this task, with realized median exploitation rates only rarely exceeding 0.2 yr^{-1}, and even in those two cases in 1981 and 1992, only just exceeding 0.2 yr^{-1} and with 95% intervals that overlapped 0.2 yr^{-1} (Fig. 5D).

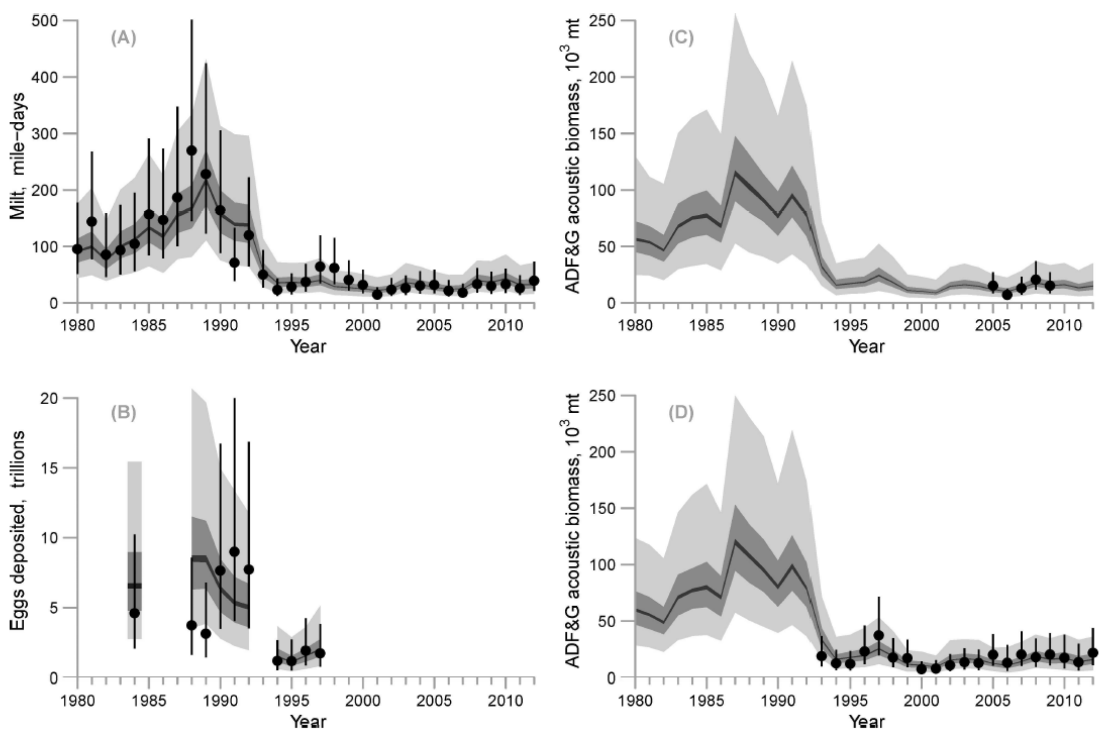

Figure 3. Model fits (shaded regions) to the four biomass time series: (A) mile-days of milt, (B) egg deposition surveys, (C) ADF&G hydroacoustic surveys, and (D) PWSSC hydroacoustic surveys (Muradian et al. 2017).

