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

Validation of Acoustic Surveys for Pacific Herring (*Clupea pallasii*) Using Direct Capture

Exxon Valdez Oil Spill Trustee Council Project 16120111-A

Final Report

Mary Anne Bishop
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Study History: This project was approved for funding by the *Exxon Valdez* Oil Spill Trustee Council in October 2011 as part of the Herring Research and Monitoring Program (project 16120111) and fieldwork commenced in November 2012. Our project's direct capture efforts were associated with two Herring Research and Monitoring Program's acoustic survey projects: Projects 16120111-F (November 2012-2016) and 16120111-E (March and April 2013-2016). We also conducted a series of trawls associated with two other Herring Research and Monitoring projects: projects 15120111-G (October 2013 – April 2014) and a short, pilot study *Integrated marine bird/humpback whale/forage fish survey at Montague Strait* (September 2014), a collaborative effort of three projects in the *Exxon Valdez* Oil Spill Trustee Council's Gulf Watch Alaska pelagic program (14120114, projects C, N, and O). 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 during the first 5-year program (2012-2016).

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. 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). 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). 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 trawls also provided fishery-independent surveys for non-herring species, thus increasing our knowledge of pelagic fishes in Prince William Sound.

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

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

doi citation:
Mary Anne Bishop. 2017. Validation of Acoustic Surveys for Pacific Herring, 2010-2016: EVOS Herring Program. Research Workspace. 10.24431/rw1k1a.

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Alaska Ocean Observing System. 1007 W. 3rd Ave. #100, Anchorage, AK 99501, 907-644-6703. http://www.aoos.org

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.

Citation:
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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 herring population has not had a strong recruitment class since 1989, when the *Exxon Valdez* Oil Spill occurred. In the *Exxon Valdez* Oil Spill settlement, herring were identified as an injured resource and they remain listed as an unrecovered species by the *Exxon Valdez* Oil Spill Trustee Council. 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.

This project was a five-year process study that addresses Objective 3 of the Herring Research and Monitoring Program*: to address assumptions in the current measurements*. The goals of this project are twofold: 1) ground truth acoustic backscatter to confirm species composition and length frequency of insonified targets; and 2) provide fish samples to other Herring Research and Monitoring projects.

Objectives specific to this project 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 Herring Research and Monitoring acoustic survey projects: Projects 16120111-F (November 2012-2016; Rand 2018a) and 15120111-G (October 2013-April 2014; Rand 2018b). We also conducted trawls for a pilot study *Integrated marine bird/humpback whale/forage fish survey at Montague Strait* (September 2014), which was a collaborative effort of three projects in the *Exxon Valdez* Oil Spill Trustee Council's Gulf Watch Alaska pelagic program (14120114, projects C, N, and O).

For the direct capture efforts associated with adult herring acoustic surveys conducted during March and April 2013-2016 (Project 16120111-E; Rand and Thorne 2017), 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 Programs, including projects 13120111-J, 14120111-J, 15120111-P, and 16120111- K and L.

Using trawl data collected in conjunction with November juvenile herring surveys (Project 16120111-F; Rand 2018a), 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 (project 15120111-G; Rand 2018b), we documented seasonal changes in juvenile herring data distribution across a seven-month period (October 2013-April 2014). 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. We discovered that 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. Detailed results are reported in Lewandoski and Bishop (2018), which is included as Appendix A in this report.

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 PWS 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.

This project was a five-year process study that addresses Objective 3 of the Herring Research and Monitoring (HRM) Program*: to address assumptions in the current measurements*. The goals of this project are twofold: 1) ground truth acoustic backscatter to confirm species composition and length frequency of insonified targets; and 2) provide fish samples to other HRM projects.

Previous juvenile herring acoustic surveys (Project 12100132-B; 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 one 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

Objectives specific to this 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 (ADF&G) for the adult herring age-structure-analyses model.

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).

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 GOA 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 2013-2016 in association with Project 16120111-F (Rand 2018a) acoustic surveys: Windy Bay, Simpson Bay, Port Gravina, Port Fidalgo, Eaglek Bay, Lower Herring Bay, Whale Bay (east and west arm), and Zaikof Bay (Fig. 1). Simpson Bay was sampled additionally between 3 October and 6 December 2013 (three cruises) and between 21 February through 6 April 2014 (four cruises) as part of Project 15120111-G (Rand 2018b). 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.

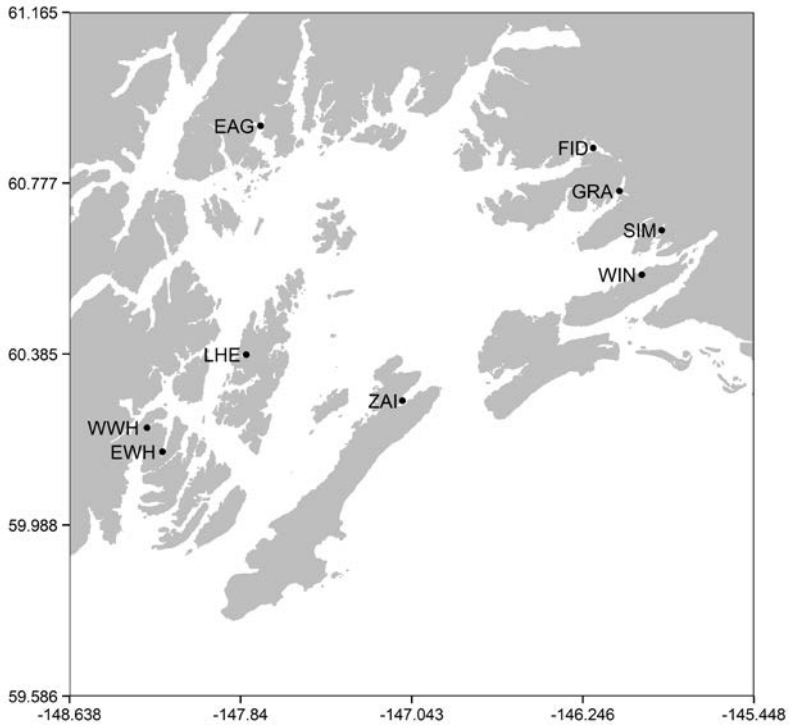

Figure 1. Map of Prince William Sound depicting the locations of juvenile herring surveys (SIM=Simpson Bay; GRA=Port Gravina; FID=Port Fidalgo; EAG=Eaglek Bay; LHE=Lower Herring Bay; WWH=west arm of Whale Bay; EWH=east arm of Whale Bay; ZAI= Zaikof Bay).

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 HRM 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 for standard length (SL), fork length (FL), and total length (TL) and weighed 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 collected in association with Projects 15120111-G and 16120111-F. All Pacific herring that measured ≤105 mm (SL) were 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 National Oceanic and Atmospheric Administration (NOAA) and US Geological Survey (USGS) laboratories for additional analyses (Table 1).

Due to concerns by ADF&G 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 ¼, 1 ½"), jigs, and castnets (6 ft; 3/16" mesh). Direct capture efforts were attempted in 2013, 2014, and 2016 and all herring given to ADF&G for their age-structure model project 16160111-T) and a genetic stock study (project 15120111-P).

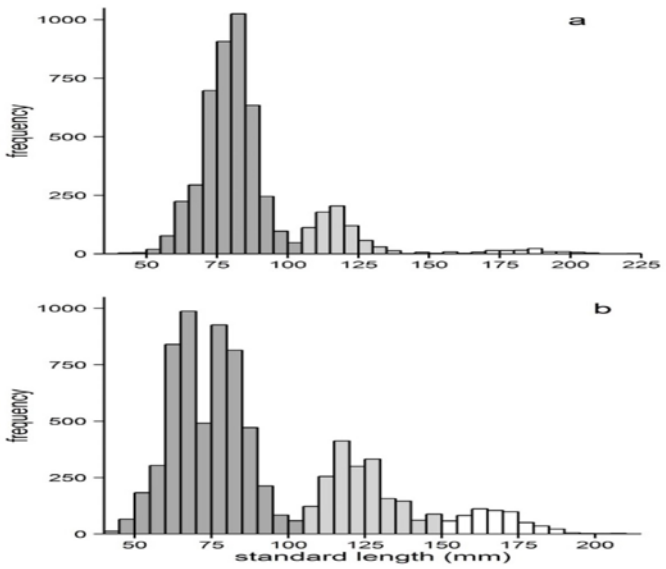

Figure 2. Frequency distribution of Pacific herring standard lengths with 5 mm bins from nine sites November 2013-2015(a) and only Simpson Bay October 2013-April 2014 (b). Age-class was assigned based on modes in the distribution of standard length measurements: dark grey bars are age-0 (≤105 mm), light grey bars are age-1 (106–150 mm), and white bars are older age classes (>150 mm).

