

*Exxon Valdez* Oil Spill  
Prince William Sound Herring Research and Monitoring Program Final Report

Validation of Acoustic Surveys for Pacific Herring (*Clupea pallasii*) Using Direct Capture  
Restoration Project 16120111-A

Final Report

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**Study History:** For this study, a detailed project description was approved for funding by the Trustee Council in October 2011. Fieldwork for the project began in November 2012. Our project's direct capture efforts were associated with the following Prince William Sound Herring Research and Monitoring Program's acoustic surveys: *Juvenile herring abundance index* (November 2012-2016) and the annual *Expanded adult herring surveys* (March and April 2013-2016). In addition, we conducted a series of trawls associated with two other HRM projects: *Juvenile herring intensive acoustic surveys* (Oct 2013 – Apr 2014) and a short, pilot study, *Integrated marine bird/whale/forage fish survey at Montague Strait* (Sept 2014). Samples were provided to various projects that were part of the Herring Research and Monitoring Program throughout the study's duration. This is the final report on activities conducted by this direct capture project.

**Abstract:** Acoustic surveys provide a relatively low-cost, remote sensing tool to estimate species-specific fish biomass and abundance. Interpreting acoustic data requires accurate ground truthing of acoustic backscatter to confirm species and length frequency of insonified targets. Pelagic trawls are the recommended method for validating species composition and for obtaining relatively unbiased information on length frequency distribution, age, and other biological information. To ground truth acoustic surveys for juvenile Pacific herring (*Clupea pallasii*), we used a low-resistance, light-weight midwater sweeper trawl and supplemented these efforts with castnets and gillnets. Our pelagic trawl surveys for juvenile herring took place in conjunction with and onboard the same vessel as two studies in the *PWS Herring Research and Monitoring program: Juvenile Herring Abundance Index* (years 2-5) and *Acoustic Consistency: Intensive Surveys of Juvenile Herring* (year 3). Using trawl data from the juvenile herring surveys, we investigated associations between catch rate and habitat covariates using generalized linear mixed models. Pacific herring was the most prevalent fish species captured in trawl tows (85.3% of total fish catch). A substantial percent of total fish catch was composed of other forage fishes including walleye pollock (11.6%) and capelin (2.3%). Our results indicated that the distribution of age-0 Pacific herring in the pelagic environment was influenced by shoreline habitat, salinity, and water depth. Age-0 Pacific herring catch rate was negatively associated with distance from eelgrass beds and tow depth, with herring favoring shallower water across the range of depths sampled (7.2–35.4 m). In addition, herring distribution was positively associated with fresher water within the sampled salinity gradient (24.1–32.3 psu). Using data from the juvenile intensive surveys, we documented seasonal changes in juvenile herring data distribution across a seven month period (October-April) at Simpson Bay. Age-0 herring tended to remain in the inner bay region throughout the seven months, while age-1 herring by spring (March-April) had shifted from the inner to the outer bay. Our project also validated acoustic surveys associated with the *PWS Herring Research and Monitoring Program: Expanded Adult Surveys* (years 2-5). For the adult herring surveys, Alaska Department of Fish and Game required gillnets and jigging for validation in lieu of trawls. In addition to ground truthing the adult and juvenile herring acoustic surveys, our project collected juvenile and adult herring samples for other projects within the Prince William Sound Herring Research and Monitoring program, including: condition index, energetics, genetics, growth, disease, and age at first spawn. Our trawls also provided fishery-independent surveys for non-herring species, thus increasing our knowledge of pelagic fishes in Prince William Sound.

**Key Words:** *Clupea pallasii*, Pacific herring, forage fish, Prince William Sound, predator avoidance, fjord, bay, estuary, eelgrass, sub-Arctic, winter, age-0, ice cover

**Project Data:** *Description of data* –Data files include measurements of collected fish, logs of gear deployment and catches, environmental data, and a master list of all survey cruises.

*Format* –All capture data is available as csv files in folder Herring capture>Data

<https://workspace.nprb.org/group/3503/project/283136/folder/1767165/data>

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## EXECUTIVE SUMMARY

Robust Pacific herring (*Clupea pallasii*) populations, suitable for exploitation by commercial fisheries, are typically sustained by periodic recruitment of strong year classes into the adult spawning population. However, the Prince William Sound (PWS) herring population has not had a strong recruitment class since 1989, when the *Exxon Valdez* Oil Spill (EVOS) occurred. In the EVOS settlement, herring were identified as an injured resource and they remain listed as an unrecovered species by the EVOS Trustee Council (EVOSTC). Understanding why herring have not recovered in Prince William Sound requires understanding potential bottlenecks in the herring life cycle. The identification of the limiting conditions to herring recovery requires a series of focused process studies combined with monitoring of the natural conditions that affect herring survival.

Our study, *Validation of Acoustic Surveys for Pacific Herring Using Direct Capture*, is a process study that addresses objective 3 of the *PWS Herring Research and Monitoring: to address assumptions in the current measurements*. The goals of this project are twofold: a) to ground truth acoustic backscatter to confirm species composition and length frequency of insonified targets; and b) provide fish samples to *PWS Herring Research and Monitoring* programs.

Objectives specific to the *Direct Capture* study included: 1) improve capture methods used for ground truthing acoustic surveys; 2) increase the sample size for identification, quantification, and measurement of juvenile (age-0+, 1+, 2+) and adult (age-3+ and older) herring schools as well as other fish schools in survey areas; 3) provide data on species composition and length frequency to aid in the interpretation of current and historical acoustic surveys; 4) provide adult herring samples to Alaska Department of Fish and Game for the adult herring age-structure-analyses model; and, 5) provide juvenile herring samples to researchers investigating juvenile herring fitness and disease.

Pelagic trawls are the recommended method for validating species composition and for obtaining relatively unbiased information on length frequency distribution, age, and other biological information. To ground truth acoustic surveys for juvenile herring, we used a low-resistance, light-weight midwater sweeper trawl and supplemented these efforts with castnets and gillnets. Our project's direct capture efforts for juvenile herring were associated with the following HRM acoustic surveys: *Juvenile herring abundance index* (Nov 2012-2016) and *Juvenile herring intensive acoustic surveys* (Oct 2013 – Apr 2014). We also conducted trawls for a short, pilot study, *Integrated marine bird/whale/forage fish survey at Montague Strait* (Sept 2014).

Our project also validated acoustic surveys associated with the *PWS Herring Research and Monitoring Program: Expanded Adult Surveys* (years 2-5). For the adult herring surveys, Alaska Department of Fish and Game required gillnets and jigging for validation in lieu of trawls. In addition to ground truthing the adult and juvenile herring acoustic surveys, our project collected juvenile and adult herring samples for other projects within the Prince William Sound Herring Research and Monitoring program (Table 1).

Using trawl data collected in conjunction with November juvenile herring surveys, we investigated associations between catch rate and habitat covariates over a three-year period (2013-2015). Pacific herring was the most prevalent fish species captured in trawl tows (85.3% of total fish catch). A substantial percent of total fish catch was composed of other forage fishes including walleye pollock (11.6%) and capelin (2.3%). We hypothesized that age-0 Pacific herring density would be associated with trawl tow depth, thermohaline conditions, and geospatial factors (distance from shore, bottom depth, and distance from

eelgrass habitat). Using generalized linear mixed models, results indicated that the distribution of age-0 Pacific herring in the pelagic environment was influenced by shoreline habitat, salinity, and water depth. Age-0 Pacific herring catch rate was negatively associated with distance from eelgrass beds and tow depth, with herring favoring shallower water across the range of depths sampled (7.2–35.4 m). In addition, herring distribution was positively associated with fresher water within the sampled salinity gradient (24.1–32.3 psu).

Using data from the juvenile intensive surveys at Simpson Bay, we documented seasonal changes in juvenile herring data distribution across a seven month period (October 2012–April 2013). We hypothesized that age-0 fish would be associated with shallow water during winter (October through February) and would migrate to deeper waters by spring (March through April). Age-1 fish were predicted to inhabit deeper water than age-0 fish throughout the year. Age-0 herring tended to remain in the inner bay region throughout the seven months, while age-1 herring by spring (March–April) had shifted from the inner to the outer bay. Additionally, catch rate of age-0 Pacific herring in areas where ice breakup had just occurred was higher than in open water, suggesting that age-0 herring preferentially select ice-covered habitats when available.

Table 1. Prince William Sound Herring Research and Monitoring projects by title, agency, and type of fish samples provided by this direct capture project.