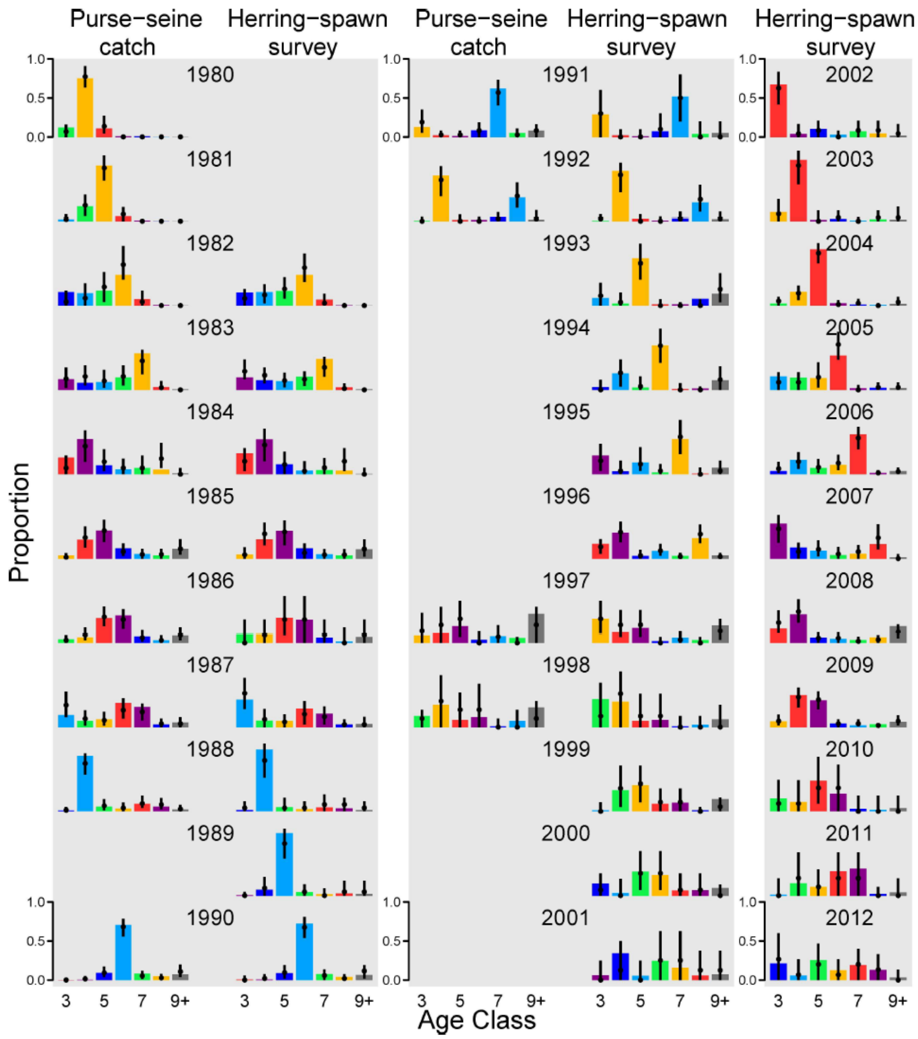

Figure 4. Model fits to the age composition data from the acoustic survey and from the commercial catches (Muradian et al. 2017).

Sensitivities to different natural mortality rates, and changes to other model parameters, did not substantially change the results of the model. In addition, retrospective peels (removing one year of data at a time) revealed no retrospective patterns indicative of model bias (Fig. 6).