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

EVOS Herring Research	**Restoration Project No.**	**Agency**	**Samples provided**
Juvenile herring abundance index	1612011-F	PWS Science Center	All species – measurements only
Juvenile herring intensive acoustic surveys	1512011-G	PWS Science Center	All species – measurements only
Expanded adult herring acoustic surveys	1612011-E	PWS Science Center	All species – measurements only
Condition index	1612011-L	PWS Science Center	Juvenile herring
Genetic stock structure	1512011-P	ADF&G	Adult herring
Age structure	16160111-T	ADF&G	Adult herring
Disease	1612011-K	USGS	Juvenile herring
Energetics	16120111-L	NOAA Auke Bay	Juvenile herring/walleye pollock
Growth RNA/DNA	13120111-J	NOAA Auke Bay	Juvenile herring
Age at first spawn	1412011-J	NOAA Auke Bay	Adult herring

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 ADF&G but, in 2016, herring were counted, bagged, and given to ADF&G unmeasured.

Environmental and geospatial data collection and data analysis

Data were obtained for a number of environmental variables based on biological rationales supporting their ability to explain juvenile herring distribution (Stokesbury et al., 2000). Depth (m), temperature (^{o}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 et al. 2008) 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 were obtained from the ShoreZone coastal mapping project (NOAA 2016). All PWS shoreline segments with continuous (visible in >50% of the shoreline unit) eelgrass in the nearshore subtidal zone were extracted from the ShoreZone database and the minimum distance from tow midpoints to eelgrass habitat was calculated using the *sp* package.

The depths of midwater tows conducted in all the sites in November 2013-2015 surveys varied substantially (7.2–35.4 m), whereas the mean temperature range was relatively narrow (8.7–11.1 ^{o}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). 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 + 1SD; 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 focused 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 2014 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 2014 in areas that were not recently iced over.

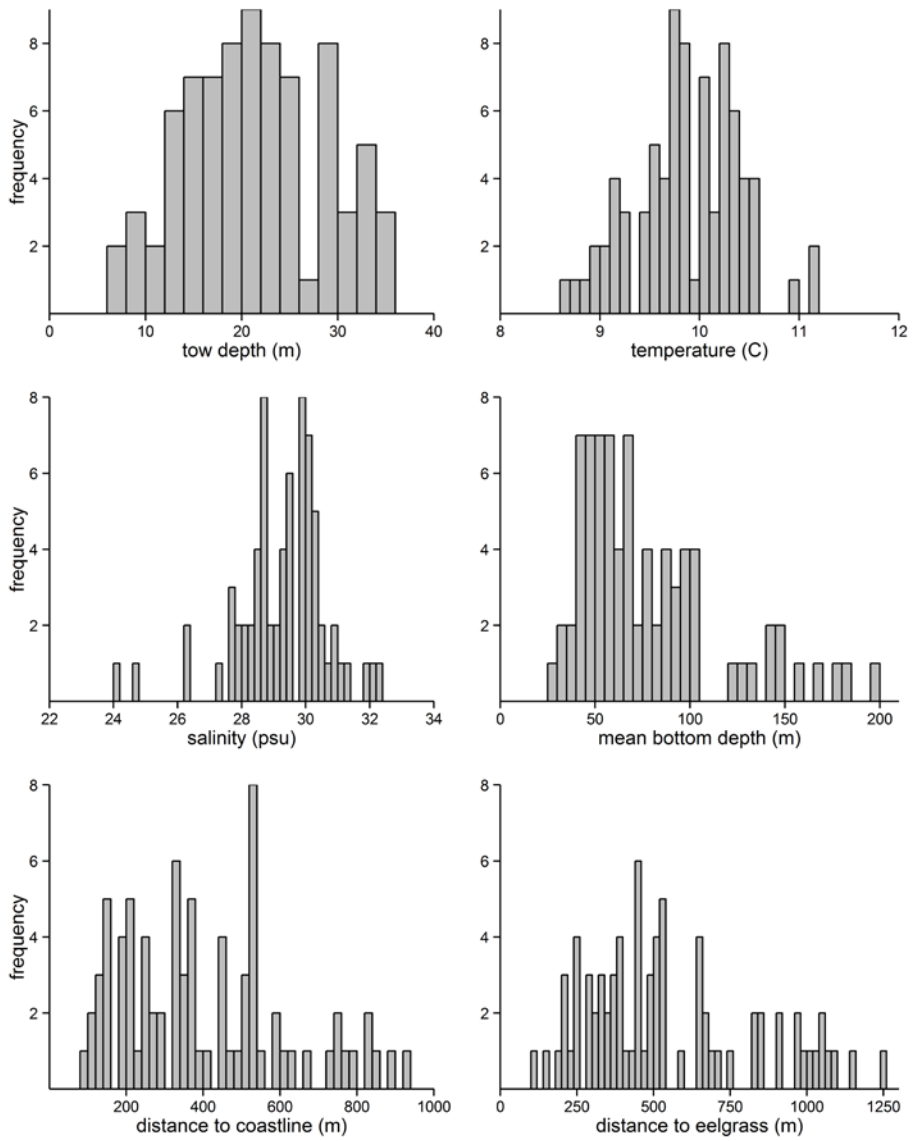

Figure 3. Frequency distribution of environmental and geospatial factors associated with tows from all nine sites during November 2013-2015 (N=78 tows).