<b><i>EVOS Herring Research</i></b>	<b>Agency</b>	<b>Samples provided</b>
Juvenile herring abundance index	PWS Science Center	All species – measurements only
Juvenile herring intensive acoustic surveys	PWS Science Center	All species – measurements only
Expanded adult herring acoustic surveys	PWS Science Center	All species – measurements only
Condition index	PWS Science Center	Juvenile herring
Genetic stock structure & age structure	ADFG	Adult herring
Disease	USGS	Juvenile herring
Energetics	NOAA Auke Bay	Juvenile herring/walleye pollock
Growth RNA/DNA	NOAA Auke Bay	Juvenile herring
Age at first spawn	NOAA Auke Bay	Adult herring

## INTRODUCTION

Robust Pacific herring (*Clupea pallasii*) populations, suitable for exploitation by commercial fisheries, are typically sustained by periodic recruitment of strong year classes into the adult spawning population. However, the Prince William Sound (PWS) herring population has not had a strong recruitment class since 1989, when the *Exxon Valdez* Oil Spill (EVOS) occurred. In the EVOS settlement, herring were identified as an injured resource and they remain listed as an unrecovered species by the EVOS Trustee Council (EVOSTC). Understanding why herring have not recovered in Prince William Sound requires understanding potential bottlenecks in the herring life cycle. The identification of the limiting conditions to herring recovery requires a series of focused process studies combined with monitoring of the natural conditions that affect herring survival.

Our study, *Validation of Acoustic Surveys for Pacific Herring Using Direct Capture*, is a process study that addresses objective 3 of the *PWS Herring Research and Monitoring: to address assumptions in the current measurements*. The goals of this project are twofold: a) to ground truth acoustic backscatter to confirm species composition and length frequency of insonified targets; and b) provide fish samples to *PWS Herring Research and Monitoring* programs.

Previous juvenile herring acoustic surveys (2009-2012) were conducted at the beginning (November) and end (March) of each winter. A variety of methods were used with limited success to ground truth these surveys. Small mid-water trawls used during fall 2007 and fall 2009 cruises also failed to catch fish. In most cases, these trawls were towed 1 day after the acoustic survey and always from a different vessel. Trawling speeds were typically 2-3 knots, producing a high level of net avoidance by the targeted fish. Variable mesh gillnets have also been used to validate acoustic surveys; however, gillnets select for faster swimming fish (Thorne et al. 1983) and in PWS, gillnet deployments have resulted in very small catch rates of juvenile herring.

Pelagic trawls are the recommended method for validating species composition and for obtaining relatively unbiased information on length frequency distribution, age, and other biological information. For this project, we used a low-resistance, light-weight midwater sweeper trawl capable of towing speeds (up to 3 knots) as a method to ground truth acoustic surveys for juvenile herring. Our trawls were conducted from the same vessel as the acoustic surveys, typically immediately after the acoustic surveys.

Objectives specific to the *Direct Capture* study included: 1) improve capture methods used for ground truthing acoustic surveys; 2) increase the sample size for identification, quantification, and measurement of juvenile (age-0+, 1+, 2+) and adult (age-3+ and older) herring schools as well as other fish schools in survey areas; 3) provide data on species composition and length frequency to aid in the interpretation of current and historical acoustic surveys; 4) provide adult herring samples to Alaska Department of Fish and Game for the adult herring age-structure-analyses model; and, 5) provide juvenile herring samples to researchers investigating juvenile herring fitness and disease.

Few analyses relating juvenile Pacific herring density to habitat characteristics have been conducted using empirical catch data. We used the juvenile herring trawl data from this study to document distribution patterns and test two hypotheses: 1) age-0 Pacific herring density are associated with trawl tow depth, thermohaline conditions, and geospatial factors (distance from shore, bottom depth, and distance from eelgrass beds; and, 2) age-0 fish are associated with shallow water during winter (October through February) and migrate to deeper waters by spring (March through April).

## STUDY AREA AND METHODS

### Study Area

Prince William Sound lies on the coast of south-central Alaska, primarily between 60° and 61° N, and is separated from the adjacent Gulf of Alaska (GOA) by large, mountainous islands. There are several large ice fields with > 20 tidewater glaciers (Molnia 2001). The coastline is rugged and extensive and includes fjords and bays with average depths ranging from <50 m to >400 m. Outside the bays are many basins and passages of varying depths up to 700 m.

Abundant rain, snow, and glacial melt result in a strong cyclonic circulation that generally travels east to west (Niebauer et al. 1994). During summer the waters of PWS are highly stratified, but during winter months they are more mixed, with Gulf of Alaska surface waters pulsing into PWS via the Alaska Coastal Current (Niebauer et al. 1994). The northern half of PWS is strongly influenced by fjord waters and tends to be colder and fresher relative to the Alaska Coastal Current-influenced waters that are warmer and more saline (Wang et al. 2001). Much of PWS is protected from the wave action that hits the exposed Alaskan coast, but winter can bring large storm systems. Annual precipitation can be as high as 5.4 m and sea surface temperatures in the fjords can be as low as 1° C in late winter, with some inner bays and fjords choked with ice (Gay and Vaughan 2001).

### Field Methods

Nine locations distributed throughout PWS were sampled for juvenile herring during November 2012-2016: Windy Bay, Simpson Bay, Port Gravina, Port Fidalgo, Eaglek Bay, Lower Herring Bay, Whale Bay (east and west arm), and Zaikof Bay (Fig. 1). The *Juvenile herring abundance index project* (JIS) was comprised of these November sampling events. In addition to the JIS, Simpson Bay was sampled from October 2013 through April 2014 as part of the *Juvenile herring intensive acoustic surveys* (Intensives). For all sampling events, juvenile herring were captured using a midwater trawl with a 38 mm mesh size dropping into 12 mm mesh at the codend (14 m × 11 m × 22 m; Innovative Net Systems, Inc., Milton, LA). Trawl tows were carried out onboard a vessel conducting hydroacoustic juvenile herring surveys. All tows were conducted at least two hours after sunset because clupeids are associated with shallower water during low light conditions (Cardinale et al., 2003; Thorne and Thomas, 1990). For 2013-2015 tows were conducted immediately following completion of hydroacoustic surveys and in areas where high acoustic backscatter had been detected (2–4 tows were conducted per night). For 2016, acoustic surveys were temporarily stopped and tows conducted when an area of high acoustic backscatter was detected. These sampling designs precluded researchers from using trawl CPUE to make inferences about total abundance within nursery areas because tows were targeted to high-density areas.

At sampling bays, additional fish were collected with juvenile herring gillnets (60' X 16'; 1/4, 5/16, 3/8" mesh) and castnets (6', 3/16" mesh) to provide samples for other herring research projects. Nets were deployed opportunistically while at anchor. Total species biomass and number collected were calculated for each tow and gillnet deployment. Additionally, up to 200 per species of collected fishes were measured (SL, FL, TL; mm) and weighed (g) onboard the research vessel, except for 2015 when fish were frozen and later measured in the lab. Age data were not collected for herring, but age classes of juvenile herring were assigned based on clear modes present in the length data from the JIS and the Intensives at Simpson Bay. All Pacific herring ≤105 mm standard length (SL) were

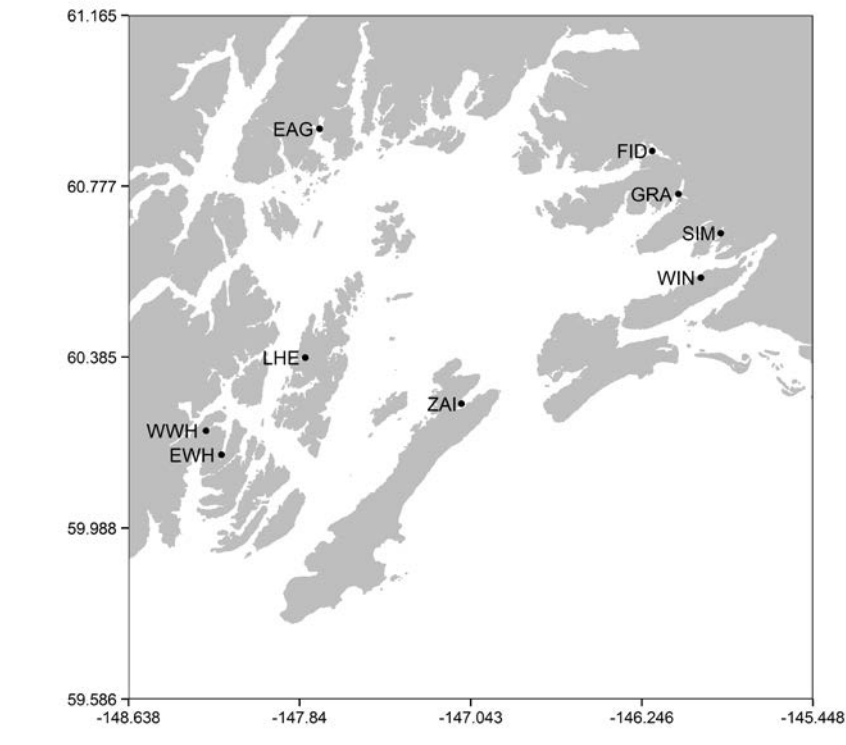


Figure 1. Map of Prince William Sound depicting the locations of juvenile herring surveys (SIM=Simpson Bay; GRA=Port Gravina; FID=Port Fidalgo; EAG=Eaglek Bay; LHE=Lower Herring Bay; WWH=west arm of Whale Bay; EWH=east arm of Whale Bay; ZAI= Zaikof Bay).

considered age-0 and Pacific herring 106–150 mm SL were considered age-1 (Fig. 2). For tows that captured more than 200 herring, total number of age-0 and age-1 herring was estimated by using length measurements from a subsample. Post measurements, some samples were frozen and sent to NOAA and USGS laboratories for additional analyses.