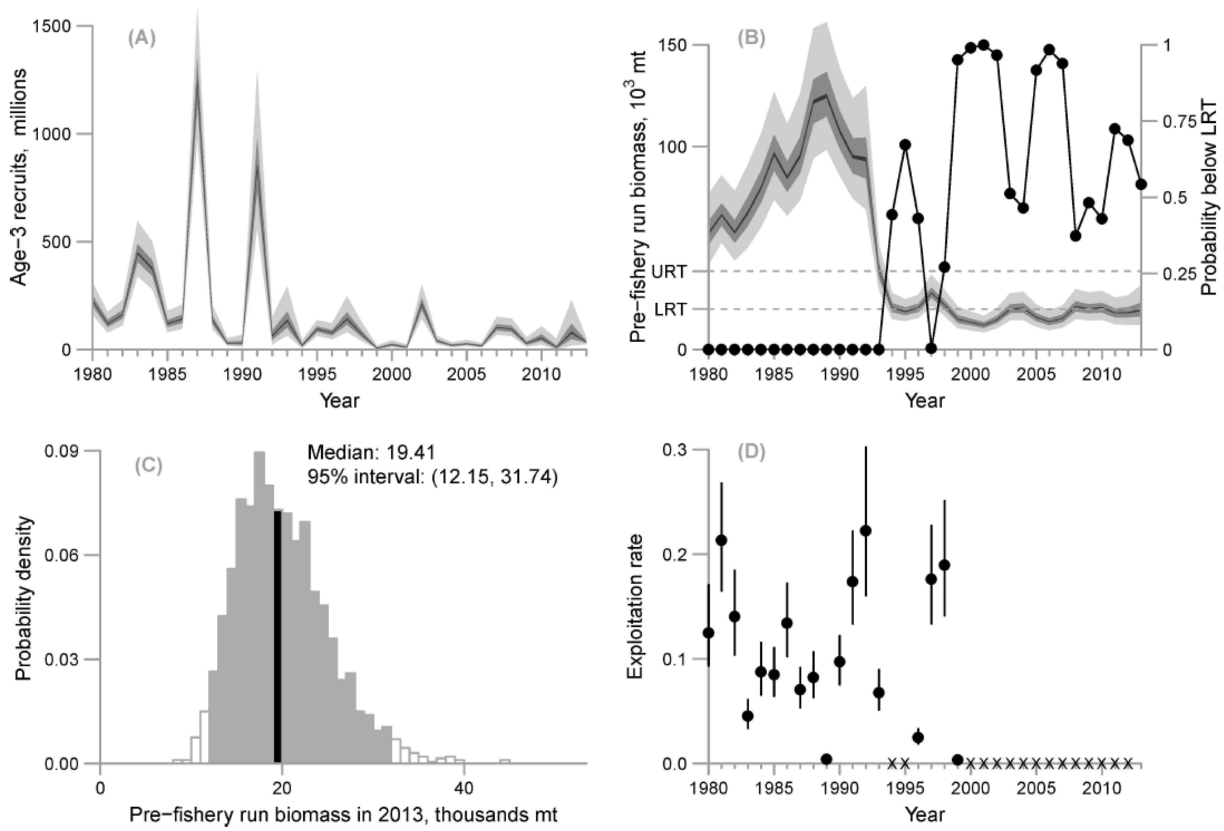

Figure 5. Model estimates of (A) recruitment, (B) spawning biomass by year and probability of falling below lower regulatory threshold (LRT) of 22,000 short tons, (C) posterior distribution of spawning biomass in 2013, and (D) annual estimates of exploitation rate (Muradian et al. 2017).

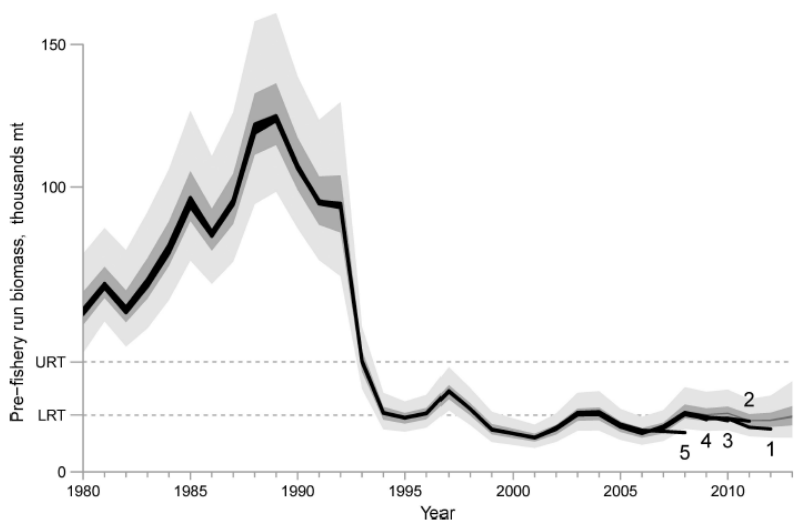

Figure 6. Results from five retrospective peels compared to the posterior distribution of the final model (Muradian et al. 2017).

Value of past information

When different data sources were removed from the BASA model one at a time, the biggest impact on model failure came from removing the disease survey (without which the model cannot explain the decline in 1993) and from removing the diver egg deposition survey (without which the model has no absolute estimate of biomass) (Table 1). Removing either of these two survey types also resulted in the highest probabilities of closing the fishery when it should be opened, or opening the fishery when it should be closed (Table 2).

Table 1. Values of extreme tail probability (ETP) for biomass in 1980 and 2013, for natural mortality, and for mean recruitment in the pre-collapse (R1) and post-collapse (R2) periods, when each survey type is removed from the model. High values of ETP translate to a high probability of model failure and values of ETP less than or equal to 0.02 imply model reliability. The last row displays the mean ETP across reference points for each case.

