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

Annual Herring Migration Cycle

Exxon Valdez Oil Spill Trustee Council Project 21170111-B
Final Report

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March 2023

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*With contributions by Jordan Bernard

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Study History: This project is a continuation of projects 14120111-B, "Tracking Seasonal Movements of Adult Pacific Herring in Prince William Sound" and 16160111-S "Annual Herring Migration Cycle: Expanding Acoustic Array Infrastructure". Methodology and results from these projects were used to perfect methods to acoustic-tag wild Pacific herring (*Clupea pallasii*) captured in prespawning aggregations, to document post-spawning herring movements, and to expand acoustic arrays at the Gulf of Alaska entrances to determine fish movement direction. Similar to the previous projects, the current project is a component of the Prince William Sound Herring Research and Monitoring Program. A detailed description of this project was approved for funding by the Trustee Council in November 2016 and field work began in April 2017. This is the final report on activities conducted by this project. Publications related to this project include Eiler and Bishop 2016, Bishop and Eiler 2018, Bishop and Bernard 2021, and Cypher et al. in press.

Abstract: One of the important knowledge gaps for the Pacific herring population in Prince William Sound is where adult herring disperse after spawning. We acoustic-tagged 726 Pacific herring in Prince William Sound during April 2017-2020 and post-release detected 96% of the fish. Most fish detected only on the spawning grounds had a final detection occurring within one month of release suggesting mortality or tag shedding. Over 70% of the tagged fish departed from the tagging grounds and by 16 July had been initially detected at one of the Gulf of Alaska entrance arrays: Hinchinbrook Entrance, Montague Strait, or one of the four Southwest Passages. We determined that Prince William Sound herring are partial migrants consisting of migratory fish that move seasonally into the Gulf of Alaska and of resident fish. Lighter fish were more likely to stay in the Prince William Sound and return to the southeast Prince William Sound spawning grounds during winter months. Except for post-spawning movements, once a herring returned it was rare for a fish to move and be detected at arrays outside of the spawning grounds. While all arrays throughout the spawning grounds had detections between September and April, fish were detected primarily along southern Orca Bay during winter months. Among the Gulf of Alaska entrance arrays, Hinchinbrook Entrance accounted for >80% of the initial, post-spawning detections, however, Montague Strait had the most detections. Migratory patterns suggest that both southern Montague Strait and the adjacent Gulf of Alaska waters serve as both post-spawning foraging and overwintering areas. Increasing weight or length (modeled separately) and tag year most often influenced the likelihood of movement from the spawning grounds to the entrance arrays and for migratory movements out into the Gulf of Alaska. Fish tagged in 2017 were less likely to move to the entrance arrays, and fish tagged in 2020 were less likely to initially move to Montague Strait/Southwest Passages arrays. Detections at the entrance arrays were characterized by short (hours) residencies and repeated returns. Migratory movements were defined by residency in Gulf of Alaska ≥ 14 d. Residency time in the Gulf of Alaska averaged 70 d with herring length positively affected residency time for fish exiting from Hinchinbrook Entrance, but not for fish exiting from Montague Strait/Southwest Passages.

Key words: Acoustic array, acoustic tags, *Clupea pallasii*, connectivity, Gulf of Alaska, migration, migratory movements, Pacific herring, Prince William Sound, post-spawning, Ocean Tracking Network, spawn site fidelity

Project Data: Biological data on herring were collected in the course of capture and tagging activities that took place during the month of April 2017-2020 in southeast Prince William Sound and at northern Montague Island (Rocky Bay) in Prince William Sound. Detections of acoustic tagged fish were obtained over the period of April 2017 through May 2022 from a series of acoustic receiver arrays deployed throughout the Sound, including the Ocean Tracking Network arrays located at the entrances to the Gulf of Alaska from Prince William Sound.

Format: All tagging data and acoustic receiver data is available as comma-delimited text files.

Data links: Ocean Tracking Network: http://oceantrackingnetwork.org/, Gulf of Alaska data portal: https://gulf-of-alaska.portal.aoos.org/#metadata/c1e401be-8d52-477b-a76b-acf5cd817686/project/folder_metadata/41882394, and DataONE: https://search.dataone.org/view/10.24431/rw1k7d0.

Dataset citations:

Bishop, M. A., E. Gallenberg, and W. S. Pegau. Annual herring migration cycle. 2017-2022, EVOSTC Herring Program. Gulf of Alaska Data Portal. https://gulf-of-alaska.portal.aoos.org/#metadata/c1e401be-8d52-477b-a76b-acf5cd817686/project/folder_metadata/41882394.

The data custodian is Carol Janzen, Director of Operations and Development, Alaska Ocean Observing System, 1007 W. 3rd Ave. #100, Anchorage, AK 99501, 907-644-6703. janzen@aoos.org. Data are archived by Axiom Data Science, a Tetra Tech Company, 1016 W. 6th Ave., Anchorage, AK 99501.

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Individuals interested in using these data are expected to follow standard, collegial guidelines such as those outlined by the U. S. Long Term Ecological Research Network’s Data Access Policy, Requirements, and Use Agreement: http://www.lternet.edu/policies/data-access. In particular, we highlight the following from the U. S. Long Term Ecological Research Network data policy: The consumer of these data (“Data User” herein) has an ethical obligation to cite it appropriately in any publication that results from its use. The Data User should realize that these data may be actively used by others for ongoing research and that coordination may be necessary to prevent duplicate publication. The Data User is urged to contact the authors of these data if any questions about methodology or results occur. Where appropriate, the Data User is encouraged to consider collaboration or coauthorship with the authors. The Data User should realize that misinterpretation of data may occur if used out of context of the original study. It is strongly recommended that careful attention be paid to the contents of the metadata file associated with these data to evaluate dataset limitations or intended use.

Citation:

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EXECUTIVE SUMMARY

This study investigated the movements of adult Pacific herring (*Clupea pallasii*) between spawning, summer feeding, and overwintering areas in Prince William Sound (PWS) and was a component of the integrated PWS Herring Research and Monitoring program. Our study expanded on an initial 2013 study of post-spawning movements by acoustic-tagged adult Pacific herring in PWS, Alaska and established that after spawning, a majority of fish moved from the spawning grounds to the Ocean Tracking Network acoustic arrays located at the entrances to the Gulf of Alaska (GOA; Eiler and Bishop 2016, Bishop and Eiler 2018). Our conclusions were limited in scope, however, because acoustic-tag life was < 9 months and because the Ocean Tracking Network acoustic arrays (hereafter referred to as the entrance arrays) consisted of single lines, precluding information on the direction of movements. With funding from the *Exxon Valdez* Oil Spill Trustee Council, in early 2017 we purchased and deployed additional receivers at the entrance arrays that would henceforth make possible determination of movement direction (i.e., back into PWS or out towards the GOA). In addition, battery life of V9 acoustic tags had improved such that herring could potentially be monitored for 25 months or more.

Objectives specific to our *Annual Herring Migration Cycle* study included:

1. Document location, timing, and direction of Pacific herring seasonal migrations between Prince William Sound and the GOA (Chapters 1 & 2).
2. Relate large-scale movements to year class and body condition of tagged individuals (Chapters 1, 2 & 3).
3. Determine seasonal residency time within PWS, at the entrances to PWS, and in the GOA (Chapters 1, 2, & 3).