Due to concerns by Alaska Department of Fish and Game (ADFG) that adult herring might be overfished, we were not permitted to use the mid-water trawl for ground-truthing acoustic surveys. Therefore we used adult gillnets (60' x 16'; 3/4, 1, 1 1/4, 1 1/2"), jigs, and and castnets (6 ft; 3/16" mesh). Direct capture efforts were attempted in 2013, 2014, and 2016 and all herring given to ADFG for their age-structure model and a genetic stock study. During 2015, no direct capture efforts occurred as the focus of the cruise was on comparing two acoustic datasets. For 2013 and 2014, adult herring were measured prior to being given to ADFG but, for 2016, herring were counted, bagged, and given to ADFG unmeasured.

#### Environmental and geospatial data collection and processing

Data were obtained for a number of environmental variables based on biological rationales supporting their ability to explain juvenile herring distribution. Depth (m), temperature (°C), and salinity (psu) were collected by attaching a sensor (Model DST, Star Oddi, Gardabaer Iceland) to the trawl head rope. Measurements were collected every five seconds and mean values were calculated for each tow. Mean bottom depth (m) for each tow was calculated from the digital elevation model (DEM) developed for PWS (8/3 arc-second resolution; Caldwell et al., 2011) using the *raster* (Hijmans, 2016) and *sp* (Bivand and Pebesma, 2013) packages for R. Distance to shore was calculated as the minimum distance between tow midpoint and shoreline using the *sp* package. Locations of coastal eelgrass beds

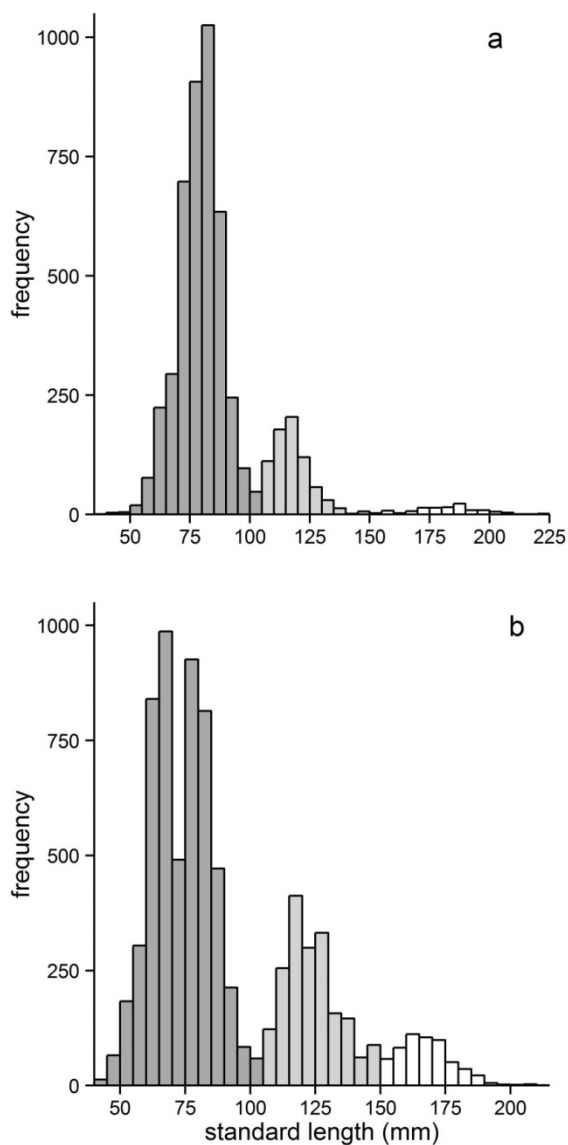


Figure 2. Frequency distribution of Pacific herring standard lengths with 5 mm bins from the Juvenile Index Survey (a) and Simpson Bay (b). Age-class was assigned based on modes in the distribution: dark grey bars are age-0 ( $\leq 105$  mm), light grey bars are age-1 (106–150 mm), and white bars are older age classes ( $> 150$  mm).

were obtained from the ShoreZone coastal mapping project (NOAA, 2016). All PWS shoreline segments with continuous (visible in  $> 50\%$  of the shoreline unit) eel grass in the nearshore subtidal zone were extracted from the ShoreZone database and the minimum distance from tow midpoints to eel grass habitat was calculated using the *sp* package.

The depths of midwater tows associated with the JIS varied substantially (7.2–35.4 m), whereas the mean temperature range was relatively narrow (8.7–11.1 °C; Fig. 3). Mean salinity had a wide range (24.1–32.3 psu), but 60% of tows were conducted in 28–30 psu. Tows were conducted 88–1,451 m from the coastline and mean bottom depth ranged from 27 to 196 m. All bays and fjords sampled contained eelgrass beds (Fig. 4), though the minimum distance between tows and eelgrass beds varied considerably (range = 111–1,699 m).

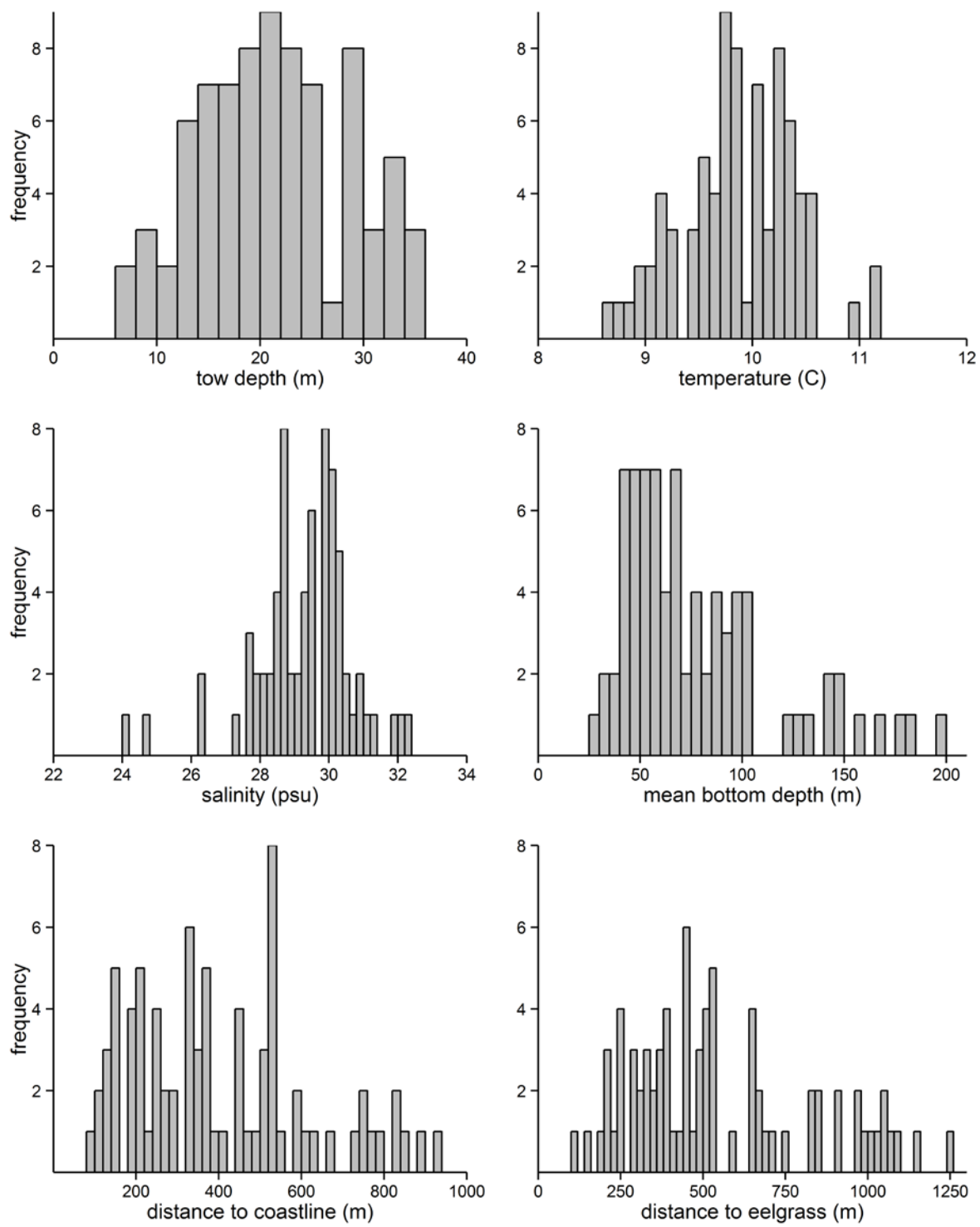


Figure 3. Frequency distribution of environmental and geospatial factors associated with tows from the Juvenile Index Survey (N=78).