Reference point	Base	Disease	Diver	ADF&G Hyd.	PWSSC Hyd.	Aerial
B_{1980}	0.01	0.19	0.03	0.03	0.01	0.03
B_{2013}	0.05	0.43	0.04	0.03	0.05	0.02
$\overline{M_1}$	0.02	NA	0.03	0.01	0.02	0.03
$\overline{M_2}$	0.18	0.56	0.36	0.13	0.15	0.08
$\overline{R_1}$	0.05	0.07	0.11	0.04	0.04	0.06
$\overline{R_2}$	0.01	0.12	0.10	0.01	0.00	0.02
Mean ETP	0.05	0.27	0.11	0.04	0.05	0.04

Table 2. Probability of false fishery closures (PFC) or false fishery openings (PFO) when each of the survey types are removed from the base model.

Metric	Base	Disease	Diver	ADF&G Hyd.	PWSSC Hyd.	Aerial
PFC	0.24	0.03	0.13	0.24	0.37	0.29
PFO	0.15	0.77	0.58	0.15	0.15	0.23

The most valuable sampling programs were the disease survey (which is relatively cheap and collects an index of additional mortality due to disease) and the diver survey (which is relatively expensive and collects an absolute index of abundance) (Fig. 7). For $10,000 a year the disease survey reduces bias and imprecision in current biomass by 34% on average, increases model reliability by 22%, and decreases by 31% the probability of a false management conclusion when regulating the fishery. For $350,000 a year the diver survey reduces bias and imprecision in the forecast by 12% on average, increases model reliability by 6%, and decreases the probability of a false management conclusion by 23%.

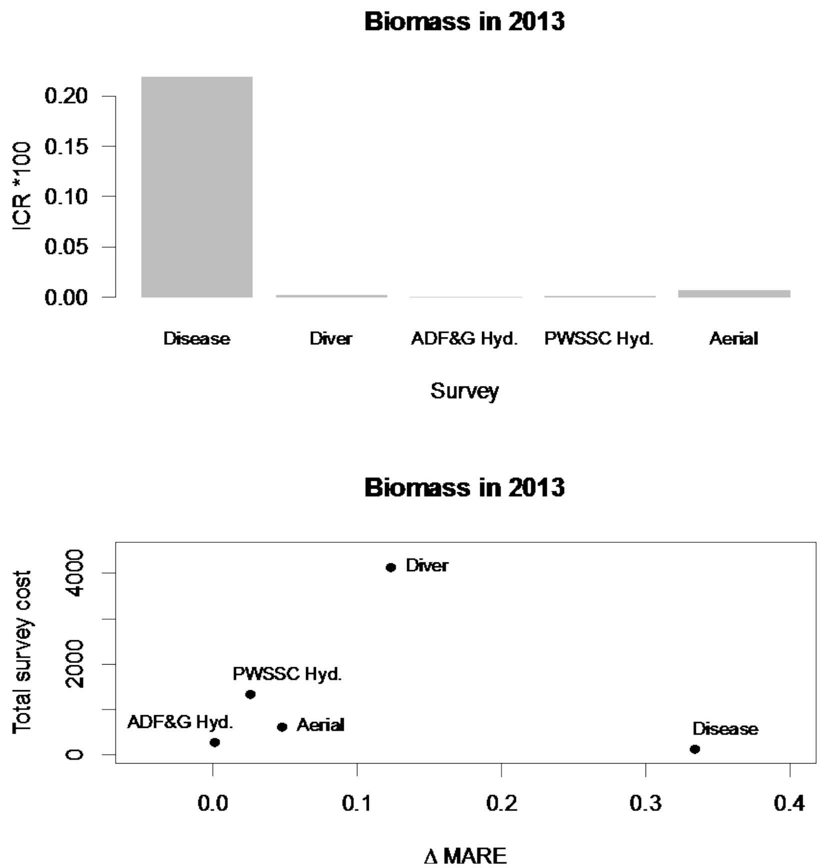

Figure 7. The top panel shows the information to cost ratio (ICR) for each survey relating to the estimate of the forecast biomass in 2013. The bottom panel shows the cost of each survey program plotted by the improvement in mean average relative error (MARE) in the forecast biomass due to the addition of that survey's data.