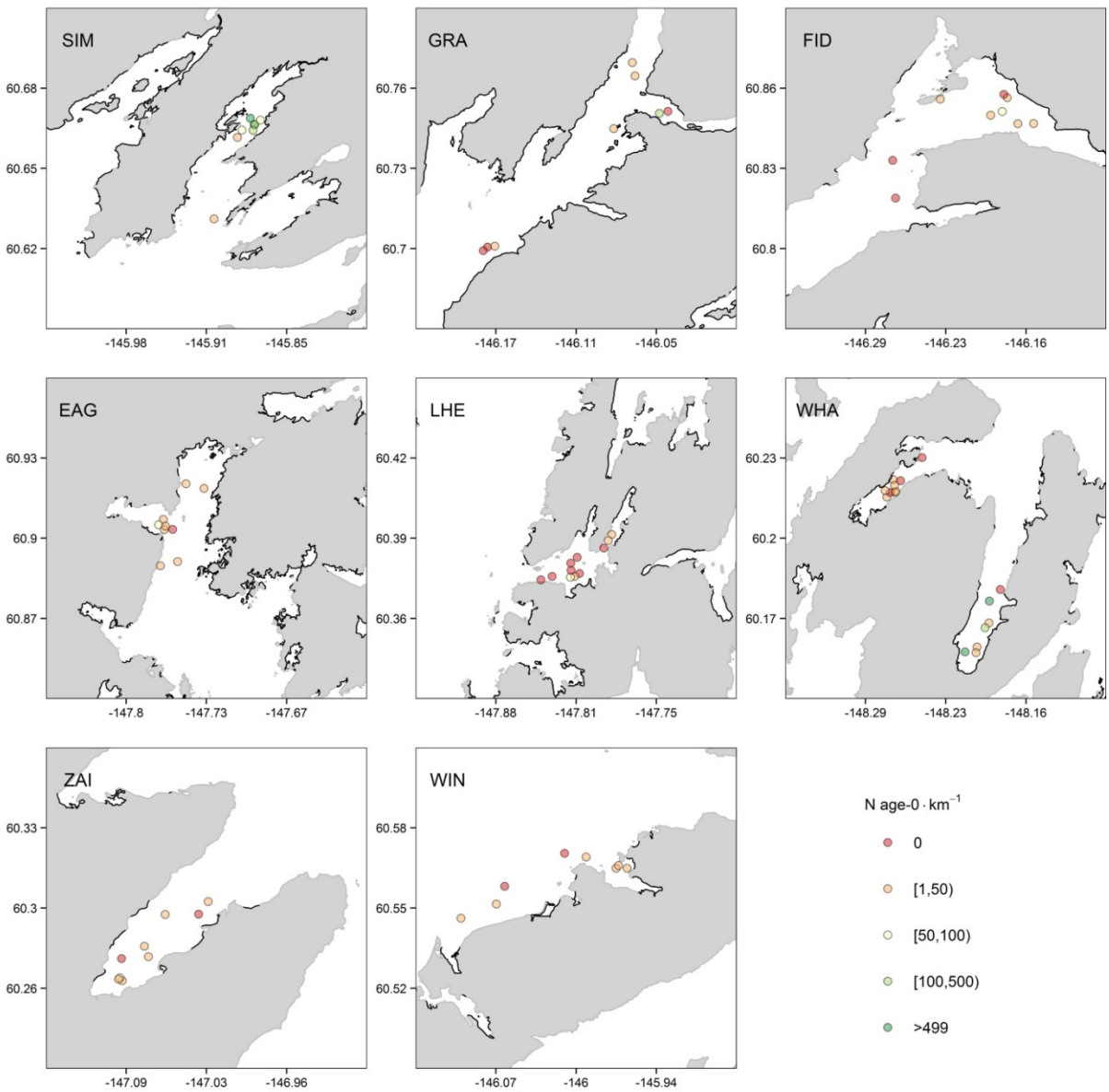

Figure 4. Maps depicting shoreline with eelgrass (bold shoreline), midpoints of trawl tows, and age-0 Pacific herring CPUE during November 2013-2015 sampling events at locations sampled (SIM=Simpson Bay; GRA=Port Gravina; FID=Port Fidalgo; EAG=Eaglek Bay; LHE=Lower Herring Bay; WWH=west arm of Whale Bay; EWH=east arm of Whale Bay; ZAI= Zaikof Bay).

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 Project 1612011-F and Project 15120111-G 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 1999) to investigate our hypotheses regarding juvenile herring distribution. The longitudinal and spatial aspects of the Project 1612011-F November surveys

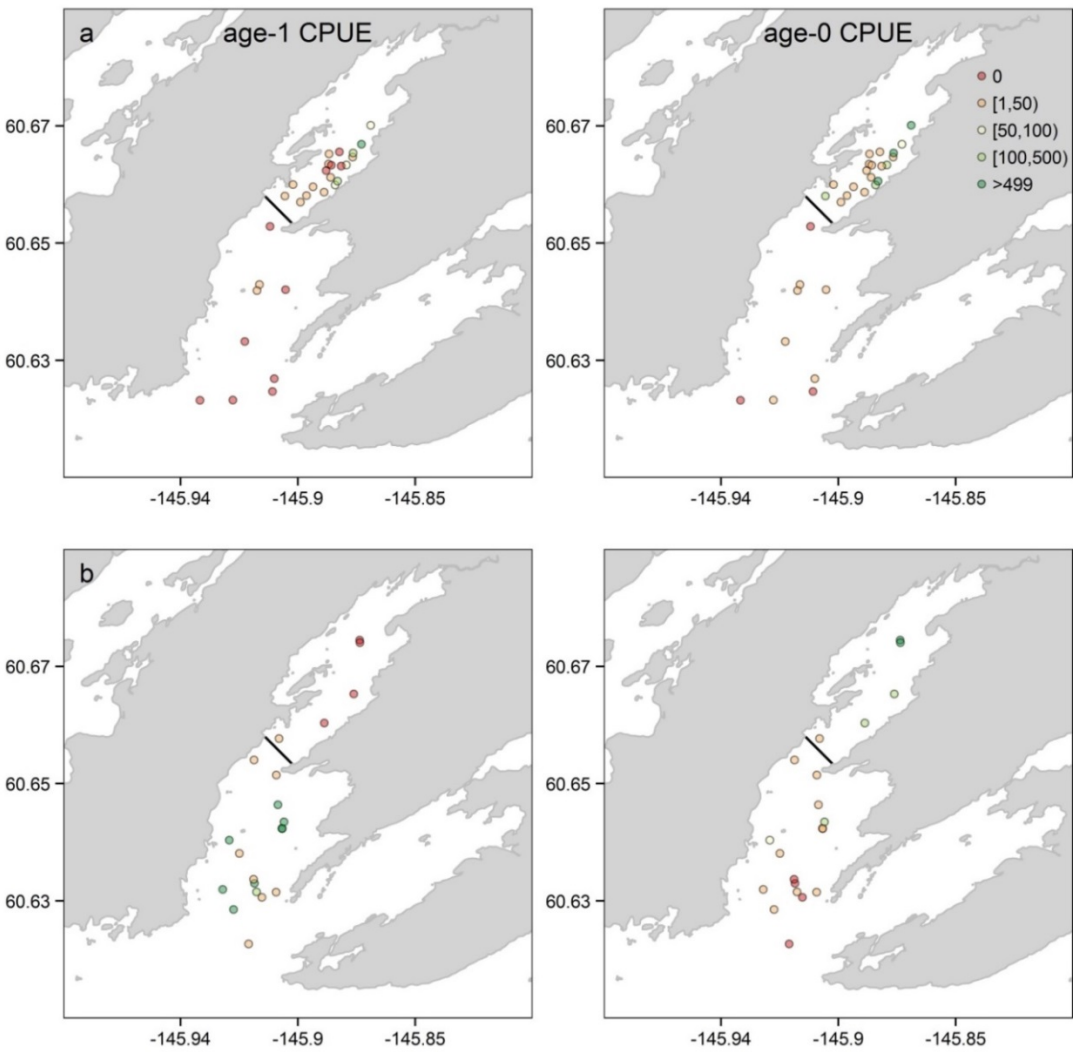

Figure 5. Midpoints of trawl tows conducted in Simpson Bay. Row (a) shows winter tows (October 2013–February 2014) and row (b) shows spring tows (March–April 2014). The inner region extends from the black line segment to the bay head and the outer region extends south to the mouth of the bay.

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 un-modeled correlation among random effects because the effect of year on catch rate was highly variable among locations.

Covariates in the project 1612011-F 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^{-1}).

All reduced models that included the random intercept and offset terms were considered. Model selection was conducted using AIC_c (Burnham and Anderson 2003). The model with the lowest AIC_c value was considered the model most parsimonious and was used for making inferences. Models with $\Delta AIC_c<2$ were considered well supported by the data, and models with $\Delta AIC_c>2$ were considered poorly supported (Burnham and Anderson 2003). 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 2014).

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-1datasets, all reduced models were considered and model selection was conducted using AIC_c. 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 HRM Program using the mid-water trawl, gillnets, and castnets (Table 1). 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 re-plumbing. 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 in conjunction with all acoustic surveys associated with Projects 15120111-G and 16120111-F. From 2013-2015, within the Project 16120111-F November 2013-2016 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 + 0.45 km). Measurements were obtained from 44% of herring collected during Project 16120111-F (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 as part of Project 15120111-G, 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 + 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, Project 16120111-E 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 of 1,625 herring were captured in gillnets and given directly to ADF&G.

Age-0 CPUE in PWS

The most supported model for PWS age-0 Pacific herring November distribution (Project 16120111-F, dataset for 2013-2015) 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 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 Project 16120111-F dataset 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

Table 2. Model selection results for age-0 Pacific herring catches all nine sites during November 2013-2015. All models contain two random intercepts (location and year nested within location) and an offset term for tow distance. Only models with ΔAIC_c <4 are listed.

model	df	log likelihood	AIC_c	ΔAIC_c
tow depth + salinity + dist2ZOS	7	-285.89	587.37	0
tow depth + salinity + temperature +	8	-285.36	588.82	1.44
bottom depth + tow depth + salinity +	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 +	8	-286.60	591.29	3.92
bottom depth + tow depth	6	-289.09	591.37	3.99

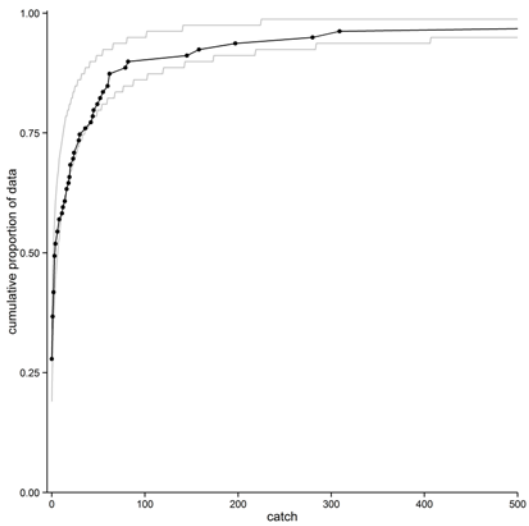

Figure 6. Observed catch data (black points) compared to expected values from the most supported model for age-0 CPUE in PWS. The 95% quantile confidence interval (grey lines) was calculated from 10,000 simulated datasets. Two observed catch values (744 and 1,410) are not shown.