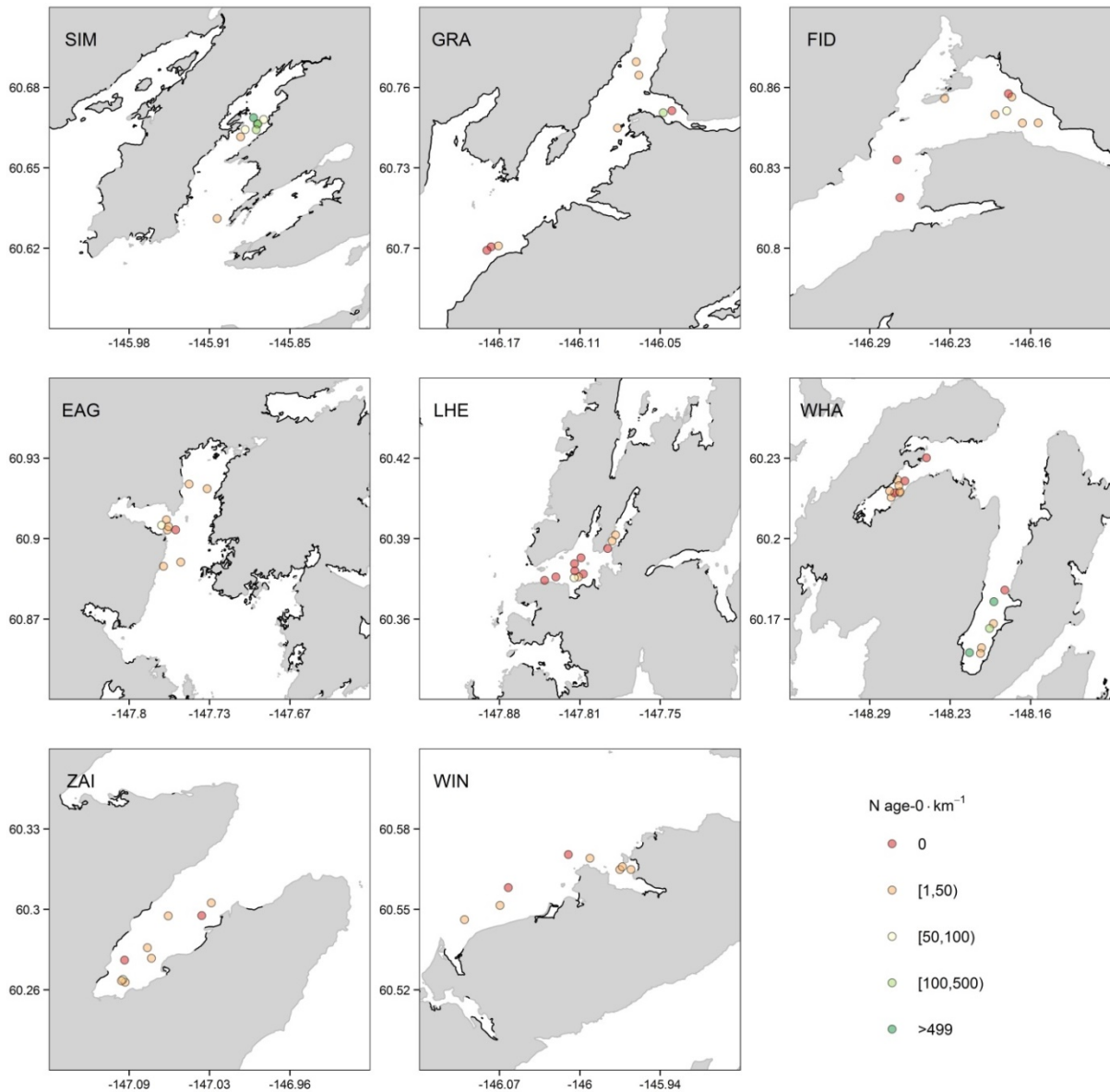


Figure 4. Maps of locations sampled during the Juvenile Index Survey depicting shoreline with eelgrass (bold shoreline), midpoints of trawl tows, and age-0 Pacific herring CPUE.

Pairwise plots between continuous covariates were generated and Pearson's correlation coefficient ( $r$ ) was calculated to examine the extent of covariance among continuous predictor variables. Distance to shore and distance to eelgrass were highly correlated ( $r = 0.73$ ) but correlations between other continuous variables were low ( $r < 0.35$ ; Dormann et al., 2013).

In Simpson Bay during winter (October 2013 through February 2014) tows were conducted at depths ranging between 10.1 and 28.4 m (mean + sd;  $18.7 + 4.2$  m) and during spring (March through April 2014) tows were conducted at depths ranging between 7.4 and 32.8 m ( $19.1 + 7.0$  m). We were interested in examining seasonal changes in distribution with this dataset, but the sample size ( $n = 50$ ) could not support a model with three continuous covariates and associated interactions with season. Therefore, changes in seasonal



distribution were investigated by partitioning Simpson bay into two regions (inner bay and outer bay) and including this spatial categorical covariate in our analyses. The inner bay region was characterized by sheltered habitat whereas the outer region was more influenced by dominant PWS circulation patterns. Our survey design was not random and CPUE may provide a biased estimate of mean density; therefore, we focus our inferences on relative comparisons of density (inner bay versus outer bay and winter versus spring). Additionally, biases in our CPUE data due to nonrandom sampling were perhaps minimal because a large number of tows were conducted in a relatively small area and spatial coverage was high (Fig. 5). Finally, during April the ice edge in Simpson Bay retreated substantially. On 6 April 2014, three tows were conducted in areas that were iced over the previous day. Catches from these three tows were compared to catches from six tows conducted during April in areas that were not recently iced over.