Meta-analysis of global herring

Comparison of PWS herring to global herring stocks revealed several ways in which PWS herring are unusual. Notably, recruits per spawner, a crucial measure of a population's ability to recover from depletion, are the lowest of any Atlantic or Pacific herring population (Fig. 8). In addition, the duration that PWS herring have spent below 30% of their maximum biomass (21 years post-collapse) is exceeded only by four other populations in the world, placing PWS herring in the lowest 10th percentile by this measure.

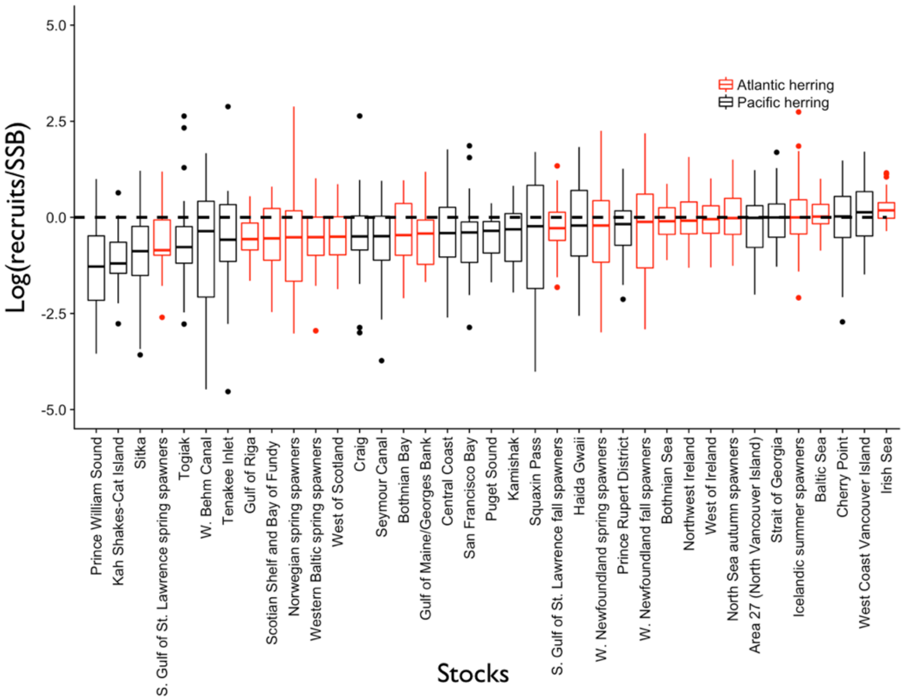

Figure 8. Log(recruits divided by spawning biomass) for all herring populations in the Atlantic (red) and Pacific (black) ordered from lowest to highest. PWS herring has the lowest median out of all populations for which data are available.

The empirical dynamic modeling approach, when applied to the database of global herring populations, did not reveal any significant environmental drivers or recovery in herring. Of all the predictors tested, sea surface temperature and sea surface height anomaly occasionally came up as significant predictors for recruits-per-spawner or spawning biomass, but even these predictors were significant for no more than 3-5 of the 25 recruits-per-spawner time series, and 1-3 of the 42 spawning biomass time series for which this analysis could be conducted. Alternative analyses similarly found no environmental predictors of recovery in herring populations.

Testing alternative hypotheses for PWS herring decline

Among recruitment hypotheses, our results support the impact of hatchery-released pink salmon and potential environmental forcing through freshwater discharge and winter mean sea level (Table 3). Both environmental indices are lagged by 2 years, indicating their impact on survival of Age-1 herring. All these covariates had effect posteriors that were significantly different from 0. Among mortality hypotheses, the effect of summer upwelling and disease (represent by 3 different data sets) are supported by DIC and their posterior distributions. Further analyses will include running a model that includes all covariates and allows the MCMC algorithm to select which of those covariates have significant impacts.