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 2013–February 2014) and spring (March–April 2014).

age class	model	df	log likelihood	AIC_c	ΔAIC_c
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
age-1					
	region * season	5	-186.11	383.58	0.00
	region * season + tow depth	6	-185.28	384.51	0.93

(ΔAIC_c = 0.93). Finally, all age-1 CPUE models without a bay region-season interaction parameter were poorly supported by the data (ΔAIC_c > 10). The most parsimonious models were used for making inferences about age-0 and age-1 Pacific herring CPUE.

Similar to the relationship detected in the November 2013-2015 dataset (Project 16120111-F), CPUE of age-0 Pacific herring in Simpson Bay for October 2013 – April 2014 (Project 15120111-G) 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 of Simpson Bay was higher than its 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 Simpson Bay 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 + 6,433; N = 3) compared to open water locations (29 + 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 +129, N = 6).

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.

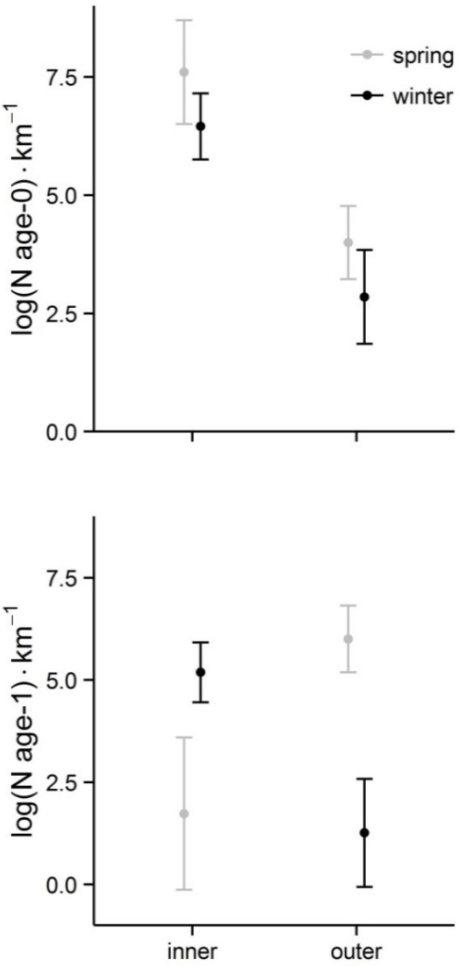

Figure 7. Mean CPUE of age-0 and age-1 Pacific herring in the inner and outer regions of Simpson Bay during winter (October 2013–February 2014) and spring (March–April 2014). Age-0 CPUE at 19 m tow depth (median tow depth from out dataset) is shown. Error bars depict 95% confidence intervals.

Finally, within Simpson Bay, the distribution patterns of age-0 and age-1 Pacific herring were similar during winter (October 2013 –February 2014) but different during spring (March–April 2014). Age-0 Pacific herring favored the inner-bay region during both seasons, whereas age-1 herring favored the inner-bay region during winter and the outer-bay region during spring. Movement into the outer-bay region during spring by age-0 herring was not observed. This was contrary to our hypothesis based on previous documentation of juvenile herring distribution patterns in PWS (Stokesbury et al. 2000). The ability of larger age-1 Pacific herring to target a wider range of prey could have driven distribution patterns in Simpson Bay. Older Pacific herring juveniles consume larger prey in additional to the smaller prey consumed by age-0 herring (Norcross et al. 2001).

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 2001, Gay and Vaughan 2001). Our 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 swim bladder 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 swim bladder 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 swim bladder 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 GOA (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 ^{o}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 November 2013-2016 surveys 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 result in inaccurate 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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Appendix A
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Distribution of juvenile Pacific herring relative to environmental and geospatial factors in Prince William Sound, Alaska

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ABSTRACT

Documenting distribution patterns of juvenile Pacific herring (*Clupea pallasii*) can clarify habitat preferences and provide insight into ecological factors influencing early life survival. However, few analyses relating juvenile Pacific herring density to habitat characteristics have been conducted. We sampled age-0 Pacific herring in nine bays and fjords distributed throughout Alaska's Prince William Sound during November over a 3-year period (2013–2015) and investigated associations between catch rate and habitat covariates using generalized linear mixed models. Our results indicated that the night-time distribution of age-0 Pacific herring in the pelagic environment was influenced by proximity to eelgrass (*Zostera marina*) beds, salinity, and water depth. Age-0 Pacific herring catch rate was negatively associated with tow depth, with herring favoring shallower water across the range of depths sampled (7.2–35.4 m). In addition, Pacific herring distribution was positively associated with fresher water within the sampled salinity gradient (24.1–32.3 psu) and proximity to eelgrass beds. Seasonal changes in juvenile Pacific herring distribution were investigated by sampling one bay over a seven month period (October-April). Age-0 Pacific herring tended to remain in the inner bay region throughout the seven months, while age-1 Pacific herring had shifted from the inner to the outer bay by spring (March-April). 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. Based on our results we recommend that habitat preferences of age-0 Pacific herring should be considered in the development of Pacific herring year-class strength indices from catch data.

1. Introduction

Pacific herring *(Clupea pallasii)* is a widely distributed pelagic forage fish with life-history adaptations that allow the species to thrive in many regional ecosystems throughout the North Pacific Ocean. They are aggregate spawners that converge on spawning grounds with remarkable synchrony (Hay, 1985). Dispersal is an important ecological process for Pacific herring larvae because spawning grounds often do not overlap spatially with nursery habitat (Norcross et al., 2001). From an evolutionary perspective, this spatial mismatch between spawning and nursery habitat indicates that habitat favorable to Pacific herring juvenile survival are not necessarily favorable to the fertilization and survival of eggs (Ciannelli et al., 2015). Larvae are transported from spawning grounds to nursery areas by oceanic currents (Norcross et al., 2001). As larval herring develop and grow in size, locomotion becomes an increasingly important dispersal mechanism because the metabolic cost of movement declines (Maes et al., 2005). Under this dispersal model, larval herring are transported by ocean currents and subsequently actively congregate in areas with favorable environmental conditions for early life survival (Hourston, 1959). However, the biological and physical characteristics of habitats that are associated with juvenile herring congregations are not well understood and further investigation is warranted (Stokesbury et al., 2000). Mechanistic distribution models relating juvenile Pacific herring density to environmental and geospatial factors (spatial data relating habitat features to local geography) can provide insight into habitat types that provide quality nursery habitat (Elith and Leathwick, 2009).

Hypotheses relating to early life survival can be investigated through examination of distribution patterns. By combining distribution data with current modeling, Ciannelli et al. (2007) examined spatiotemporal trends in survival of age-0 Atlantic cod (*Gadus morhua*). Survival was negatively associated with older conspecifics and age-0 abundance, suggesting that predation and competition were important mechanisms influencing survival (Ciannelli et al., 2007). Bottom-up control on juvenile capelin *(Mallosus villosus)* and age-0 walleye pollock (*Gadus chalcogrammus)* was examined using trawl catch data (Logerwell

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et al., 2010). Distribution of capelin and walleye pollock was influenced by densities of preferred zooplankton prey and both species exhibited pelagic habitat selection (Logerwell et al., 2010). Finally, changes in juvenile red snapper (*Lutjanus campechanus*) distribution among years with varying hypoxia severity revealed that age-0 juveniles were driven into deeper, cooler habitat during years with high hypoxia severity (Switzer et al., 2015). Based on this observed habitat shift and an association between hypoxia severity and adult recruitment, Switzer et al. (2015) hypothesized that hypoxic conditions reduced the extent of high quality nursery habitat. These examples illustrate that when relevant covariates are measured, empirical distribution data can be used to clarify ecological mechanisms influencing distribution and survival of juvenile fishes.