During April 2017-2020, we acoustic-tagged 714 Pacific herring in prespawning aggregations in southeast PWS and 12 herring at northern Montague Island (2019 only). Depending on the tag type, acoustic tags had an expected life of ~8.5 months for smaller V8 tags and ~26 months or longer for the larger V9 tags. We targeted fish weighing <100 g for the smaller V8 tags. Biological data collected for each individual during tagging included weight (g), standard length (mm), and sex. In 2019 and 2020 we collected a scale from each tagged herring and were able to determine age for 278 herring.

Using data from 2017 and 2018 tagged fish, we developed an Arnason-Schwarz multistate model, a generalization of the Cormack-Jolly-Seber mark-recapture model, to estimate the probability at which PWS herring move between geographic locations while accounting for uncertainty of fish locations and mortality rates in the PWS and GOA. We implemented a Bayesian version of the Arnason-Schwarz model where fish direction information recorded at the entrance arrays was incorporated into the model using informative priors on the movement probabilities at the entrance arrays.

Our multistate model results suggest that the Sound's herring are partial migrants. That is, the PWS Pacific herring population consists of both migratory fish that move seasonally between PWS and the GOA and resident fish. Lighter fish were shown to be more likely to stay in the Sound and return to the spawning grounds during winter months. Because weight is positively correlated with length and age, our results suggest that the heavier, longer, and older fish are more likely to migrate than smaller, younger fish. Comparing movement patterns between entrance arrays, we found that although heavier fish were more likely to move from PWS to Montague Strait during the and summer season, weight was not found to have a significant influence on the probability of movement from the PWS to Hinchinbrook Entrance during the spring and summer. We also found evidence that the tagging procedure had a differential effect on herring survival over time. When we analyzed mortality in the initial months following tagging, our results show that in 2017, mortality was higher in both the Sound and the Gulf during the first half of the spring and summer season compared to the second half of the season. The same trend appeared in the Gulf for the fish tagged in 2018.

Next, we examined post-spawning movements for all four tag years (2017-2020), including detections at entrance arrays from April 2017 through June 2021. Post release, we detected >96% of tagged individuals either on the spawning grounds or at the entrance arrays. Approximately 71% of the 714 herring tagged at the southeast Prince William Sound spawning grounds subsequently moved to an entrance array. Most fish arrived during April and May and by 16 July over 98% of initial GOA entrance array detections had taken place. Located ~20-55 km from the tagging grounds, Hinchinbrook Entrance was the initial entrance array for 86% of the herring, while 12% first travelled to the Montague Strait array (~110-130 km distance) and only 2% to the Southwest Passages (~120-170 km distance).

Using logistic regression, we found that the likelihood of movement from the spawning grounds to an entrance array increased with weight and depended on the tag year with fish tagged in 2017 less likely to move to the entrance arrays. There was no significant support that sex or age affected the likelihood of moving to the entrance arrays. However, lack of support for age may have been due to the small sample size (278 of 726 fish aged) and skewed distribution of age 4+ fish. Models with standard length and tag year or condition and tag year were also fit, and results were similar to the model with weight. Similarly, when we modeled the likelihood of herring moving first to Montague Strait/Southwest Passage arrays, weight and tag year were found to significantly affect the probability. As weight increased the probability of first moving to Montague Strait/Southwest Passages increased with 2020 tag year having the lowest probability. There was no evidence that either age of condition significantly affected movement probability.

Residency at the entrance arrays tended to be relatively short. Using data from the first residency event at an entrance, residencies averaged 10.22 h (range = 0.02 – 185.98 h; n = 487 fish). The Montague Strait array had the highest number of days (nonconsecutive) and residency events, averaging 12.2 d and 6.7 events over the entire tracking period.

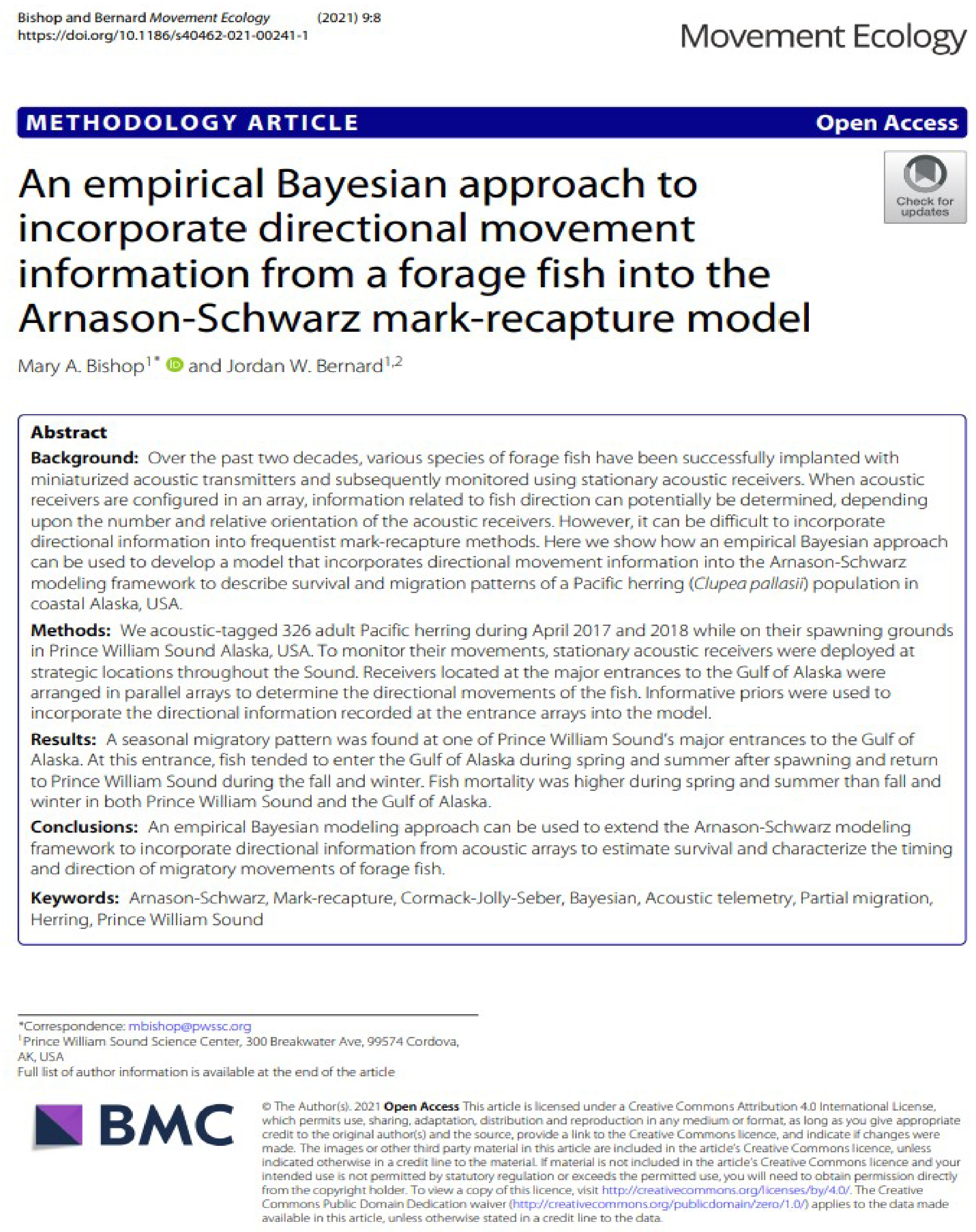
We defined a migratory movement into the GOA as an exit from and return to the Sound from the outermost arrays, and having a duration $\geq$ 14 d. Even though Hinchinbrook Entrance accounted for >80% of the first entrance array detections, it was used as an exit into the GOA exclusively during the spring and summer months. In contrast, Montague Strait was by far the most important exit and return entrance and, except for during spawning, was used by migrant herring throughout the year. Average residency time in the GOA was estimated 67.3 d (range 14-309 d). Of the 162 occurrences where we could estimate residency time, almost 25% (40/162) were in the GOA for >3 months. Modeling results indicated that the interaction of standard length and exit array had a significant effect on the GOA residency time. Herring length positively affected average GOA residency time for fish exiting from Hinchinbrook Entrance, but not for fish exiting from Montague Strait/Southwest Passage. For condition and weight models, no variables were found to significantly affect average residency time in the GOA.