Table 3. Comparison of the Deviance Information Criterion (DIC) and estimated effects of covariates on juvenile survival (recruitment) and adult survival. Values in bold text indicate…

Model	△DIC	Covariate effect Median	95% credibility interval	
Recruitment covariate				
Null model	7.27	NA	NA	
PWS freshwater discharge (lagged 3 years)	8.99	-0.15	(-0.66,0.30)	
PWS freshwater discharge (lagged 2 years)	**2.55**	**-0.52**	**(-0.94,-0.12)**	
PWS winter SST (lagged 2 years)	9.48	0.06	(-0.43,0.47)	
PWS wild juvenile pink salmon (lagged 1 year)	8.55	-0.18	(-0.67,0.31)	
PWS hatchery juvenile pink salmon (lagged 2 years)	**0.00**	**-0.63**	**(-1.02,-0.26)**	
PWS hatchery adult pink salmon (lagged 2 years)	**3.94**	**-0.49**	**(-0.94,-0.12)**	
PWS wild adult pink salmon (lagged 1 year)	8.17	0.26	(-0.19,0.69)	
PWS hatchery adult pink salmon (lagged 1 year)	6.27	-0.37	(-0.80,0.06)	
PWS winter air temperature (lagged 2 years)	8.33	-0.19	(-0.67,0.19)	
PWS spring air temperature (lagged 3 years)	7.81	0.25	(-0.23,0.68)	
PWS winter sea level (lagged 2 years)	**1.23**	**-0.54**	**(-1.00,-0.19)**	
PWS spring sea level (lagged 3 years)	8.16	0.14	(-0.30,0.61)	
PWS summer sea level (lagged 3 years)	8.44	-0.23	(-0.67,0.23)	
Adult mortality covariate				
Null model	52.65	NA	NA	
Humpback whale predation	40.51	0.05	(0.03,0.08)	
Freshwater discharge	50.11	0.04	(0.00,0.08)	
Winter SST	55.27	0.01	(-0.02,0.04)	
Winter air temperature	21.42	0.08	(0.06,0.09)	
Winter mean sea level	54.61	0.02	(-0.02,0.06)	
Spring air temperature	44.76	-0.06	(-0.10,-0.02)	
Spring mean sea level	51.78	-0.03	(-0.07,0.00)	
Summer mean sea level	55.60	0.01	(-0.03,0.05)	
Summer mean sea level (lag 1)	36.37	-0.10	**(-0.14,-0.06)**	
Summer upwelling index (summer prior)	**0.00**	**0.11**	**(0.09,0.13)**	
Disease	**10.91**	**0.02**	**(0.01,0.03)**	*(I. hoferi survey 1994-2006)*
		-0.21	**(-0.28,-0.10)**	*(I. hoferi survey 2007-2012)*
		-0.73	**(-0.93,-0.43)**	*(VHSV survey 1994-2012)*

DISCUSSION

The updated Bayesian model (BASA) confirms the existing ADF&G model conclusions that PWS herring collapsed in 1993 and has generally remained at low levels since. The most valuable survey time series in the past were the disease surveys and the diver egg deposition survey. This is because the disease surveys provide an explanation for the sudden decline in biomass in 1993, without which the high mortality cannot be explained. The egg deposition surveys, which were conducted during intermittent years during 1984 through 1997, are crucial since they alone provide an estimate of absolute biomass. Counter-intuitively, the milt surveys and hydroacoustic surveys are not highlighted as being important, however, this is because these two survey types return very consistent estimates of relative herring biomass over time: removing any one of these results in similar model estimates, but removing both the milt and hydroacoustic surveys would result in no information about population trends since 1997, and no way of assessing population recovery. Future analyses of the value of data collection should include the scenario where both the milt surveys and hydroacoustic surveys are removed.

Meta-analysis revealed several ways in which the prolonged duration of low biomass in PWS herring is unusual. Notably, this population has the fourth longest duration of biomass below 30% of maximum biomass (more than 20 years) and the lowest recruits-per-spawner observed in any herring population in the database. As is common for recruitment in fisheries, we were unable to find any consistent environmental covariate that could explain recruitment in the database assembled.

Multiple factors were highlighted for the decline and lack of recovery, although these results are preliminary and may change. These include pink salmon production, freshwater discharge into PWS, winter mean sea level height, summer upwelling, and disease, in addition to previously identified impacts from the oil spill. Should these results hold up to further analysis, this suggests a suite of factors may be playing a role in depressing the population of PWS herring.