In southcentral Alaska, the Prince William Sound (PWS) Pacific herring population historically supported regionally important commercial fisheries. These fisheries were closed in 1989 due to contamination concerns from the 1989 *Exxon Valdez* oil spill, intermittently reopened, and closed again in 1999 due to precipitous biomass declines (Botz et al., 2013). While the cause and timing of the biomass decline are debated (Carls et al., 2002; Pearson et al., 2012; Thomas and Thorne, 2003; Thorne and Thomas, 2015, 2008), reduced biomass levels have persisted (Botz et al., 2013).

Early life survival and disease-induced mortality are hypothesized drivers of PWS Pacific herring population dynamics. The disease hypothesis was supported by modeling efforts: stock-assessment models for PWS Pacific herring were improved by including time-varying natural mortality rates associated with indices of disease prevalence (Marty et al., 2003). Additionally, several hypotheses regarding ecological controls on early life survival have been proposed: predation by marine birds and fishes (Bishop et al., 2015; Bishop and Powers, 2013), variable zooplankton transport from the Gulf of Alaska into PWS (Kline, 1999), competition and predation from hatchery-reared juvenile pink salmon (*Oncorhynchus gorbuscha*; Pearson et al., 2012), poor nutrition associated with oceanic factors (Pearson et al., 2012), and overwinter survival of age-0 herring (Norcross et al., 2001). These mechanisms are related; reduced zooplankton availability can lead to lowered body condition which, in turn, increases susceptibility to disease. Lowered body condition, poor nutrition, reduced overwinter survival, and high predation rates are all associated with reduced early life survival.

Juvenile Pacific herring distribution and habitat preferences provide insight into early life survival strategies. Thus, management and conservation of Pacific herring in PWS could be advanced by increased understanding of juvenile distribution patterns. Previous research indicates that juvenile Pacific herring tend to aggregate in sheltered pelagic areas near the heads of bays (Abookire et al., 2000; Hourston, 1959; Stokesbury et al., 2000). Additionally, seasonal distribution patterns have been documented (Stokesbury et al., 2000). However, the factors influencing juvenile herring distribution are unclear because few analyses relating juvenile Pacific herring density to specific habitat characteristics have been conducted.

We developed predictive models of juvenile herring distribution by investigating associations between juvenile herring catch rates and environmental and geospatial factors. Catch data from night-time midwater trawl tows conducted during November in PWS bays and fjords thought to contain relatively high densities of juvenile Pacific herring were used to accomplish this objective. Bottom depth and distance to shore, geospatial factors negatively associated with inner-bay habitat, were considered potential predictors of juvenile Pacific herring distribution. Juvenile Pacific herring density was hypothesized to be negatively associated with bottom depth and distance from shore based on previous documentation of aggregations near bay heads in PWS (Stokesbury et al., 2000). However, the predictive capacity of distance from shore may depend upon shoreline habitat. Age-0 herring catch rates were higher in habitats containing eelgrass (*Zostera marina*) compared to kelp (Laminariales) or rock in PWS nearshore habitats during the summer (Johnson et al., 2010). As such, we hypothesized that proximity to shoreline containing eelgrass habitat may be a better predictor of juvenile herring distribution than proximity to shoreline.

Thermohaline conditions were also considered potential predictive factors. Salinity was hypothesized to be positively associated with juvenile Pacific herring distribution because PWS has a considerable salinity gradient due to large freshwater inputs (Niebauer et al., 1994) and salinity is positively associated with the distribution of other estuarine fishes (Boehlert and Mundy, 1988). We hypothesized that juvenile herring would tend to congregate in higher temperature areas because temperatures within PWS bays and fjords were highest near bay heads during October (Gay and Vaughan, 2001), suggesting that temperature could be an important aspect of inner-bay habitat driving distribution of juvenile Pacific herring. Finally, clupeids tend to congregate higher in the water column at night (Cardinale et al., 2003; Huse and Korneliussen, 2000; Thorne and Thomas, 1990). Based on this behavior, we predicted that tow depth would be negatively associated with juvenile Pacific herring catch rates.

We also investigated temporal dynamics of distribution patterns in one location (Simpson Bay) to determine if seasonal changes depended upon age class. We hypothesized that both age-0 and age-1 herring would tend to occupy inner-bay habitat during winter and move into outer-bay habitat during spring. Age-0 and age-1 PWS Pacific herring have previously been documented in mixed schools within inner-bay regions during October and farther offshore by March (Stokesbury et al., 2000). Differences in seasonal distribution may be due to forage availability. During October zooplankton densities are higher and can support energetic requirements of higher densities of juvenile herring, whereas during March zooplankton densities are lower and finding adequate forage may require dispersal throughout a larger area (Norcross et al., 2001).

Finally, ice cover may be a characteristic of inner-bay habitat important to juvenile herring. Within PWS, sea surface temperatures in the fjords can be as low as 1 °C in late winter and some inner bays and fjords become choked with ice (Gay and Vaughan, 2001). We qualitatively assessed the effects of ice cover on juvenile herring distribution patterns by sampling areas near the head of Simpson Bay within 24 h of ice breakup. This comparison allowed us to investigate the influence of ice cover on juvenile herring distribution patterns.

2. Materials and methods

2.1. Study area

Prince William Sound is a large embayment along the coast of south-central Alaska, primarily between 60° and 61° N, and is separated from the adjacent Gulf of Alaska by large, mountainous islands. A number of marine passageways provide access to the sound, including Hinchinbrook Entrance and Montague Strait (Fig. 1). The PWS coastline is rugged and irregular with numerous islands, fjords, and bays. Bays and fjords are diverse, with average depths ranging from < 50 m (typically referred to as bays) to > 400 m (typically fjords). Outside the bays and fjords are basins and passages of varying depths down to 700 m. There are several large icefields and more than 20 tidewater glaciers (Molnia, 2001). The northern half of PWS is strongly influenced by glacial runoff in the fjords and tends to be colder and fresher relative to the ACC-influenced waters that are warmer and more saline (Wang et al., 2001). Abundant rain, snow, and glacial melt result in a strong cyclonic circulation that generally travels east to west (Niebauer et al., 1994). Finally, during summer the waters of PWS are highly stratified, but during winter months they are more mixed (Niebauer et al., 1994).

2.2. Field methods

Nine locations distributed throughout PWS were sampled for juvenile herring during November 2013, 2014, and 2015: Windy Bay, Simpson Bay, Port Gravina, Port Fidalgo, Eaglek Bay, Lower Herring

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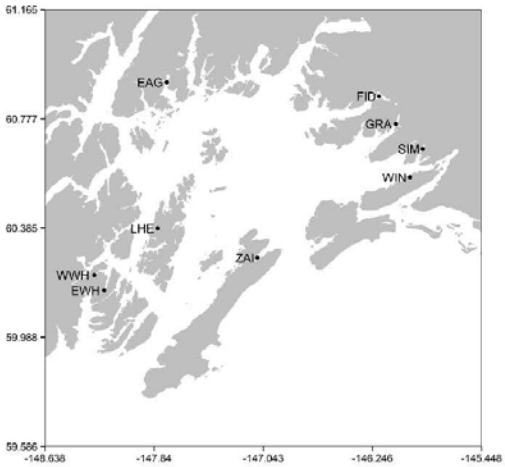

Fig. 1. Map of Prince William Sound depicting the locations of sampled bays and fjords (SIM = Simpson Bay; GRA = Port Gravina; FID = Port Fidalgo; EAG = Eaglek Bay; LHE = Lower Herring Bay; WWH = west arm of Whale Bay; EWH = east arm of Whale Bay; ZAI = Zaikof Bay).

Bay, Whale Bay (east and west arm), and Zaikof Bay (Fig. 1). The Juvenile Index Survey (JIS) comprises these November sampling events. In addition to the JIS, Simpson Bay was sampled from October 2013 through April 2014. For all sampling events, juvenile Pacific herring were captured using a midwater trawl (Stokesbury et al., 2000) 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 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). Finally, tows were conducted immediately following completion of hydroacoustic surveys and in areas and at depths where high acoustic backscatter had been detected (2–4 tows were conducted per night). This sampling design precluded researchers from using trawl catch per unit effort (CPUE) to make inferences about total abundance within sampled locations because tows were targeted to high-density areas.