We examined spawning site fidelity throughout the annual cycle. Herring generally began to return from the GOA entrance arrays in September and October. Depending on the tag year, 10% - 15% of V8-tagged herring returned to the spawning grounds with numbers generally increasing from September until December when transmitter batteries expired. For V9-tagged fish, numbers increased across winter with largest numbers arriving during the March-April spawning season. Depending on the tag year, 8% - 20% of V9-tagged fish returned within the first year and 3% - 11% the second year. Except for post-spawning movements to the GOA entrances, once a herring returned it was rare for a herring to move and be detected at arrays away from the spawning grounds. In winter herring were detected primarily along southern Orca Bay while during spring fish were detected most often around southern Port Gravina.

Logistic regression showed that the probability of an early (September-November) return to the southeast PWS spawning grounds was related to fish weight and length, with smaller herring significantly more likely to return than larger herring. Post-tagging movements to the GOA entrance arrays (Hinchinbrook Entrance, Montague Strait and/or the Southwest Passages) also influenced return rates to the southeast PWS spawning grounds. Herring with detections solely at the Hinchinbrook Entrance array had a significantly higher return rate to the southeast PWS spawning grounds than fish that returning from Montague Strait/Southwest Passage arrays.

To determine the seasonal return rate of fish to the southeast PWS spawning grounds while accounting for imperfect detection and apparent mortality, we used a multistate mark-recapture framework. Estimates of monthly survival from spring to winter were either lower than or similar to estimates from winter to spring, depending on the year. This suggests increased mortality, tag loss/failure, and/or permanent emigration from spring to winter. For fish on the spawning grounds in winter, the probability that they were on the spawning grounds in spring was significantly greater than the probability for fish that were elsewhere in winter. That is, fish elsewhere in winter were more likely to spawn in other areas of PWS than fish on the southeast PWS spawning grounds in winter, who were almost certain to remain and spawn in the area.

CHAPTER 1 AN EMPIRICAL BAYESIAN APPROACH TO INCORPORATE DIRECTIONAL MOVEMENT INFORMATION FROM A FORAGE FISH INTO THE ARNASON-SCHWARZ MARK-RECAPTURE MODEL



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METHODOLOGY ARTICLE Open Access

An empirical Bayesian approach to incorporate directional movement information from a forage fish into the Arnason-Schwarz mark-recapture model

Mary A. Bishop[1*] and Jordan W. Bernard[1,2]

Abstract

Background: Over the past two decades, various species of forage fish have been successfully implanted with miniaturized acoustic transmitters and subsequently monitored using stationary acoustic receivers. When acoustic receivers are configured in an array, information related to fish direction can potentially be determined, depending upon the number and relative orientation of the acoustic receivers. However, it can be difficult to incorporate directional information into frequentist mark-recapture methods. Here we show how an empirical Bayesian approach can be used to develop a model that incorporates directional movement information into the Arnason-Schwarz modeling framework to describe survival and migration patterns of a Pacific herring (*Clupea pallasii*) population in coastal Alaska, USA.

Methods: We acoustic-tagged 326 adult Pacific herring during April 2017 and 2018 while on their spawning grounds in Prince William Sound Alaska, USA. To monitor their movements, stationary acoustic receivers were deployed at strategic locations throughout the Sound. Receivers located at the major entrances to the Gulf of Alaska were arranged in parallel arrays to determine the directional movements of the fish. Informative priors were used to incorporate the directional information recorded at the entrance arrays into the model.

Results: A seasonal migratory pattern was found at one of Prince William Sound's major entrances to the Gulf of Alaska. At this entrance, fish tended to enter the Gulf of Alaska during spring and summer after spawning and return to Prince William Sound during the fall and winter. Fish mortality was higher during spring and summer than fall and winter in both Prince William Sound and the Gulf of Alaska.

Conclusions: An empirical Bayesian modeling approach can be used to extend the Arnason-Schwarz modeling framework to incorporate directional information from acoustic arrays to estimate survival and characterize the timing and direction of migratory movements of forage fish.

Keywords: Arnason-Schwarz, Mark-recapture, Cormack-Jolly-Seber, Bayesian, Acoustic telemetry, Partial migration, Herring, Prince William Sound

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Background

Abundant, and occurring in large schools, forage fish comprise 20–30% of the global fish catch [1]. These small fish also play a key role in the pelagic food web by transferring energy from primary or secondary producers to a wide variety of higher trophic level predators including seabirds, marine mammals, and other fish species [2]. Despite their importance in the marine ecosystem, little is known about the movement of forage fish. Because of their small size, and in some species the sensitivity to handling [3], most movement studies of forage fish have relied on fishery-dependent methods including traditional mark-recapture [4, 5] or catch-per-unit effort (cpue) [6] analyses. However, with characteristically low recapture rates (e.g. <1% [5]) data from traditional mark-recapture and cpue methods usually lack the temporal and spatial resolution to understand the timing and amount these fish move.

Knowing more about the movements of forage fish would help us better understand their population dynamics, food webs, and provide for better fisheries management. Forage fish often make long migrations between their spawning, foraging and wintering grounds. These migration patterns can shift due to multiple external factors including population collapses and recoveries, prey distributions, abiotic conditions, and climate [7–11], impacting predator populations as well as commercial fisheries management [10–12]. For example, commercially important capelin (*Mallotus villosus*) stocks in the North Atlantic have regularly experienced population collapses. Following the 1991–92 collapse of the Newfoundland stock, capelin became less migratory and remained inshore year-round. With the shift to inshore waters, capelin stocks were closer to seabird colonies and became a significant proportion of seabird diets [11]. In the case of Norwegian spring-spawning herring (*Clupea harengus*), the world's largest commercially fished herring stock, over a 60-year period, spawning, feeding, and wintering migration routes and locations have changed [12, 13]. The establishment of new and discrete wintering ground locations in this herring population have been attributed to numerically dominant first-time spawners when the social learning process was disrupted due to high fishing pressure on and a scarcity of older herring [10, 12, 14].