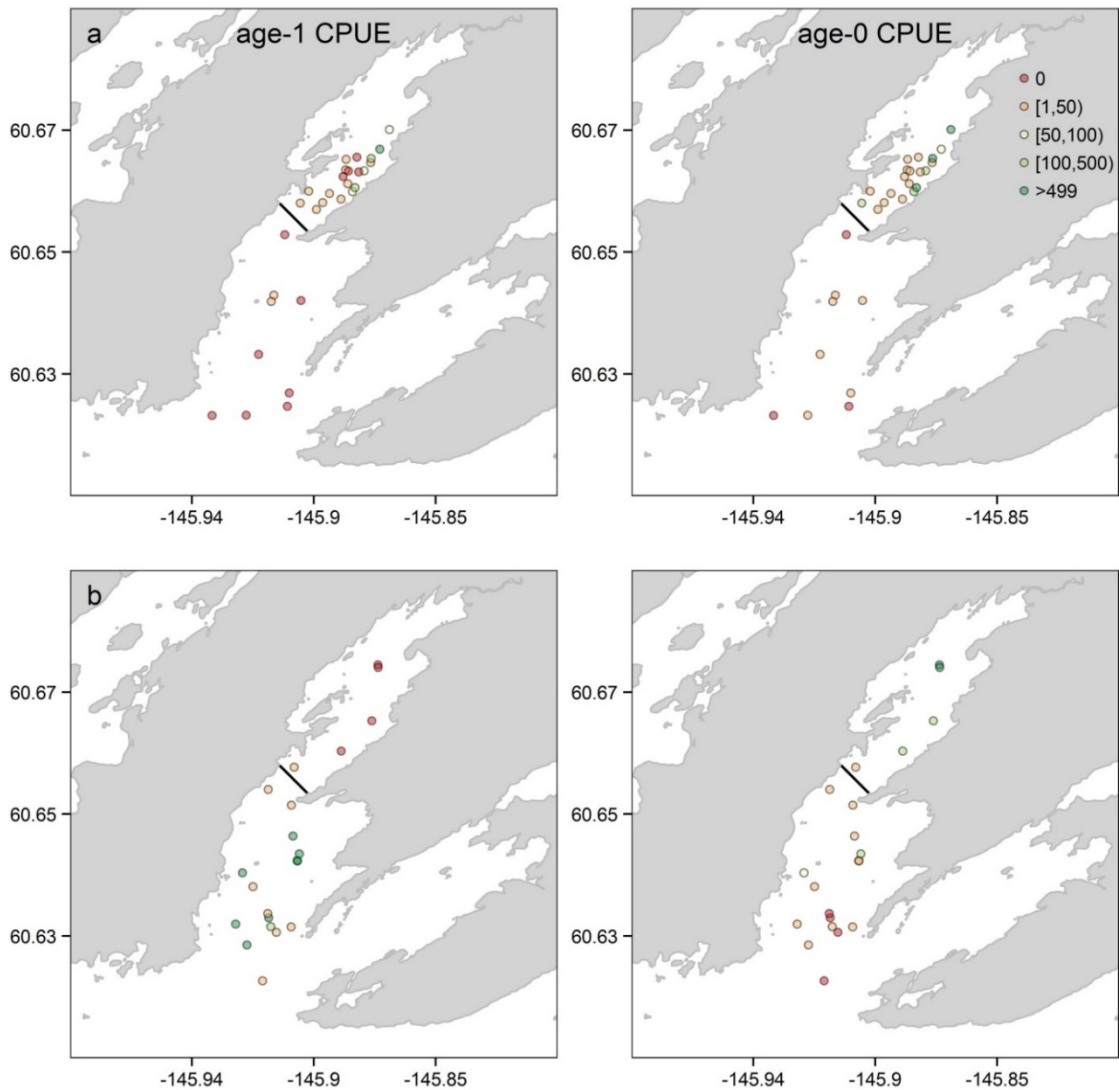


Figure 5. Midpoints of trawl tows conducted in Simpson Bay. Row (a) shows winter tows (October 2013–February 2014) and row (b) shows spring tows (March–April 2014). The inner region extends from the black line segment to the bay head and the outer region extends south to the mouth of the bay.

#### Model development and selection

After their first summer, age-0 herring exhibit schooling behavior and are not randomly distributed. Our catch data from both the JIS and from Simpson Bay were probably overdispersed based on the long tails in the frequency distributions. Therefore, we used the negative binomial distribution (Burke et al., 2013; Power and Moser, 1997) to investigate our hypotheses regarding juvenile herring distribution.

The longitudinal and spatial aspects of the JIS were accounted for by including random intercept parameters in the model for location (nine locations) and year nested within location. A nested random effect structure was used because three years of sampling were insufficient for estimating interannual variability. This simplification likely did not introduce substantial unmodeled correlation among random effects because the effect of year on catch rate was highly variable among locations.

Covariates in the JIS global model for PWS age-0 Pacific herring November distribution included salinity, temperature, tow depth, bottom depth, and either distance to shore or distance to eel grass habitat (models including both distance to shore and distance to eelgrass were excluded due to high collinearity). Additionally, catch data were standardized by including an offset term in the model for tow distance (km). Thus, model output was catch per unit effort (CPUE; n. km<sup>-1</sup>).

All reduced models that included the random intercept and offset terms were considered. Model selection was conducted using AICc (Burnham and Anderson, 2002). The model with the lowest AICc value was considered the model most parsimonious, but all models with  $\Delta AICc < 2$  were considered well supported by the data (Burnham and Anderson, 2002). All models were fit using the *glmer.nb* function from the *lme4* package (Bates et al., 2014) for R version 3.1.2 (R Core Team).

Excess zeros in ecological count data can be problematic and result in overdispersion and poor agreement between model predictions and the data. Datasets containing excess zeros can be appropriately analyzed using zero inflation or hurdle-type models (Zuur and Ieno, 2012). An approximate overdispersion parameter estimate for our global model was obtained by comparing the sum of squared Pearson residuals (SSQ) to the appropriate chi-squared distribution (residual  $df = 70$ ;  $\chi^2 = 37.1$ ;  $p = 0.99$ ). The apparently low overdispersion indicated that there were not substantial excess zeros in the data and our data were appropriately modeled using the negative binomial distribution. We further tested for excess zeros and agreement between model predictions and the data by simulating datasets ( $n=10,000$ ) from parameter estimates and random effects from the most parsimonious model and observed covariate data. The resulting mean response and 95% quantile confidence interval was plotted and visually compared to the observed data.

Our hypotheses concerning seasonal distribution patterns of age-0 and age-1 Pacific herring in Simpson Bay were investigated by developing models with parameters for tow depth, bay region (inner or outer), and season. We investigated if the spatial distribution of juvenile herring changed seasonally by including a season-bay region interaction term in the global model. For both age-0 and age-1 datasets, all reduced models were considered and model selection was conducted using AICc. Models were fit in R using the *glm.nb* function from the MASS package (Venables and Ripley, 2013).

## RESULTS

### Data overview

We collected juvenile and adult herring samples for a total of nine projects within the Prince William Sound Herring Research and Monitoring program using the mid-water trawl, gillnets, and castnets (see Table 1, Executive summary). Due to hydraulic compatibility issues between our reel/winches and the charter vessel during the initial November 2012 survey, we were unable to obtain sufficient power to successfully deploy and haul our mid-water sweeper trawl, despite several attempts at system modifications and replumbing. Therefore, within each November 2012 survey bay variable mesh adult and juvenile herring gillnets were deployed and allowed to soak overnight in areas of high acoustic signature as an alternative validation method.

Beginning in October 2013, the mid-water trawl was used for all JIS and Intensive herring surveys. From 2013-2015, within the JIS trawl dataset ( $n = 79$ ), one tow in Windy Bay was only 0.04 km and was removed from the dataset prior to analyses. Tow distance for the remaining 78 tows ranged from 0.15–2.8 km ( $0.91 \pm 0.45$  km). Measurements were obtained from 44% of herring collected during the JIS (total collected = 5,205). Based on the 105 mm maximum length criterion, 82% of the total catch was age-0 herring. Age-0 Pacific herring were captured in all nine locations sampled (7–11 trawl tows per location).

In Simpson Bay, tows were conducted during winter (October 2013 through February 2014;  $n = 29$ ) and spring (March through April 2014;  $n = 21$ ; Fig. 5). Tow distance ranged from 0.08–1.58 km ( $0.66 \pm 0.30$ ). Measurements were obtained from 45% of collected Pacific herring. Age-0 herring were most abundant (68% of total herring catch), but substantial numbers of age-1 herring were captured (25% of total herring catch).

Pacific herring was the most prevalent fish species captured in trawl tows (85.3% of total fish catch). A substantial percent of total fish catch was composed of other forage fishes including walleye pollock (11.6%) and capelin (2.3%). In addition to fish species, tows often captured high numbers of cnidarians and ctenophores. By weight, these invertebrate species made up 80.9% of the total biomass captured in trawl tows.

Direct captures using gillnets, jigs, and castnets associated with the spring, expanded adult herring surveys were limited in 2013 and 2014. In 2013, a total of 317 herring were captured and measured ( $SL = 210.4 \pm 19.9$  mm,  $mass = 125.8 \pm 43.9$  g). In 2014, only 92 adult herring were captured ( $SL = 221.9 \pm 20.2$  mm;  $mass = 137.6 \pm 37.7$  g). In 2016, a total of 1,625 herring were captured in gillnets and given directly to ADFG.

### Age-0 CPUE in PWS

The most supported model for PWS age-0 Pacific herring November distribution (JIS dataset) contained parameters for tow depth, salinity, and distance from eelgrass beds (Table 2). Furthermore, models with an additional parameter for water temperature ( $\Delta AIC_c = 1.44$ ) or bottom depth ( $\Delta AIC_c = 1.70$ ) were well supported by the data. All other models were not well supported by the data ( $\Delta AIC_c > 2$ ; Table 2).