Pacific herring were measured (standard length to nearest mm) onboard the research vessel to infer age class. Juvenile herring were assigned to an age class based on clear modes present in the length data. All Pacific herring ≤105 mm standard length (SL) were considered age-0 and Pacific herring 106–150 mm SL were considered age-1 (Fig. 2). Catches were enumerated by species and up to 200 herring were measured from each tow. 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. In total, measurements were obtained from 44% of herring collected during the JIS and Simpson Bay sampling.

Within the JIS trawl dataset (n = 79; 7–11 trawl tows per location), one tow in Windy Bay was only 0.04 km and was removed from the dataset prior to the analyses. Tow distance for the remaining 78 tows ranged from 0.15 to 2.8 km (mean ± sd; 0.91 ± 0.45 km). In Simpson Bay, tows were conducted during winter (October through February; n = 29) and spring (March through April; n = 21; Fig. 5). Tow distance ranged from 0.08 to 1.58 km (0.66 ± 0.30 km).

2.3. Environmental and geospatial data collection and processing

Depth (m), temperature (°C), and salinity (psu) were collected by

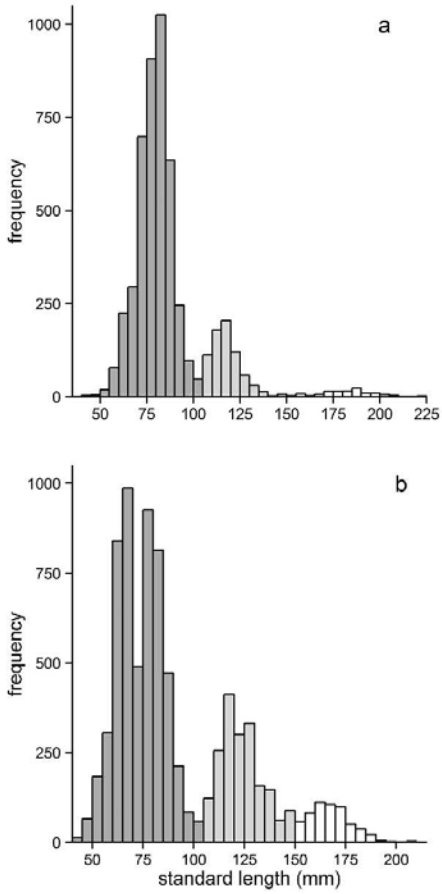

Fig. 2. Frequency distribution of Pacific herring standard lengths with 5 mm bins collected during the Juvenile Index Survey (a) and winter and spring tows conducted in Simpson Bay (b). Age-class was assigned based on modes in the distribution: dark grey bars are age-0 (≤105 mm), light grey bars are age-1 (106–150 mm), and white bars are older age classes (> 150 mm).

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 for each tow was calculated from the digital elevation model developed for PWS (8/3 arc-second resolution; Caldwell et al., 2011) using the *raster* (Hijmans, 2016) and *sp* (Bivand et al., 2008) packages for R. Distance to shore (m) was calculated as the minimum distance between tow midpoint and shoreline using the *sp* package. Locations of coastal eelgrass beds 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

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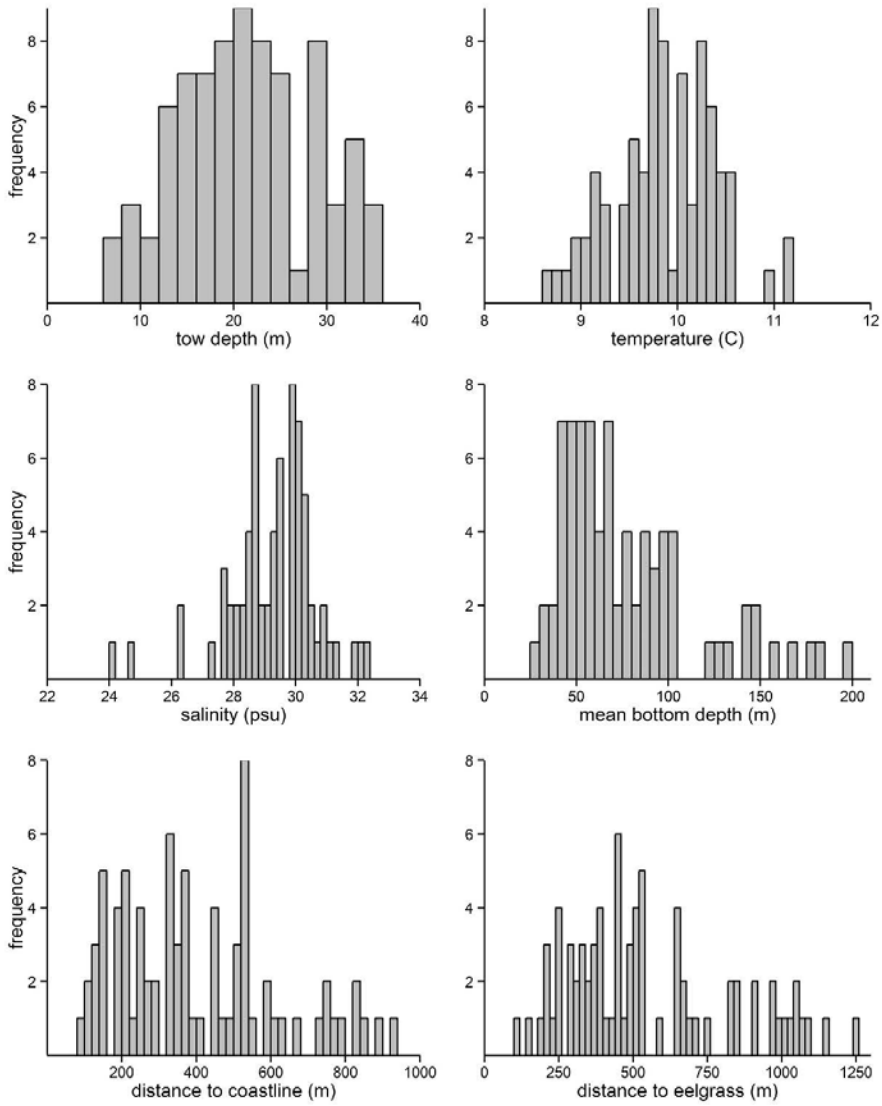

Fig. 3. Frequency distribution of environmental and geospatial factors associated with tows from the Juvenile Index Survey (n = 78).

(24.1–32.3 psu), but 60% of tows were conducted in 28–30 psu. Tows were conducted 88–1451 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 = 111–1699 m). 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 (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