Pacific herring (*C. pallasii*) in the North Pacific Ocean is a widely distributed pelagic forage fish that supports important commercial fisheries. In Alaska's Prince William Sound (Sound), the herring population historically supported five fisheries, representing an annual commercial harvest of up to 20,000 metric tonnes [15]. In 1989 the *Exxon Valdez,* an oil tanker, ran aground in the Sound and spilled approximately 35,000 metric tonnes of crude oil. Four years after the spill, the Sound's adult herring population collapsed and has yet to recover [16, 17]. Conservation concerns about the lack of recovery of the Sound herring population make it increasingly important to document migration patterns to improve our understanding of adult herring survival [3]. Two important knowledge gaps for the Sound herring population are where post-spawning adults go to feed during the summer and fall and where they overwinter. Elsewhere after spawning, Pacific herring may feed and overwinter in different areas separated by as much as 1000s of kilometers. And within a spawning aggregation, herring migration patterns can vary by local populations with both resident and migratory adult Pacific herring often occurring within the same stock [18], a phenomenon known as partial migration [19].

Over the past two decades miniaturized acoustic transmitters that emit ultrasonic signals have been used successfully to study movements and survival in forage fish species including juvenile salmon (*Oncorhynchus spp.*) [20, 21], adult capelin [22], and adult herring (*Clupea spp.*) [3, 23]. Passive acoustic telemetry has numerous advantages over traditional mark-recapture methods in that fish can be repeatedly located without being physically recaptured. With this tracking method, when a tagged fish swims within the detection range of a submerged hydrophone receiver, an encoded identification and date/time stamp are recorded by the receiver. While mobile acoustic receivers can be used for active tracking, more often acoustic receivers are positioned in stationary grid formations or in a line of receivers deployed as a curtain for continuous, passive monitoring [24].

Methods to analyze individual fish movements based on detections from spatial arrays have ranged from interpolation among locations of receivers [25–27], to state-space models [28, 29]. Another approach is the Arnason-Schwarz (AS) [30] model which generalizes the Cormack-Jolly-Seber mark-recapture model [31–33] so that multiple geographic locations can be accounted for. AS models, including Bayesian versions of the model, have been used to examine animal migration by describing the rates at which animals transition between geographic regions while accounting for mortality and state uncertainty [34–37]. However, a major shortcoming of these techniques for movement analyses when applied to spatial arrays is that information related to the direction of animal movement is not incorporated, which increases state uncertainty.

Incorporating directional movement reduces state uncertainty and therefore improves estimates of when fish transition between geographic locations. Using an empirical Bayesian approach, we show how directional information can be incorporated into the AS modeling framework through the use of informative priors. Our approach refines estimates of survival and movement and allows the AS modeling framework to be applied to new systems with complex geography such as sounds and estuaries. We describe collective migration patterns of acoustic-tagged Pacific herring based on detections at a series of acoustic receiver arrays, deployed at strategic locations throughout the Sound, to showcase the benefits of our modeling approach.

Previously in the Sound, we used acoustic telemetry to investigate post-spawn movements of herring and found that 62% of the 69 acoustic-tagged herring moved to six acoustic arrays located at the entrances of the marine passageways (hereafter referred to as the entrance arrays) that connect the Sound to the Gulf of Alaska (Gulf). During the following fall, we also observed pulses of tagged herring at one of the entrance arrays, suggesting herring were returning from the Gulf. However, the single-line configuration of the entrance arrays prevented confirmation that herring were migrating out into and returning from the Gulf [27]. In 2017, a second line of receivers was added at each of the entrance arrays that made possible the determination of movement direction.

Here we present results from acoustic-tagging Pacific herring while on the spawning grounds in the Sound during spring 2017 and 2018. We hypothesized that if herring were to migrate seasonally between the Sound and the Gulf the movement probabilities from the entrance arrays back into the Sound and from the entrance arrays out into the Gulf would each oscillate seasonally and would alternate in magnitude by season. We used these same movement probabilities to determine if there were seasonal differences in the use of entrance arrays. Finally, we hypothesized that neither physical characteristics of the fish (including length, weight, and sex) nor tag-burden influenced herring movement and survival rates.

Methods

Tagging procedures

We captured and tagged adult Pacific herring during April 2017 (n = 124) and 2018 (n = 202) in the vicinity of and around spring spawning areas in the eastern Sound (Fig. 1). Details regarding the methods to capture and tag the fish have been described previously [3]. Briefly, fish were captured while in prespawning aggregations, anesthetized, and then weighed to the nearest 0.1 g, and measured (standard length, mm). We made a small incision along the ventral midline of the fish to determine sex and surgically implant an acoustic transmitter (Models V9-2x or V8-4x, 69 kHz; Vemco, Halifax, Nova Scotia, Canada). Operational life of the transmitters was estimated at 246 d (Model V8-4x; n=60) and 755-763d (Model V9-2x; n=266). Post-surgery, both tagged and untagged (i.e. not sedated, measured, or tagged) herring from the capture event were held together in a tank to determine when tagged herring had recovered from sedation and exhibited normal swimming and schooling behavior. Tagged and untagged herring were released together.

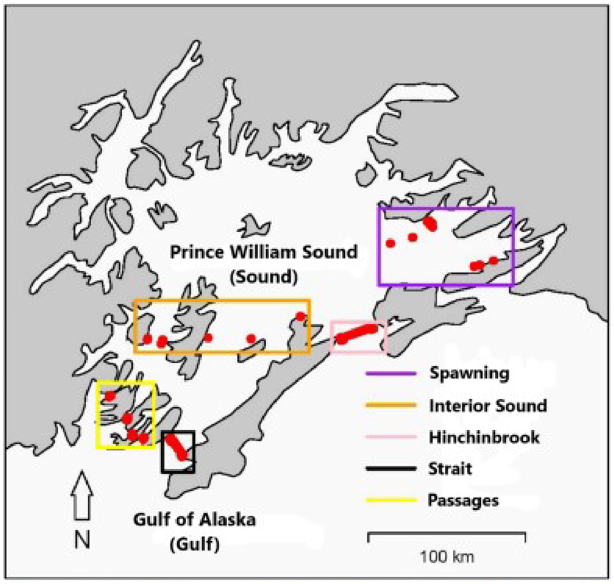

Fig. 1 Map of Prince William Sound (the Sound) showing the location of the acoustic receivers (red circles), the spawning area, additional interior arrays, and the three principal passageways into the Sound from the Gulf of Alaska (the Gulf)

Tracking procedures

To monitor the fish we tethered acoustic receivers (Models VR2W, VR2AR, VR3, and VR4; Vemco, Halifax, Nova Scotia, Canada) to stationary moorings on the ocean floor at depths ranging from 3 to 359 m and with distances between adjacent receivers ranging from 378 to 835 m. Fish swimming within reception range of a receiver were detected and the date, time, and unique identity of the fish recorded. Previous range tests for the V9, 145 dB transmitters found that signals were regularly detected (>88% of the time) at distances between 200 and 400 m from receivers [3]. We assumed that detection rates were similar, but slightly less with the V8, 144 dB transmitters. Depending on the year, a total of 59 to 65 receivers were deployed throughout the Sound (Fig. 1), including up to 10 receivers within known spawning grounds in the eastern Sound, and five receivers within the inside waters of the Sound (hereafter referred to as interior Sound receivers).