Based on parameter estimates from the most supported model, juvenile herring CPUE in PWS was strongly associated with tow depth ( $p = 0.001$ ). Our hypothesis that age-0 Pacific herring tend to occupy shallow depths at night was supported; a 1-m increase in mean tow depth was associated with an 11% decrease in CPUE (95% CI: 4-17% decrease). Additionally, salinity was strongly associated with CPUE ( $p = 0.013$ ). Age-0 Pacific herring

Table 2. Model selection results for age-0 Pacific herring catches from the Juvenile Index Survey. All models contain two random intercepts (location and year nested within location) and an offset term for tow distance. Only models with  $\Delta AIC_c < 4$  are listed.

model	df	log likelihood	AIC <sub>c</sub>	$\Delta AIC_c$
tow depth + salinity + dist2ZOS	7	-285.89	587.37	0
tow depth + salinity + temperature + dist2ZOS	8	-285.36	588.82	1.44
bottom depth + tow depth + salinity + dist2ZOS	8	-285.50	589.01	1.70
bottom depth + tow depth + salinity	7	-287.26	590.12	2.75
bottom depth + tow depth + salinity + temperature + dist2ZOS	9	-285.01	590.67	3.30
tow depth + salinity	6	-288.91	591.00	3.63
tow depth + dist2ZOS	6	-288.97	591.11	3.74
bottom depth + tow depth + salinity + temperature	8	-286.60	591.29	3.92
bottom depth + tow depth	6	-289.09	591.37	3.99

densities were higher in fresher water and a 0.1 psu increase in salinity was associated with a 5% decrease in catch rate (95% CI: 1-9% decrease). Finally, CPUE was strongly associated with minimum distance to eelgrass beds ( $p = 0.014$ ). A 100 m increase in distance from eelgrass was associated with an 18% decrease in CPUE (95% CI: 4–30% decrease). Juvenile herring were patchily distributed in the pelagic environment and the count distribution of catches from the JIS had a long tail. While the maximum catch was 1,410 age-0 herring, 71 trawls (90%) contained 0–82 fish. However, based on simulation results, this overdispersion was accounted for by the negative binomial distribution and the model fit the catch reasonably well, although the model tended to over-predict the frequency of catches containing 10–20 age-0 herring (Fig. 6). The observed proportion of zero catches (0.28) was similar to simulated proportions of zero catches (median = 0.28, 95% CI: 0.20–0.38) indicating that the data were adequately modeled without including a zero-inflation component.

#### Age-0 and age-1 seasonal CPUE in Simpson Bay

The most supported model for Simpson Bay age-0 CPUE included bay region, season, and tow depth (Table 3). However, a model without a season parameter was also well supported by the data ( $\Delta AIC_c = 0.39$ ). For age-1 CPUE, the most supported model included bay region, season, and an interaction parameter between bay region and season (Table 3). An additional parameter for tow depth was also included in a model well-supported by the data ( $\Delta AIC_c = 0.93$ ). Finally, all age-1 CPUE models without a bay region-season interaction parameter were poorly supported by the data ( $\Delta AIC_c > 10$ ). The most parsimonious models were used for making inferences about age-0 and age-1 Pacific herring CPUE.

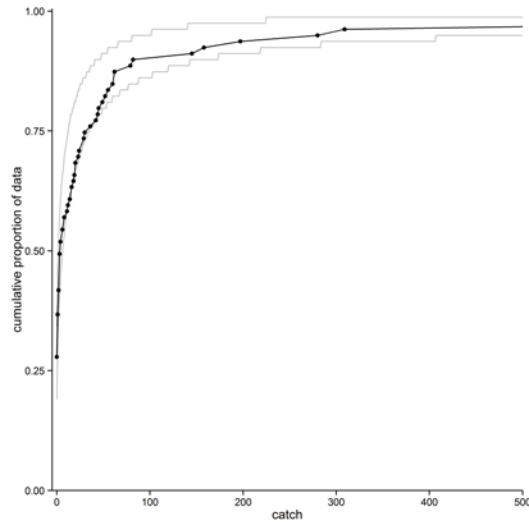


Figure 6. Observed catch data (black points) compared to expected values from the most supported model for age-0 CPUE in PWS. The 95% quantile confidence interval (grey lines) was calculated from 10,000 simulated datasets. Two observed catch values (744 and 1410) are not shown.

Table 3. Model selection results for Simpson Bay juvenile Pacific herring catch data. Region is location within Simpson Bay and season is a categorical covariate with two levels, winter (October–February) and spring (March–April).

age class	model	df	log likelihood	AIC <sub>c</sub>	Δ AIC <sub>c</sub>
age-0	region + season + tow depth	5	-213.84	439.04	0.00
	region + tow depth	4	-215.27	439.42	0.39
	region * season + tow depth	6	-213.84	441.63	2.59
	region + season	4	-217.43	443.74	4.71
	region * season	5	-216.60	444.57	5.53
	season + tow depth	4	-223.44	455.77	16.74
	region	3	-224.66	455.84	16.80
	tow depth	3	-224.78	456.09	17.05
	season + tow depth	3	-235.45	477.42	38.38
age-1	intercept only	2	-239.03	482.31	43.28
	region * season	5	-186.11	383.58	0.00
	region * season + tow depth	6	-185.28	384.51	0.93
	region + season	4	-195.50	399.89	16.31
	season	3	-197.13	400.78	17.20
	intercept only	2	-198.31	400.87	17.29
	region + season + tow depth	5	-195.07	401.51	17.92
	region	3	-197.82	402.17	18.59
	season + tow depth	4	-196.68	402.24	18.66
	tow depth	3	-197.90	402.33	18.75
	region + tow depth	4	-197.39	403.68	20.09

Similar to the relationship detected in the JIS dataset, CPUE of age-0 Pacific herring in Simpson Bay was negatively associated with tow depth ( $p < 0.001$ ). A 1- m increase in tow depth was associated with a 15% decrease in CPUE (95% CI: 5-25% decrease). Tow depth was not strongly associated with age-1 CPUE. After accounting for tow depth, mean age-0 CPUE in the inner bay was higher than outer bay CPUE during both winter and spring (Fig. 7). For both inner and outer bay regions, age-0 mean CPUE was higher in spring than in winter, although 95% confidence intervals overlapped (Fig 7). The relationship between bay region and age-1 CPUE varied seasonally. Mean age-1 CPUE in the inner bay was higher than outer bay CPUE during winter whereas, during spring, mean age-1 CPUE was highest in the outer bay (Fig. 7).

Within the Simpson Bay inner bay region, the CPUE of age-0 and age-1 Pacific herring were influenced by ice cover. CPUE of age-0 Pacific herring tended to be higher in the recently ice-covered locations ( $7,357 \pm 6,433$ ;  $n = 3$ ) compared to open water locations ( $29 \pm 40$ ;  $n = 6$ ), whereas CPUE of age-1 herring tended to be lower in recently ice-covered locations ( $0$ ;  $n = 3$ ) compared to open water locations ( $185 \pm 129$ ,  $n = 6$ ).

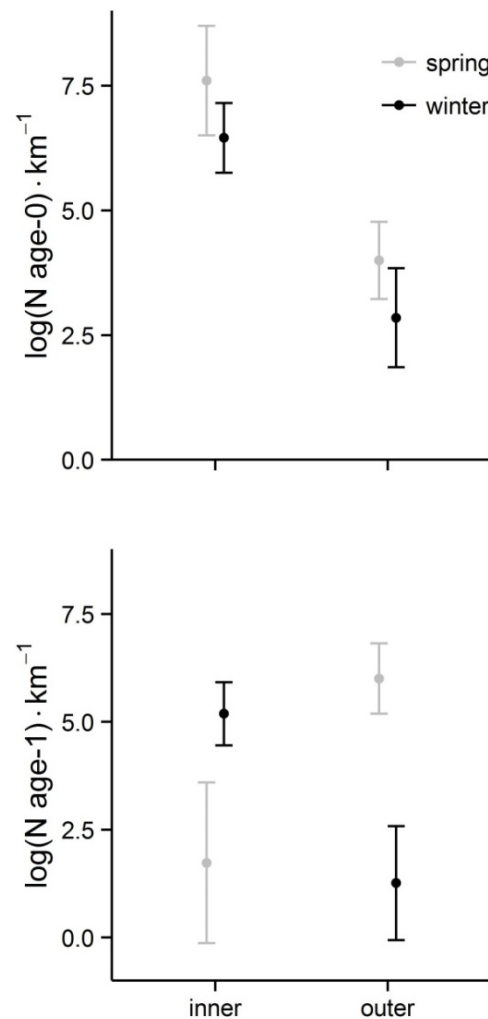


Figure 7. Mean CPUE of age-0 and age-1 Pacific herring in the inner and outer regions of Simpson Bay during winter (October–February) and spring (March–April). Age-0 CPUE at 19 m tow depth (median tow depth from out dataset) is shown. Error bars depict 95% confidence intervals.