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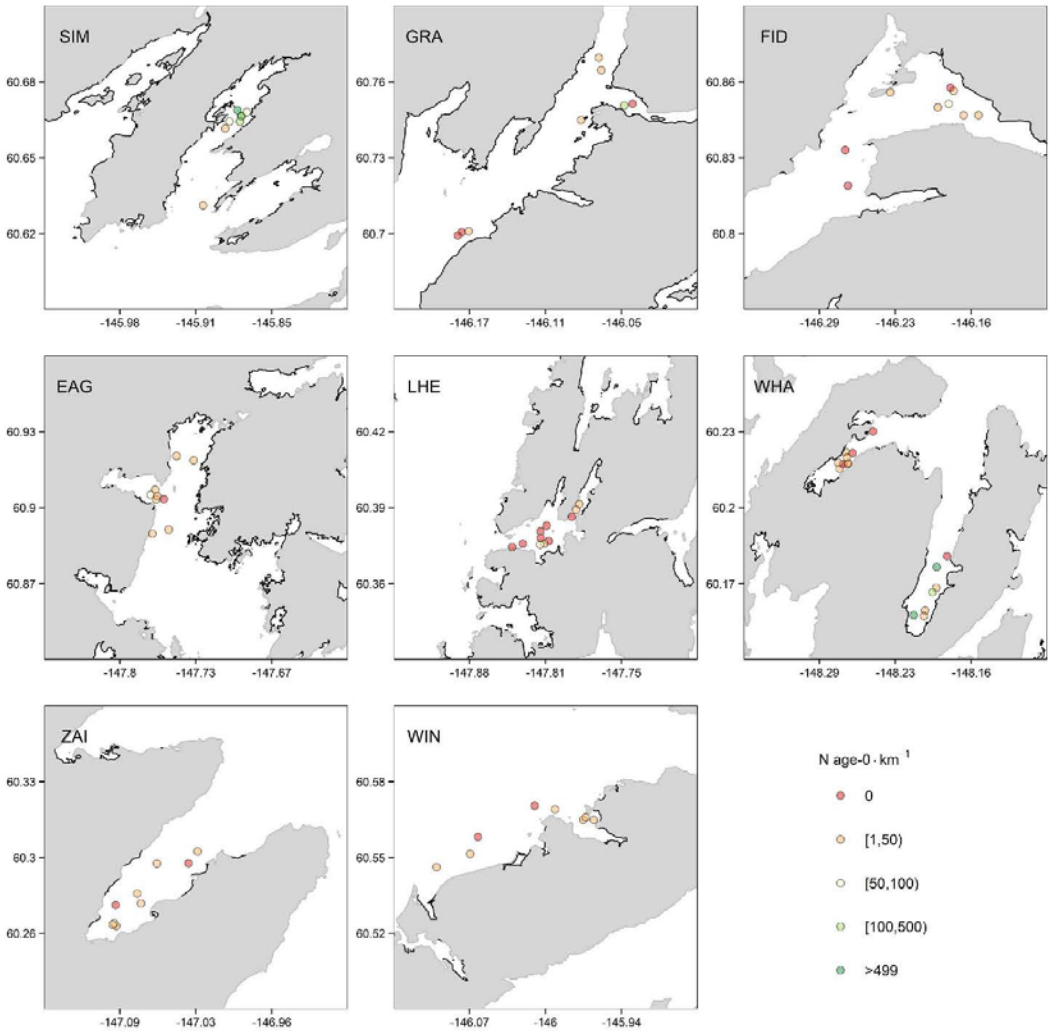

Fig. 4. Maps of individual bays and fjords sampled during the Juvenile Index Survey depicting shoreline with eelgrass (bold shoreline), midpoints of trawl tows, and age-0 Pacific herring CPUE.

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.

2.4. Model development and selection

After their first summer, age-0 herring exhibited schooling behavior and were 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, 1999) 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

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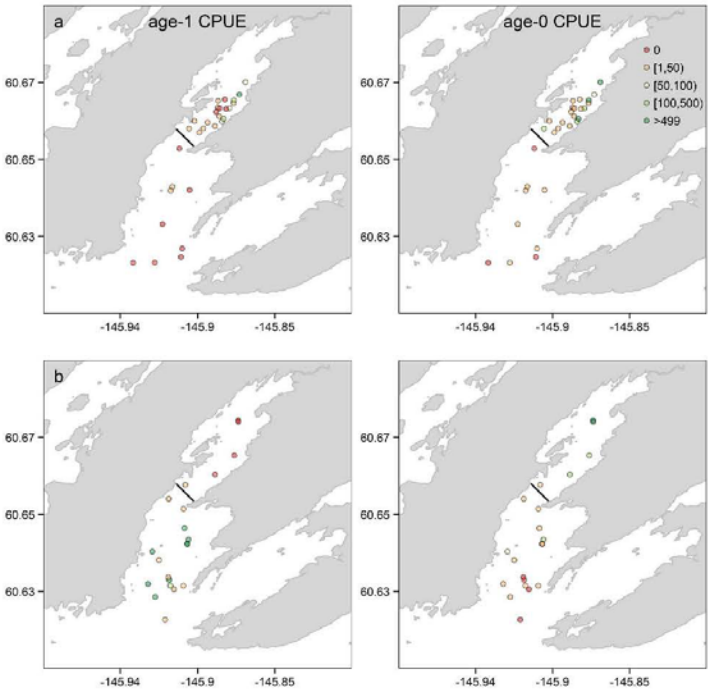

Fig. 5. Midpoints of trawl tows conducted in Simpson Bay. Row (a) shows winter tows (October–February) and row (b) shows spring tows (March–April). The inner region extends from the black line segment to the head of the bay and the outer region extends south to the mouth of the bay.

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 proximity to shore or proximity to eel grass habitat (models including both proximity to shore and proximity 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^{-1}).

All reduced models that included the random intercept and offset terms were considered. Model selection was conducted using Akaike's information criterion corrected for small sample size (AIC_c; Burnham and Anderson, 2003). The model with the lowest AIC_c value was considered the model most parsimonious and was used for making inferences. Models with $\Delta AIC_c < 2$ were considered well supported by the data, and models with $\Delta AIC_c > 2$ were considered poorly supported (Burnham and Anderson, 2003). 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, 2014).

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 models (Zuur et al., 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 (winter, October-February, or spring, March-April). 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-1datasets, all reduced models were considered and model selection was conducted using AIC_c. Models were fit in R using the *glm.nb* function from the MASS package (Venables and Ripley, 2013).

3. Results

3.1. Data overview

Age-0 Pacific herring were captured in all nine locations sampled during the JIS. Based on the 105 mm maximum length criterion, 82% of the JIS herring catch was age-0 herring. Age-0 herring were also abundant in Simpson Bay trawl tows (68% of herring catch), but substantial numbers of age-1 herring were captured (25% of herring catch).

Pacific herring was the most abundant 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.

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Table 1
Model selection results for age-0 Pacific herring catches from the Juvenile Index Surveys, November 2013–2015. All models contain two random intercepts (location and year nested within location) and an offset term for tow distance. Only models with ΔAICc < 4 are listed.

Model	df	log likelihood	AICc	ΔAICc
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

3.2. 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 1). 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. Finally, all models containing distance to shore were poorly supported by the data ($\Delta AIC_c > 4$).

Juvenile herring CPUE was strongly negatively 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 negatively associated with CPUE ($p = 0.013$). Age-0 Pacific herring 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 positively associated with proximity 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 1410 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.

3.3. 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 2). 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 2). 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 ($\Delta AIC_c > 10$).

Similar to the relationship detected in the JIS dataset, CPUE of age-0 Pacific herring in Simpson Bay was strongly 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

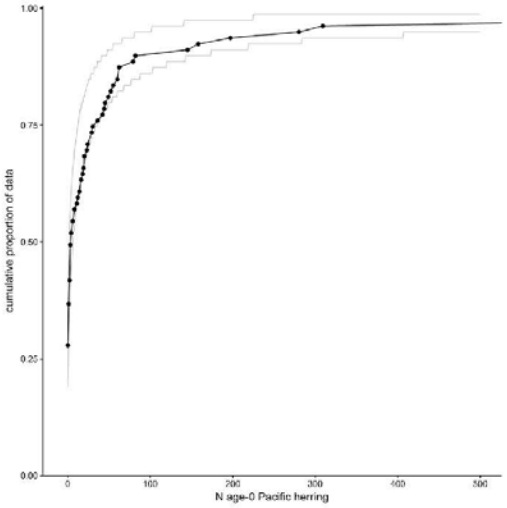

Fig. 6. Observed catch data (black points) compared to expected values from the most supported model for age-0 CPUE in PWS. The 95% quantile confidence interval (grey lines) was calculated from 10,000 simulated datasets. Two observed catch values (744 and 1410) are not shown.

Table 2
Model selection results for Simpson Bay juvenile Pacific herring catch data. Region has two levels, inner bay and outer bay, and season is a categorical covariate with two levels, winter (October–February) and spring (March–April).