At the six major entrances connecting the Sound to the Gulf, receivers were arranged in two parallel lines so that information related to the direction of fish movement was recorded. Coverage included 14 receivers at the four southwest passages (Passages), 15 at Montague Strait (Strait), and 20 receivers at Hinchinbrook Entrance (Hinchinbrook). These six arrays located in the Passages, the Strait, and Hinchinbrook collectively comprise the entrance arrays. A 2013 pilot study found that 96–100% of the initial detections at Hinchinbrook and the Strait arrays occurred at the receivers closest to the shoreline [27]. For this reason, we also installed a partial parallel line consisting of two receivers on both sides of Hinchinbrook and the Strait (Fig. 1).

Data were downloaded from the receivers periodically. In our analysis we considered all detections occurring over the 24-month period beginning April 2017. We also assumed that an acoustic-tagged fish was present at an array when two or more detections occurred with a 24 h period.

Statistical methods

The likelihood

In developing the mathematical framework of the likelihood, we begin by indexing individual fish tagged by $i = 1, 2, \cdots, m = 326$. Let M denote the set of all fish indexes, c_i be the release time of the i^{th} fish, and l_i be the estimated transmitter life for the i^{th} fish where $c_i = 0$ when the i^{th} fish was the first to be released into the system. We assumed that an individual's transmitter is active for the duration of the manufacturer's estimated battery life. With this assumption the detection periods for which the transmitter is active can be represented by $N_i = \{c_i + 1, c_i + 2, \cdots, c_i + l_i\}$. Finally, we let f be the final possible detection period corresponding to the 31 March 2019 end date. The AS modeling framework requires a discrete number of detection (or capture) occasions. The fastest fish moved from the spawning receivers to Hinchinbrook in roughly four days; however, it took longer (>2 weeks) for the majority of fish that moved between the two arrays. In order to accurately capture the large scale (i.e. seasonal) movements of the fish while satisfying computational constraints, one-week detection periods were used.

Let Z_{ij} be a state variable where $i \in M$ and $j \in N_i \cup \{c_i\}$, and let the state space be labeled as $S = \{1, 2, 3, 4, 5, 6, 7, 8\}$. Referring the reader to Fig. 2, we define $Z_{ij} = 1$ to be the event that the i^{th} fish has expired at detection period j; $Z_{ij} = 2$ that the fish is present at a Sound spawning ground receiver; $Z_{ij} = 3$, that the fish is present at an interior Sound receiver; $Z_{ij} = 4$, that the fish is present within the Sound but not present at a receiver; $Z_{ij} = 5$, that the fish is present at a Hinchinbrook receiver; $Z_{ij} = 6$, that the fish is present at a Strait receiver; $Z_{ij} = 7$, that the fish is present at a Passages receiver; and $Z_{ij} = 8$, that the fish is present in the Gulf.

Let X_{ij} be a detection variable where $i \in M$ and $j \in N_i$. The detection variables differ from the state variables in a fundamental way. While a tagged fish is always assigned

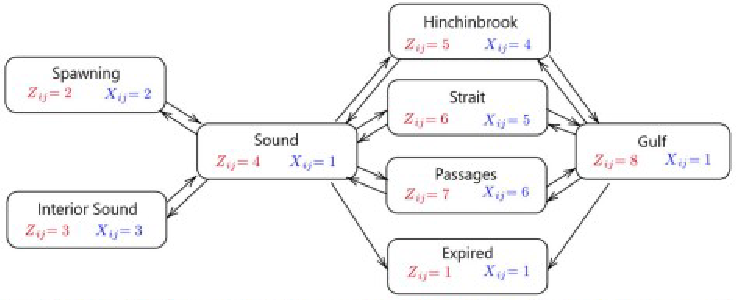

Fig. 2 Schematic of model. Arrows pointing to the expired state represent mortality probabilities. All other arrows between nodes illustrate movement probabilities between states. For each node, model states are denoted by Z_{ij} while model detection events are denoted by X_{ij}

to a state, detections are only possible when a fish passes within the detection range of a receiver. No detections of an acoustic-tagged fish can occur under three scenarios: 1) the fish has expired; 2) the fish is present in the inside waters of the Sound but not within range of any receivers; or, 3), the fish is present in the Gulf. To encode this information, the observation space is defined to be $T = \{1, 2, 3, 4, 5, 6\}$ where $X_{ij} = 1$ is the event where no detection is made for the i^{th} fish during detection period j; $X_{ij} = 2$, that the fish is detected at a spawning grounds receiver; $X_{ij} = 3$, that the fish is detected at an interior Sound receiver; $X_{ij} = 4$, that the fish is detected at a Hinchinbrook receiver; $X_{ij} = 5$; that the fish is detected at a Strait receiver; and $X_{ij} = 6$, that the fish is detected at one the Passages receivers. The scheme used to encode the state and detection variables is detailed further in Fig. 2.

According to the AS modeling framework, when the individual fish are assumed to act independently of one another, the joint likelihood of **Z** and **X** can be factored as

$$p(\mathbf{z}, \mathbf{x}) = \prod_{i \in M} p(z_{ic_i}) \prod_{j \in N_i} p(z_{ij}|z_{i(j-1)})p(x_{ij}|z_{ij})\mathrm{I}(j \leq f) \qquad (1)$$

In this equation, $p(z_{ic_i})$ describes the initial state of the i^{th} fish. Here, we let $P(X_{ic_i} = 2) = 1$. That is, the initial state of a fish corresponds to its release on the Sound spawning grounds. Additionally, $p(z_{ij}|z_{i(j-1)})$ describes how the current state of a fish relates to its previous state, and $p(x_{ij}|z_{ij})$ relates the current state of a fish to its detection data. We define $p(z_{ij}|z_{i(j-1)})$ and $p(x_{ij}|z_{ij})$ further in the next section. The indicator variable $\mathrm{I}(j \leq f)$ essentially states that the model only considers the detections that occurred before April 2019.

Model parameters

Here, we parameterized the model in order to capture the geography of the Sound and Gulf regions and the seasonal movement of herring between these regions. The model is parameterized according to the notation presented by Dupuis and others [38]. Let ϕ_{ij}^{rs} and p_{ij}^{rt} be transition and emission (detection) probabilities, respectively. Let $r, s \in S$ and $t \in T$. Formally, we define ϕ_{ij}^{rs} and p_{ij}^{rt} as $\phi_{ij}^{rs} = P\left(Z_{i(j+1)} = s|Z_{ij} = r\right)$, and $p_{ij}^{rt} = P(X_{ij} = t|Z_{ij} = r)$. Then ϕ_{ij}^{rs} is the probability the i^{th} fish is alive and in state s at time $j + 1$ given that it was alive and in state r at time j. The parameter p_{ij}^{rt} is the probability that the i^{th} fish is detected as t at time j given that it is in state r at time j. Two additional parameters (ψ and S) are introduced into the model in order to distinguish survival from movement. The movement parameter ψ_{ij}^{rs} is interpreted as the conditional probability that the i^{th} fish in state r at time j is in state s at time $j + 1$ given that the fish is alive at time $j + 1$. The survival parameter S_{ij}^{r} is interpreted as the probability that the i^{th} fish survives to time $j + 1$ given that the fish is alive and in state r at time j. To separate movement and survival it is assumed that $\phi_{ij}^{rs} = S_{ij}^{r}\psi_{ij}^{rs}$.