CONCLUSIONS

PWS herring remain at low levels and show no evidence of recovery more than 20 years after their collapse a few years after the oil spill. A variety of factors are identified to explain their failure to recover, but environmental factors typically have low predictive value in explaining trends in other herring populations. The development of a new modeling tool, a Bayesian age-structured model of PWS herring, provided the basis for examining the value of information, trends in abundance, and examination of alternative hypotheses for the decline and lack of recovery of PWS herring.

ACKNOWLEDGEMENTS

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LITERATURE CITED

Atkinson, A., S. L. Hill, M. Barange, E. A. Pakhomov, D. Raubenheimer, K. Schmidt, S. J. Simpson, and C. Reiss. 2014. Sardine cycles, krill declines, and locust plagues: revisiting 'wasp-waist' food webs. Trends in Ecology and Evolution doi: 10.1016/j.tree.2014.03.011.

Cury, P. M., I. L. Boyd, S. Bonhommeau, T. Anker-Nilssen, R. J. M. Crawford, R. W. Furness, J. A. Mills, E. J. Murphy, H. Österblom, M. Paleczny, J. F. Piatt, J.-P. Roux, L. Shannon, and W. J. Sydeman. 2011. Global seabird response to forage fish depletion—one third for the birds. Science 334:1703-1706.

Deriso, R. B., M. N. Maunder, and W. H. Pearson. 2008. Incorporating covariates into fisheries stock assessment models with application to Pacific herring. Ecological Applications 18:1270-1286.

Fournier, D. A., H. J. Skaug, J. Ancheta, J. Ianelli, A. Magnusson, M. N. Maunder, A. Nielsen, and J. Sibert. 2012. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optimization Methods & Software 27:233-249.

Hilborn, R., and D. Eggers. 2000. A review of the hatchery programs for pink salmon in Prince William Sound and Kodiak Island, Alaska. Transactions of the American Fisheries Society 129:333-350.

Hulson, P.-J. F., S. E. Miller, T. J. Quinn II, G. D. Marty, S. D. Moffitt, and F. Funk. 2008. Data conflicts in fishery models: incorporating hydroacoustic data into the Prince William Sound Pacific herring assessment model. ICES Journal of Marine Science 65:25-43.

Marty, G. D., P.-J. F. Hulson, S. E. Miller, T. J. Quinn II, S. D. Moffitt, and R. A. Merizon. 2010. Failure of population recovery in relation to disease in Pacific herring. Diseases of Aquatic Organisms 90:1-14.

Muradian, M. L. 2015. Modeling the population dynamics of herring in the Prince William Sound, Alaska. M.S. thesis, Quantitative Ecology and Resource Management, University of Washington, Seattle.

Muradian, M. L., T. A. Branch, S. D. Moffitt, and P.-J. F. Hulson. 2017. Bayesian stock assessment of Pacific herring in Prince William Sound, Alaska. PLoS One 12:e0172153.

Pearson, W. H., R. B. Deriso, R. A. Elston, S. E. Hook, K. R. Parker, and J. W. Anderson. 2012. Hypotheses concerning the decline and poor recovery of Pacific herring in Prince William Sound, Alaska. Reviews in Fish Biology and Fisheries 22:95-135.

Rodionov, S. 2006. Use of prewhitening in climate regime shift detection. Geophysical Research Letters 33:L12707.

Rodionov, S. N. 2004. A sequential algorithm for testing climate regime shifts. Geophysical Research Letters 31:L09204.

Smith, A. D. M., C. J. Brown, C. M. Bulman, E. A. Fulton, P. Johnson, I. C. Kaplan, H. Lozano-Montes, S. Mackinson, M. Marzloff, L. J. Shannon, Y.-J. Shin, and J. Tam. 2011. Impacts of fishing low-trophic level species on marine ecosystems. Science 333:1147-1150.

Sugihara, G., R. M. May, H. Ye, C.-H. Hsieh, E. R. Deyle, M. Fogarty, and S. B. Munch. 2012. Detecting causality in complex ecosystems. Science 338:496-500.

Teerlink, S. F., O. Von Ziegesar, J. M. Straley, T. J. Quinn II, C. O. Matkin, and E. L. Saulitis. 2014. First time series of estimated humpback whale (*Megaptera novaeangliae*) abundance in Prince William Sound. Environmental and Ecological Statistics doi: 10.1007/s10651-014-0301-8.