Age class	Model	df	log likelihood	AICc	Δ AICc
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
	intercept only	2	−239.03	482.31	43.28
age-1					
	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

was only moderately 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, age-0 Pacific herring were positively associated with ice cover whereas age-1 herring were negatively associated. The CPUE of age-0 Pacific herring was higher in the

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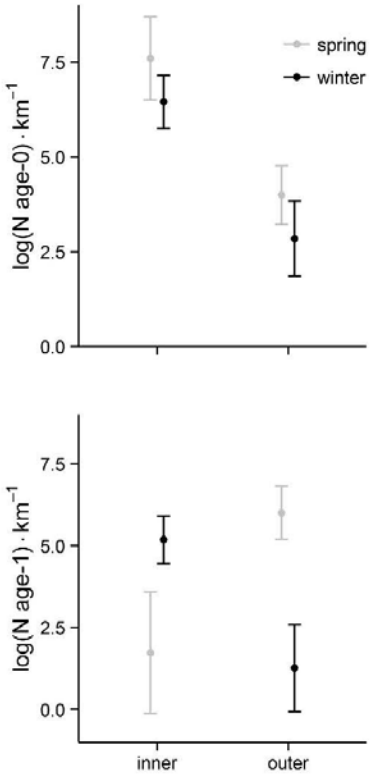

Fig. 7. Mean CPUE of age-0 and age-1 Pacific herring in the inner and outer regions of Simpson Bay during winter (October–February) and spring (March–April). Age-0 CPUE at 19 m tow depth (median tow depth from our dataset) is shown. Error bars depict 95% confidence intervals.

recently ice-covered locations (7357 ± 6433; $n = 3$) compared to open water locations (29 ± 40; $n = 6$). Zero age-1 herring were captured in recently ice-covered locations ($n = 3$) and CPUE was substantially higher in open water locations (185 ±129, $n = 6$).

4. Discussion

4.1. Juvenile herring distribution patterns

Understanding of age-0 Pacific herring distribution patterns in PWS was advanced by using generalized linear mixed models and model selection techniques to identify habitat characteristics associated with age-0 Pacific herring density. Based on catch data from night-time November trawl tows, age-0 Pacific herring densities in PWS bays and fjords were positively associated with proximity to eelgrass beds and lower salinity waters. Surprisingly, models containing parameters for distance to shore and bottom depth were not well supported by the data.

Vertical distribution was also examined and deeper trawl tows during the JIS tended to catch fewer age-0 Pacific herring. Thus, over the range of depths sampled (7.2–35.4 m) age-0 Pacific herring preferentially occupied more shallow depths during the night. Analyses of winter and spring age-0 catch data from Simpson Bay revealed that this tendency to occupy shallower depths at night was consistent during multiple seasons. Within Simpson Bay only moderate support for an association between age-1 Pacific herring CPUE and depth was detected, indicating that older juveniles were more evenly distributed in the midwater column at night compared to age-0 juveniles.

Finally, within Simpson Bay, the distribution patterns of age-0 and age-1 Pacific herring were similar during winter (October–February) but different during spring (March–April). Age-0 Pacific herring favored the inner-bay region during both seasons, whereas age-1 herring favored the inner-bay region during winter and the outer-bay region during spring. Movement into the outer-bay region during spring by age-0 herring was not observed. This was contrary to our hypothesis based on previous documentation of juvenile herring distribution patterns in PWS (Stokesbury et al., 2000). The ability of larger age-1 Pacific herring to target a wider range of prey could have driven distribution patterns in Simpson Bay. Older Pacific herring juveniles consume larger prey in additional to the smaller prey consumed by age-0 herring (Norcross et al., 2001).

4.2. Environmental and geospatial factors

Trawl 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 h 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, 2001; 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. Dual-frequency identification sonar (DIDSON) cameras can effectively measure the size structure and density of forage fish schools (Boswell et al., 2008). Mounting DIDSON cameras on remote-operated vehicles is a promising approach for monitoring juvenile Pacific herring in ice-covered habitat (K. Boswell, Florida International University, personal communication). This methodology could provide insight into the influence of ice cover on juvenile herring behavior and early life survival.

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 compared to the outer bay with higher salinity and little stratification (Abookire et al., 2000). The tendency to aggregate in 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 Pacific 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% and 50% of their energy budget on osmoregulation (Boeuf and Payan, 2001). Feeding behavior, growth, and food conversion rates are also influenced by salinity (Boeuf and Payan, 2001). Laboratory research investigating how the metabolism, growth, and behavior of juvenile Pacific herring are influenced by the range of salinities found in PWS bays and fjords could provide insight into how salinity influences nursery habitat quality.

Appendix A
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Age-0 Pacific herring have been documented in nearshore eelgrass habitat during the summer (Johnson et al., 2010), but our results indicate that proximity to eelgrass beds also influences their distribution in the pelagic environment during 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, positive association between age-0 Pacific herring density and proximity to eelgrass 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) and filter feeding requires less energy output than visual foraging 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. Eelgrass densities in Prince William Sound during early winter were below peak seasonal levels, which typically occur during late summer at high latitudes (Clausen et al., 2014). However, eelgrass beds likely provided sheltering habitat during our November sampling because eelgrass beds exhibit low seasonal aboveground biomass variation at high latitudes and living eelgrass has been documented under Arctic ice during winter (Clausen et al., 2014; McRoy, 1969).

Age-0 Pacific herring distribution in PWS during November was not strongly influenced by temperature. However, there was a narrow temperature gradient during the period sampled (8.7–11.1 °C). Age-0 Pacific herring distribution within PWS may be influenced by temperature when larger temperature gradients are present because 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). Furthermore, in the inner region of the northern Eastern Bering Sea an association between juvenile Pacific herring (mean length < 150 mm) distribution and temperature was observed. CPUE was slightly higher and distribution was more contracted during cold years compared to warm years (Andrews et al., 2015).

4.3. Future research and management implications

Modeling differences in age-0 herring densities among nursery areas as a random effect was an effective way to investigate juvenile herring habitat preferences because spatial correlations in the data were accounted for. However, we did not explore the causes of variability in densities among nursery areas because trawl data alone from the JIS survey were 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. Juvenile Pacific herring surveys designed to provide an unbiased index of density within nursery areas throughout PWS could be used to test hypotheses relating large-scale distribution patterns to larval recruitment, juvenile survival, and active dispersal to nursery areas. Using a larval drift model predicting dispersal from known spawning areas (Norcross et al., 2001; Werner et al., 1997) as a null model, alternative hypotheses could be tested by including associations among biological and environmental factors and juvenile survival (e.g. Ciannelli et al., 2007), juvenile movement, or both and assessing model fit. Investigating the underlying ecological processes driving large-scale distribution patterns in PWS would increase understanding of Pacific herring recruitment dynamics.

Natural resource managers who set harvest levels for Pacific herring are challenged with predicting recruitment to the spawning stock. Harvest rules can be too liberal or overly cautious if recruitment dynamics are not well understood because a single year class can make up a large proportion of total spawning biomass (Schweigert et al., 2009). Measurements of spawning extent or spawning stock biomass can conceptually provide insight into the number of recruits entering the spawning stock, but variable survival during the egg and early larval stages limit reliability of this approach. An alternative method, using an index of post-metamorphosis age-0 herring abundance to predict age-3 recruits, appears promising. Age-0 Pacific herring abundance was correlated with age-3 recruits in British Columbia stocks (Schweigert et al., 2009). The correlation was sufficient to be useful to natural resource managers; information on the strength of upcoming age-3 year classes was available prior to the fishing season and total allowable catch could be modified accordingly (Schweigert et al., 2009). This approach is heuristic, but juvenile density indices can also be incorporated directly into stock assessment models. For example, walleye pollock Gulf of Alaska stock assessment includes age-1 and age-2 abundance indices as well as spawning stock biomass estimates to better forecast recruitment to the fishery (Dorn et al., 2016).

Management approaches incorporating age-0 Pacific herring survey data are only effective if abundance indices developed from survey data accurately track changes in abundance. Including relevant habitat related covariates in the development of abundance indices from catch data can improve their reliability (Bigelow and Maunder, 2007) and, as a result, year-class strength predictions. Some habitat characteristics that influence age-0 Pacific herring distribution in PWS (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 may not be adequately accounted for by standardized survey transects. 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.

5. Conclusions

Age class influenced how juvenile Pacific herring distribution patterns changed seasonally. Age-0 distribution was relatively consistent between winter and spring, whereas the distribution of age-1 herring changed from the inner-bay to the outer-bay. Additionally, we developed a mechanistic model for age-0 Pacific herring distribution and determined that CPUE in PWS nursery bays and fjords was associated with proximity to eelgrass beds and low salinity waters during November. The distribution model can be used to guide conservation and research hypotheses by identifying habitat predicted to contain high densities of juvenile Pacific herring (Elith and Leathwick, 2009). Strong associations between juvenile herring densities and environmental and geospatial factors were detected, but the ecological processes driving these distribution patterns are unclear. Further research into the top-down and bottom-up drivers of juvenile herring distribution would improve our understanding of what habitat characteristics constitute quality nursery habitat for Pacific herring.

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Appendix A
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