Additional assumptions are added to the model in order to capture the geographic region of interest, to decrease the computational expense of estimating parameters, improve the fit of the model, and to increase the robustness of the parameter estimates. We made two assumptions regarding transition probabilities: fish only expire in the Gulf or within the Sound but not within reception range of a receiver array and survival and movement probabilities are binned by season. Spring and summer season is defined as April through August and fall and winter season as September through March. Spring and summer season corresponds to when herring spawn and then move to feeding grounds; fall and winter season are a period when herring move to deeper overwintering grounds while their gonads ripen [39]. We also assumed that emission probabilities do not depend upon the individual fish or detection time and that an undetected fish is in the Sound but away from receivers, or is in the Gulf, or has expired. Finally, we assumed an acoustic-tagged fish is always detected when it passes by an array. Because a series of receivers are located at each array and most fish move along the sides of the Sound's passages which are lined with two sets of receivers, there is a high probability of fish detection [3].

The transition and emission probabilities can be expressed as matrices (referred to as transition and emission matrices respectively). For the i^{th} fish at detection period j, the transition matrix is defined to be $T_{rs}^{(ij)} = \phi_{ij}^{rs}$ and the emission matrix to be $E_{tr}^{(ij)} = p_{ij}^{rt}$. Supposing that there are M seasons and that B_k is the set of all detection times in the k^{th} season, the transition and emission matrices for the i^{th} fish at detection period j are defined to be

$$T^{(ij)} = \begin{Bmatrix} 1 & 0 & 0 & \phi_{ik}^{14} & 0 & 0 & 0 & \phi_{ik}^{18} \\ 0 & \phi_{ik}^{22} & 0 & \phi_{ik}^{24} & 0 & 0 & 0 & 0 \\ 0 & 0 & \phi_{ik}^{33} & \phi_{ik}^{34} & 0 & 0 & 0 & 0 \\ 0 & \phi_{ik}^{42} & \phi_{ik}^{43} & \phi_{ik}^{44} & \phi_{ik}^{45} & \phi_{ik}^{46} & \phi_{ik}^{47} & \phi_{ik}^{48} \\ 0 & 0 & 0 & \phi_{ik}^{54} & \phi_{ik}^{55} & 0 & 0 & \phi_{ik}^{58} \\ 0 & 0 & 0 & \phi_{ik}^{64} & 0 & \phi_{ik}^{66} & 0 & \phi_{ik}^{68} \\ 0 & 0 & 0 & \phi_{ik}^{74} & 0 & 0 & \phi_{ik}^{77} & \phi_{ik}^{78} \\ 0 & 0 & 0 & 0 & \phi_{ik}^{85} & \phi_{ik}^{86} & \phi_{ik}^{87} & \phi_{ik}^{88} \end{Bmatrix}$$

$$E^{(ij)} = \begin{Bmatrix} 1 & 0 & 0 & 1 & 0 & 0 & 0 & 1 \\ 0 & 1 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \end{Bmatrix}$$

where $j \in B_k$. In understanding the movement and survival dynamics of the fish, we first considered $M = 4$

seasons (two spring and summer and two fall and winter). Here, B_1 was defined to be the set of detection times ranging from April through August 2017; B_2, September 2017 through March 2018; B_3, April through August 2018; and B_4, September 2018 through March 2019. The transition matrix was developed to reflect the model schematic in Fig. 2.

In our modeling framework, tag shedding cannot be distinguished from mortality. Additionally, mortality cannot be distinguished from permanent immigration to the Gulf. Because mortality cannot be distinguished from permanent immigration in the Gulf, mortality rates in the Gulf are positively biased. However, as the rates at which herring migrate permanently into the Gulf is expected to be relatively low, we refer to the Gulf mortality and immigration rates as the Gulf mortality rates.

Determining the factors that influence survival and movement

A linear constraint was incorporated into the model to understand which factors influence the survival and movement rates. Here, a logit link function was used to model the movement and survival probabilities as a function of a categorical variable. The variables considered were standard length, weight, condition (weight × length^{-3}), sex, and tag-burden (tag weight/fish weight). The median was used as the break point in separating the variable of interest into two levels. In the weight model, we let y_i be an indicator variable where $y_i = 0$ when the i^{th} fish weighs less than or equal to the median weight and $y_i = 1$ when the i^{th} fish weighs more than the median weight. The survival probabilities are now modeled as $\text{logit}\left(S^{r}_{ik}\right) = \beta^{r}_{0k} + \beta^{r}_{1k} y_i$ and the movement probabilities are modeled as $\text{logit}\left(\psi^{rs}_{ik}\right) = \beta^{rs}_{0k} + \beta^{rs}_{1k} y_i$. Analogous to a simple linear regression, the parameters β^{r}_{1k} and β^{rs}_{1k} can be used to determine if the variables length, weight, condition, sex, or tag-burden influence herring survival and movement. Because the survival and movement probabilities do not depend upon the individual fish, $S^{rs}_{y_i k}$ and $\psi^{rs}_{y_i k}$ will henceforth be used to denote S^{rs}_{ik} and ψ^{rs}_{ik}. We built five constrained models, one for each covariate. Additionally, we built an unconstrained version of the model with no covariates. We drop the subscript i when referring to parameters within this unconstrained model as the survival and movement probabilities do not depend upon characteristics of individual fish.

To determine if mortality increased during the initial months following the tagging procedure, two different variations of the model were run. In the first variation, fish tagged in 2017 were used to estimate the mortality rates in the Sound and the Gulf during the first and second half of the 2017 spring and summer season; in the second variation, fish tagged in 2018 were used to estimate the mortality rates in the first and second half of the 2018 spring and summer season. If fish were to expire immediately after the tagging procedure, the mortality rates would be higher during the first half of both the 2017 and 2018 spring and summer.

Priors

If some information about a model parameter is known before the start of an experiment, a prior density reflecting the degree of subjective belief about the parameter can be selected so that the posterior density is a compromise between the likelihood and the prior. On the other hand, if no information is known about a model parameter at the start of an experiment, an uninformative prior can be selected. Because fine scale directional data recorded at the six entrance arrays were not considered in developing the likelihood, an informative prior was placed on the transition probabilities at the entrance arrays (Hinchinbrook, the Strait, and the Passages) to incorporate the directional data. For the Sound spawning grounds and the interior Sound receivers, non-informative priors are placed on the transition probabilities as directional information is not recorded at these locations. Non-informative priors are also placed on the survival probabilities in the Sound and the Gulf.

Informative priors at the entrance arrays

To determine the passage direction associated with detections made at each of the six entrance arrays, we used an algorithm to determine the first and last receiver(s) where detections occurred. The algorithm considers a fish to move from the Sound to the Gulf if the fish is detected by an entrance array's inner line of receivers first and the outer line last; a fish is considered to move from the Gulf to the Sound if the fish is detected by the entrance array's outer line first and the inner line last. In our implementation, a fish was considered to have left the entrance array if it was undetected for a 24-h period after the last detection.