## DISCUSSION

### Juvenile herring distribution patterns

We determined that age-0 Pacific herring densities in PWS bays and fjords were positively associated with both eelgrass habitat and lower salinity pelagic waters during November. Additionally, we found that deeper tows tended to catch fewer age-0 herring. Thus, over the range of depths sampled (7.2–35.4 m) age-0 herring appear to preferentially occupy more shallow depths during the night. This conclusion was corroborated by our analyses of winter and spring age-0 catch data from Simpson Bay. Within Simpson Bay no strong association between age-1 CPUE and depth was detected, indicating that older juveniles were more evenly distributed in the midwater column at night compared to age-0 juveniles.

Within Simpson Bay, the distribution patterns of age-0 and age-1 were similar during winter (October–February). However, age-0 Pacific herring tended to inhabit areas near the head of the bay during spring (March–April), whereas age-1 herring tended to inhabit less sheltered areas toward the mouth of the bay. We predicted high age-0 CPUE in the outer bay region during the spring based on previous documentation of juvenile herring distribution patterns (Stokesbury et al. 2000), but this pattern was not observed in this study. Age-0 CPUE in the outer bay region remained lower than age-0 CPUE in the inner bay region during the spring. Additionally, our prediction that age-1 CPUE would be higher in the outer bay region during both seasons was not supported; age-1 CPUE during the winter was highest in the inner bay region.

### Environmental and geospatial factors

Portions of Simpson Bay were ice covered from February through April, limiting our ability to sample near the head of the bay during this time. However, prior to ice cover and immediately after breakup we documented high age-0 CPUE in the inner bay region. Furthermore, tows conducted in non-ice covered areas during April had relatively low catches of age-0 herring, whereas tows conducted in locations that were previously iced over (tows were conducted within 24 hours of ice breakup) had high catches of age-0 herring. This pattern could have been caused by age-0 Pacific herring preferentially selecting ice covered habitats within nursery areas or by higher age-0 survival rates in ice covered habitats compared to open water habitats. Ice covered habitat may facilitate high overwinter juvenile Pacific herring survival by providing cover from avian and marine mammal predators and cool, stable water temperatures optimal for lowering energy expenditure during forage-limited winter periods (Foy and Norcross 2000; Gay and Vaughan 2001). Inability to sample in ice-covered habitat with the midwater trawl and low sample size prevented rigorous exploration of this observation, but further investigations into the effects of ice cover on juvenile Pacific herring behavior and survival are warranted.

Catch rates of age-0 Pacific herring were higher in shallower tows, indicating that age-0 Pacific herring are not evenly distributed in the upper water column at night. Diel vertical migration is common among clupeids and is thought to be linked with swimbladder inflation via gulping air at the surface (Thorne and Thomas 1990), predator avoidance, bioenergetics optimization, and tracking diel vertical migration of zooplankton (Cardinale et al. 2003). Gulping air at the surface at night prior to descent may confer an energetic advantage by allowing juvenile herring to be neutrally buoyant at deep depths during the day (Thorne and Thomas 1990). Furthermore, juvenile herring swimbladder gas can be lost through diffusion in 2–3 days (Blaxter and Batty 1984) and therefore individuals remaining at constant depth would also require periodic gas input to achieve neutral buoyancy. Based on

this previous research, intake of swimbladder gas may be a physiological driver of vertical migratory behavior of age-0 Pacific herring. The zooplankton tracking hypothesis may further explain our documented association between age-0 Pacific herring and water depth. Age-0 Pacific herring forage primarily on euphausiids and calanoids during autumn (October–November) in PWS (Sturdevant et al. 2000) and the nocturnal density of several species of euphausiids (*Thysanoessa spinifera*, *Thysanoessa inermis*, *Euphausia pacifica*, *Thysanoessa longpipes*) and calanoids (*Neocalanus plumchrus*, *Neocalanus flemingeri*, and *Metridia pacifica*) was highest at 0–20 m depth in the northern Gulf of Alaska (Coyle and Pinchuk 2005). However, herring feeding is limited in PWS during winter (December–March) and, therefore, physiological and energetic factors may be the dominant drivers of herring distribution in the winter (Foy and Norcross 2001).

Age-0 Pacific herring in PWS tended to congregate in areas with lower salinity. Similar patterns have been documented in Pacific herring populations elsewhere in Alaska. Within Cook Inlet, AK, summertime juvenile Pacific herring catch rates were higher in the sheltered inner bay with low salinity surface compared to the outer bay with higher salinity and little stratification (Abookire et al. 2000). This documented association with fresher water could be a result of juvenile Pacific herring using salinity as an environmental cue to modify their behavior. Salinity cues are a hypothesized mechanism for orienting estuarine larval and juvenile fishes to presumably high quality nursery habitat (Boehlert and Mundy 1988). Thus, the observed tendency of age-0 herring to congregate in fresher water could be a result of an evolved behavioral mechanism that facilitates movement towards estuarine habitat with environmental conditions favorable for survival. Furthermore, salinity itself can influence habitat quality. Fishes inhabiting saline conditions above or below optimal conditions can expend between 10–50% of their energy budget on osmoregulation (Boeuf and Payan 2001). Additionally, feeding behavior, growth, and food conversion rates are influenced by salinity (Boeuf and Payan 2001).

Age-0 Pacific herring have been documented in nearshore eelgrass habitat during the summer (Johnson et al. 2010), but our results indicate that shoreline habitat also influences their distribution in the pelagic environment during the winter. A possible explanation for this distribution pattern is that environmental conditions favorable to the formation of eelgrass beds are also favorable to age-0 herring survival. Eelgrass beds are an indicator of sheltered coastlines with little wave influence (Harper and Morris 2011); therefore, the pelagic conditions near shorelines containing eelgrass beds may promote age-0 herring survival or retention. Alternatively, this distribution pattern could be due to nocturnal migrations from nearshore eelgrass habitat into the pelagic environment. Herring may inhabit sheltered eelgrass habitat during the day to minimize predation risk and migrate into the pelagic environment at night to feed when they are less vulnerable to visually oriented predators. Herring are adapted to filter feeding in low-light conditions using gill rakers (Batty et al. 1990). In clupeids, filter feeding requires less energy output than visual foraging and is an important feeding strategy when forage is limited. Thus, inhabiting the pelagic environment during the night and sheltered eelgrass habitat during the day could be a strategy for optimizing growth while minimizing predation risk.

Our data did not strongly support a relationship between juvenile Pacific herring density and temperature. However, Pacific herring recruitment was found to be correlated with sea surface temperature (Williams and Quinn 2000) and Pacific herring CPUE was influenced by large-scale temperature regimes in the Bering Sea (Andrews et al. 2015). Moreover, temperature is an important regulator of metabolism (Clarke and Fraser 2004) and can influence the development and survival of pelagic fishes during early life history stages (Pepin 1991). Thus, water temperature is likely an important environmental factor driving



the distribution juvenile herring, but relatively homogenous temperatures among trawl tows (8.7–11.1 °C) likely limited our power to detect an association between juvenile herring density and temperature. Sampling across a wider temperature gradient could further our understanding of how temperature influences the distribution of age-0 Pacific herring.

#### Future research and management implications

Modeling differences in age-0 herring densities among nursery areas as a random effect was an effective way to account for spatial correlation in our data and investigate juvenile herring habitat preferences. However, we did not explore the causes of variability among nursery areas because trawl data alone from the JIS survey was not intended to provide unbiased estimates of density. Tows were targeted to regions of high abundance and therefore mean density within each nursery area may have not been linearly related to CPUE. Further investigations into associations among biological and environmental factors and larval recruitment (either by local retention or larval drift), age-0 survivorship, and juvenile movement between nursery areas would help researchers develop a holistic understanding of recruitment dynamics in PWS. Larval drift models (Werner et al. 1997; Norcross et al 2001) and a more extensive empirical juvenile herring distribution dataset could be used to test hypotheses relating larval recruitment, age-0 survivorship, and juvenile movements to large-scale distribution patterns.

Density indices of age-0 Pacific herring can be a useful tool for forecasting recruitment to the spawning stock (Schweigert et al. 2009). However, a key assumption of this approach is that catch data can provide an unbiased estimate of age-0 Pacific herring density. We suggest that Pacific herring recruitment indices based on catch data should incorporate habitat preferences because our results indicate that habitat characteristics influence age-0 Pacific herring distribution. Exclusion of relevant habitat related covariates in the development of population-level density indices from catch data can lead to misinterpretations of abundance trends (Bigelow and Maunder 2007) and, as a result, year-class strength predictions. Some associations we detected (tow depth, distance from eelgrass beds, region within bay) can be accounted for by standardization of survey transect locations and depths among years. However, salinity, a more ephemeral habitat characteristic, may not be adequately accounted for by standardized survey transects. Based on documented associations between age-0 density and habitat characteristics, we suggest that standardized survey transects and collection of in situ environmental data can facilitate development of more robust Pacific herring recruitment indices from age-0 catch data.