At Hinchinbrook and the Strait arrays, only the receivers closest to the east and west shorelines had both inner and outer line receivers. Therefore, passage direction was not assigned when a fish was detected at inner line receivers that lacked a complementary outer line. In addition, passage direction was not assigned when the first or last detections coincided between inner and outer line receivers. Inner and outer line detections coincided $<$ 10% of all detections. A histogram of the April–August 2018 detections at the entrance arrays where passage direction was assigned is depicted in Fig. 3.

In defining the informative priors at the entrance arrays, let y represent a particular fish class. For example, $y = 0$ may represent the class of fish with weights less than or equal to the median weight of the tagged fish. Now let d^{r8}_{yk} be the number of well-defined Sound to Gulf directional detections for the y^{th} class during the k^{th} season at

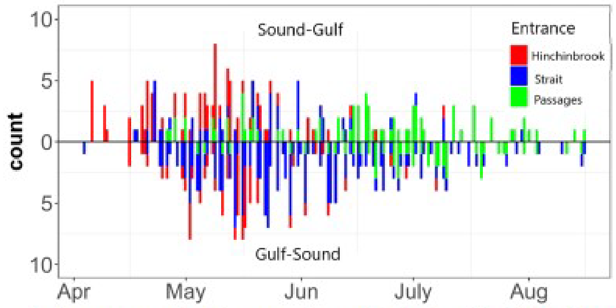

Fig. 3 Directional detections at the three arrays situated at the entrances between the Sound and the Gulf, April-August 2018. The histogram depicts the detections at Hinchinbrook, the Strait, and the Passages where our algorithm assigned a direction

the r^{th} entrance array, and let d_{yk}^{r4} be the number of well-defined Gulf to Sound directional detections for the y^{th} class during the k^{th} season at the r^{th} entrance array. Here, $r \in \{5,6,7\}$ where $r = 5$ corresponds to Hinchinbrook, $r = 6$ to the Strait, and $r = 7$ to the Passages. Let q_r be the number of fish that stayed at the r^{th} entrance array divided by the number of fish that left the entrance array between consecutive detection occasions. We then estimate the number of fish in the y^{th} class that stay at the r^{th} entrance between consecutive detection periods relative to the number of fish that leave as $d_{yk}^{rr} = q_r\left(d_{yk}^{r4} + d_{yk}^{r8}\right)$. The counts $\left(d_{yk}^{r4}, d_{yk}^{rr}, d_{yk}^{r8}\right)$ can be seen as arising from a Multinomial $\left(\psi_{yk}^{r4}, \psi_{yk}^{rr}, \psi_{yk}^{r8}\right)$ distribution; therefore, in order to incorporate the fine-scale directional information, the prior densities for the movement probabilities at the entrance arrays are distributed as

$$\left(\psi_{yk}^{r4}, \psi_{yk}^{rr}, \psi_{yk}^{r8}\right) \sim \text{Dirichlet}\left(d_{yk}^{r4} + 1, d_{yk}^{rr} + 1, d_{yk}^{r8} + 1\right).$$

Here, the informative Dirichlet priors placed on the movement probabilities at the entrance arrays incorporate directional fish count information into the model.

Non-Informative priors

Because directional information was not recorded at the receiver arrays located at either the Sound spawning grounds or the interior Sound, non-informative prior densities were placed on the remaining movement probabilities. Here, we continue with the Dirichlet family of distribution. Specifically, the prior distributions on the movement probabilities at: Sound spawning grounds arrays, Sound interior arrays, areas within Sound waters but away from the arrays, and Gulf waters are defined as

$$\left(\psi_{yk}^{22}, \psi_{yk}^{24}\right) \sim \text{Dirichlet}(2,2)$$
$$\left(\psi_{yk}^{33}, \psi_{yk}^{34}\right) \sim \text{Dirichlet}(2,2)$$
$$\left(\psi_{yk}^{42}, \psi_{yk}^{43}, \psi_{yk}^{44}, \psi_{yk}^{45}, \psi_{yk}^{46}, \psi_{yk}^{47}\right) \sim \text{Dirichlet}(2,2,2,2,2,2)$$
$$\left(\psi_{yk}^{85}, \psi_{yk}^{86}, \psi_{yk}^{87}, \psi_{yk}^{88}\right) \sim \text{Dirichlet}(2,2,2,2)$$

Non-informative Beta priors were placed on the survival probabilities in the Sound and in the Gulf. Here,

$$S_{yk}^{4} \sim \text{Beta}(2,2)$$
$$S_{yk}^{8} \sim \text{Beta}(2,2)$$

The product of the previously defined informative and not-informative priors defines the joint prior density.

Computation and convergence diagnostics

The entire analysis was carried out using the programming language R [40]. For the Markov Chain Monte Carlo (MCMC) step, the Gibbs sampler JAGS [41] and R interface Rjags [42] were used to approximate the posterior density. Four chains were run for 200,000 iterations each with a burn-in period of 10,000 iterations and a thinning period of 25 iterations. Trace and Gelman-Rubin-Brooks plots [43] were used to ensure that the chains had converged. Different variations of the model were run and the Deviance Information Criterion (DIC) was used as the metric to compare the fit of the models.

Results

We obtained 322,258 detections at the receivers over the 24-month study period. A total of 178,284 of these detections occurred at the spawning ground arrays, 2,506 detections at the interior Sound arrays, and 141,468 detections at the entrance arrays. Most of the entrance array detections came from the Strait (54,044 detections) and the Passages (56,820 detections). Of the 124 herring

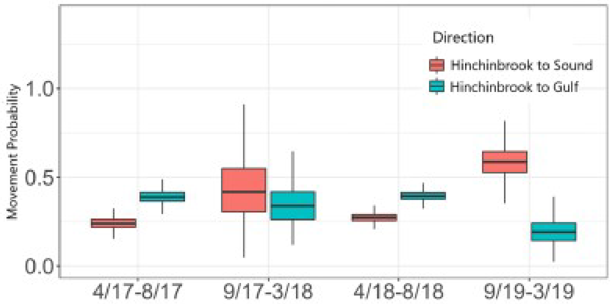

Fig. 4 Pacific herring seasonal movement probabilities between Hinchinbrook and the Sound (ψ_j^{54}) and between Hinchinbrook and the Gulf (ψ_j^{58}). Probabilities are based on weekly time periods. The Hinchinbrook to Sound and the Hinchinbrook to Gulf movement probabilities oscillate by season. During the spring and summer season (April-August) fish are more likely to move from the Sound to the Gulf than from the Gulf to the Sound. During the fall and winter season (September-March) the trend reverses

tagged in 2017, 1 was never detected, 64 were detected at spawning grounds receivers only, and 59 were detected at receivers outside of the spawning grounds; of the 202 herring tagged in 2018, 17 were never detected, 48 were detected at spawning grounds receivers only, and 137 were detected at receivers outside of the spawning grounds. Fish were detected at Hinchinbrook, the Strait, and the Passages arrays on 397, 611, and 178 separate occasions, respectively.