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## LITERATURE CITED

- Abookire, A.A., Piatt, J.F., Robards, M.D., 2000. Nearshore fish distributions in an Alaskan estuary in relation to stratification, temperature and salinity. *Estuar. Coast. Shelf Sci.* 51, 45–59.
- Andrews, A.G., Strasburger, W.W., Farley, E.V., Murphy, J.M., Coyle, K.O., 2015. Effects of warm and cold climate conditions on capelin (*Mallotus villosus*) and Pacific herring (*Clupea pallasii*) in the eastern Bering Sea. *Deep-Sea Res. Pt. II: Top. Stud. Ocean* <http://dx.doi.org/10.1016/j.dsr2.2015.10.008i>.
- Bates, D., Mächler, M., Bolker, B., Walker, S., 2014. Fitting linear mixed-effects models using lme4. *arXiv preprint arXiv:1406.5823*.
- Batty, R.S., Blaxter, J.H.S., Richard, J.M., 1990. Light intensity and the feeding behaviour of herring, *Clupea harengus*. *Mar. Biol.* 107, 383–388.
- Bigelow, K.A., Maunder, M.N., 2007. Does habitat or depth influence catch rates of pelagic species? *Can. J. Fish. Aquat. Sci.* 64, 1581–1594.
- Bivand, R.S., Pebesma, E.J., Gomez-Rubio, V., 2008. *Applied spatial data analysis with R*. Springer-Verlag, New York.
- Blaxter, J.H.S., Batty, R.S., 1984. The herring swimbladder: loss and gain of gas. *J. of the Mar. Bio. Ass. of the U. K.* 64, 441–459.
- Boehlert, G.W., Mundy, B.C., 1988. Roles of behavioral and physical factors in larval and juvenile fish recruitment to estuarine nursery areas, in: *Am. Fish. Soc. Symp.* 3(5), 1–67.
- Boeuf, G., Payan, P., 2001. How should salinity influence fish growth? *Comp. Biochem. Phys. C* 130, 411–423.
- Burke, B.J., Liermann, M.C., Teel, D.J., Anderson, J.J., Fleming, I., 2013. Environmental and geospatial factors drive juvenile Chinook salmon distribution during early ocean migration. *Can. J. Fish. Aquat. Sci.* 70, 1167–1177.
- Burnham, K.P., Anderson, D.R., 2003. *Model selection and multimodel inference: a practical information-theoretic approach*. Springer-Verlag, New York.
- Caldwell, R.J., Eakins, B.W., Lim, E., 2011. *Digital Elevation Models of Prince William Sound, Alaska: Procedures, Data Sources, and Analysis*. NOAA Marine Geology and Geophysics Division., National Geophysical Data Center, Tech. Memorandum NESDIS NGDC-40, <http://www.ngdc.noaa.gov/dem/squareCellGrid/getReport/735>.
- Cardinale, M., Casini, M., Arrhenius, F., Haakansson, N., 2003. Diel spatial distribution and feeding activity of herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) in the Baltic Sea. *Aquat. Liv. Res.* 16, 283–292.
- Clarke, A., Fraser, K.P.P., 2004. Why does metabolism scale with temperature? *Funct. Ecol.* 18, 243–251.
- Coyle, K.O., Pinchuk, A.I., 2005. Seasonal cross-shelf distribution of major zooplankton taxa on the northern Gulf of Alaska shelf relative to water mass properties, species depth preferences and vertical migration behavior. *Deep Sea Res. Part II: Topical Studies in Oceanogr.* 52, 217–245.
- Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., others, 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36, 27–46.
- Foy, R.J. and Norcross, B.L., 2001. Temperature effects on zooplankton assemblages and juvenile herring feeding in Prince William Sound, Alaska. *Herring: expectations for a new millennium*. Edited by F. Funk, J. Blackburn, D. Hay, AJ Paul, R. Stephensen, R. Toreson, and D. Witherell. University of Alaska Sea Grant AK-SG-01-04, Fairbanks, pp.21-35.

- Gay, S., Vaughan, S.L., 2001. Seasonal hydrography and tidal currents of bays and fjords in Prince William Sound, Alaska. *Fish. Oceanogr.* 10, 159–193.
- Harper, J.R., Morris, M.C., 2011. Alaska ShoreZone coastal habitat mapping protocol. Nuka Research and Planning LCC of Seldovia, Alaska for the Bureau of Ocean Energy Management (BOEM), Anchorage, AK.
- Hijmans, R.J., 2016. Introduction to the ‘raster’ package, 1-27.
- Johnson, S.W., Thedinga, J.F., Neff, A.D., Harris, P.M., Lindeberg, M.R., Maselko, J.M., Rice, S.D., 2010. Fish assemblages in nearshore habitats of Prince William Sound, Alaska. *Northwest Sci.* 84, 266–280.
- Molnia, 2001. *Glaciers of Alaska: Alaska Geographic* 28.
- NOAA, 2016. Alaska ShoreZone Coastal Mapping and Imagery, accessed 3 March 2016, <<https://alaskafisheries.noaa.gov/habitat/shorezone>>.
- Niebauer, H.J., Royer, T.C., Weingartner, T.J., 1994. Circulation of Prince William Sound, Alaska. *J. Geophys. Res.: Oceans* 99, 14113–14126.
- Norcross, B.L., Brown, E.D., Foy, R.J., Frandsen, M., Gay, S.M., Kline, T.C., Mason, D.M., Patrick, E.V., Paul, A.J., Stokesbury, K.D., 2001. A synthesis of the life history and ecology of juvenile Pacific herring in Prince William Sound, Alaska. *Fish. Oceanogr.* 10, 42–57.
- Pepin, P., 1991. Effect of temperature and size on development, mortality, and survival rates of the pelagic early life history stages of marine fish. *Can. J. Fish. Aquat. Sci.* 48, 503–518.
- Power, J.H., Moser, E.B., 1999. Linear model analysis of net catch data using the negative binomial distribution. *Can. J. Fish. Aquat. Sci.* 56, 191–200.
- R Core Team, 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Schweigert, J.F., Hay, D.E., Theriault, T.W., Thompson, M., Haegele, C.W., 2009. Recruitment forecasting using indices of young-of-the-year Pacific herring (*Clupea pallasii*) abundance in the Strait of Georgia (BC). *ICES J. Mar. Sci.* 66, 1681–1687.
- Sturdevant, M.V., Brase, A.L., Hulbert, L.B., 2001. Feeding habits, prey fields, and potential competition of young-of-the-year walleye pollock (*Theragra chalcogramma*) and Pacific herring (*Clupea pallasii*) in Prince William Sound, Alaska, 1994-1995. *Fish. Bull.* 99, 482–482.
- Stokesbury, K.D.E., Kirsch, J., Brown, E.D., Thomas, G.L., Norcross, B.L., 2000. Spatial distributions of Pacific herring, *Clupea pallasii*, and walleye pollock, *Theragra chalcogramma*, in Prince William Sound, Alaska. *Fish. Bull.* 98, 400–409.
- Thorne, R.E., Thomas, G.L., 1990. Acoustic observations of gas bubble release by Pacific herring (*Clupea harengus pallasii*). *Can. J. of Fish. and Aquat. Sci.* 47, 1920–1928.
- Venables, W.N., Ripley, B.D., 2013. *Modern applied statistics with S-PLUS*. Springer-Verlag, New York.
- Wang, J., Jin, M., Patrick, E.V., Allen, J.R., Eslinger, D.L., Mooers, C.N., Cooney, R.T., 2001. Numerical simulations of the seasonal circulation patterns and thermohaline structures of Prince William Sound, Alaska. *Fish. Oceanogr.* 10, 132–148.
- Werner, F.E., Quinlan, J.A., Blanton, B.O., Luettich, R.A., 1997. The role of hydrodynamics in explaining variability in fish populations. *J. Sea Res.* 37, 195–212.
- Williams, E.H., Quinn II, T.J., 2000. Pacific herring, *Clupea pallasii*, recruitment in the Bering Sea and north-east Pacific Ocean, II: relationships to environmental variables and implications for forecasting. *Fish. Oceanogr.* 9, 300-315.
- Zuur, A.F.S., Ieno, A.A., Ieno, 2012. *Zero inflated models and generalized linear mixed models with R*. Highland Statistics. Newburgh, Scotland, UK