Seasonal migration between the sound and the gulf

We determined seasonal migration patterns of the tagged herring using the unconstrained model. If a portion of the tagged herring were to migrate seasonally between the Sound and the Gulf, both the entrance arrays to the Sound and the entrance arrays to the Gulf movement probabilities (ψ_j^{r4} and ψ_j^{r8} with $r \in \{5,6,7\}$) would oscillate seasonally (eg $\psi_1^{r4}, \psi_3^{r4} > \psi_2^{r4}, \psi_4^{r4}$ and $\psi_1^{r8}, \psi_3^{r8} < \psi_2^{r8}, \psi_4^{r8}$). Additionally, probabilities for the entrance arrays to the Sound and entrance arrays to the Gulf would alternate in magnitude by season (eg $\psi_1^{r4} > \psi_1^{r8}$, $\psi_2^{r4} < \psi_2^{r8}$, $\psi_3^{r4} > \psi_3^{r8}$, and $\psi_4^{r4} < \psi_4^{r8}$). This trend is especially important as it distinguishes seasonal migration from non-seasonal movement.

We confirmed these oscillating patterns in the movement probabilities at one of the three entrances. At Hinchinbrook during the spring and summer the rate at which herring pass into the Gulf was higher than the rate at which herring passed into the Sound, whereas the opposite trend was reflected during fall and winter (Fig. 4). However, this pattern was not observed in the movement probabilities at the Strait or the Passages arrays (Table 1).

To determine if there was a seasonal difference in the use of entrance arrays, we calculated movement probabilities between the Sound and the entrance arrays and between the Gulf and the entrance arrays (ψ_j^{4r} and ψ_j^{8r} with $r \in \{5,6,7\}$). During the spring and summer season herring entered the Gulf primarily through Hinchinbrook whereas, during the fall and winter season herring returned to the Sound from the Gulf primarily through the Strait (Table 2). An exception was in the fall and winter season of 2017/2018 when a large portion of fish moved from the Gulf to the Passages during September.

Table 1 Pacific herring movement probabilities at Hinchinbrook, the Strait, and the Passages. The table details the full set of movement probabilities between the entrance arrays and the Sound (ψ_j^{r4}) and between the entrance arrays and the Gulf (ψ_j^{r8}). A seasonal back and forth pattern is found at Hinchinbrook. However, this pattern is not found at the Strait or the Passages

Location	**Weekly probability of movement (median estimate; 90% CI)**			
from-to	**4/17-8/17**	**9/17-3/18**	**4/18-8/18**	**9/19-3/19**
Hinchinbrook-Sound	0.24; (0.19, 0.30)	0.42; (0.17, 0.72)	0.27; (0.24, 0.32)	0.59; (0.44, 0.73)
Hinchinbrook-Gulf	0.39; (0.33, 0.45)	0.34; (0.10, 0.63)	0.39; (0.35,0.44)	0.19; (0.09, 0.32)
Strait-Sound	0.18; (0.14,0.24)	0.23; (0.18,0.27)	0.36; (0.33,0.39)	0.13; (0.11,0.16)
Strait-Gulf	0.37; (0.31,0.43)	0.21; (0.17,0.26)	0.12; (0.10,0.14)	0.39; (0.36,0.43)
Passages-Sound	0.22; (0.15,0.31)	0.25; (0.16,0.35)	0.21; (0.18,0.25)	0.31; (0.17,0.49)
Passages-Gulf	0.35; (0.26,0.45)	0.32; (0.22,0.42)	0.29; (0.26,0.33)	0.33; (0.18,0.50)

Table 2 Seasonal movement probability point estimates and credible intervals for acoustic tagged Pacific herring moving between the Sound and the entrance arrays $\left(\psi_j^{4r}\right)$ and between the Gulf and the entrance arrays $\left(\psi_j^{8r}\right)$. The entrance arrays include those in Hinchinbrook, the Strait, and the Passages. During spring and summer season (April–August) fish move from the Sound to the Gulf primarily through Hinchinbrook. During the fall and winter months (September—March) fish move from the Gulf to the Sound through the Strait

Date (month/year)	Location (from-to)	Weekly probability of movement (median estimate; 90% CI)
4/17 to 8/17	Sound-Hinchinbrook	0.09; (0.07, 0.12)
4/17 to 8/17	Sound-Strait	0.05; (0.04, 0.07)
4/17 to 8/17	Sound-Passages	0.05; (0.04, 0.07)
4/18 to 8/18	Sound-Hinchinbrook	0.10; (0.08, 0.11)
4/18 to 8/18	Sound-Strait	0.05; (0.04, 0.06)
4/18 to 8/18	Sound-Passages	0.05; (0.04, 0.06)
9/17 to 3/18	Gulf-Hinchinbrook	0.02; (0.01, 0.04)
9/17 to 3/18	Gulf-Strait	0.05; (0.03, 0.08)
9/17 to 3/18	Gulf-Passages	0.05; (0.03, 0.07)
9/18 to 3/19	Gulf-Hinchinbrook	0.02; (0.01, 0.03)
9/18 to 3/19	Gulf-Strait	0.09; (0.07, 0.11)
9/18 to 3/19	Gulf-Passages	0.01; (0.00, 0.01)

The constrained model was run separately on each variable of interest (length, weight, condition, sex, and tag-burden). Length, weight, and condition were each found to have a significant effect on the rate at which herring move from the Sound to the entrance arrays. Sex and tag burden did not have a significant effect on the rates of herring movement. For brevity, we have chosen to summarize the results for the weight variable only. Here, heavier fish were more likely to move from the Sound to the Strait entrance during the spring and summer season (90% CIs: β_{11}^{46} [-1.24, -0.02]; β_{13}^{46} [-1.43, -0.14]) while lighter fish were shown to be more likely to move from the Sound to the spawning grounds arrays during the fall and winter season (90% CIs: β_{12}^{42} [0.51, 2.15]; β_{14}^{42} [0.44, 1.37]).

Survival

The unconstrained model was used to estimate the seasonal mortality rates in the Sound $(1-S_j^4)$ and Gulf $(1-S_j^8)$. These parameters were not found to differ significantly from each other. Because the estimated mortality rate in the Gulf is positively biased, true mortality was not found to be higher in the Sound than in the Gulf. In the Sound, mortality was significantly higher during the spring and summer than the fall and winter. In the Sound, the weekly mortality rate was estimated to be 0.16 and 0.09 in the spring/summer of 2017 and 2018 compared to 0.01 an 0.03 in the fall and winter of 2017 and 2018. In the Gulf, the median point estimates reflect the same seasonal trend as in the Sound: the mortality rates were higher during the spring and summer than the fall and winter (Fig. 5a). Given the lifespan of Pacific herring in the Sound (8–13 years), mortality rates were higher than expected during the spring and summer season. For instance, during spring and summer 2017 the weekly death rate in the Sound was estimated to be 0.15. These trends would appear if mortality was higher for newly tagged fish.

When we analyzed mortality in the initial months following the tagging procedure, our results show that in 2017, mortality was higher in both the Sound and the Gulf during the first half of the spring and summer season compared to the second half of the season. The same trend appeared in the Gulf for the fish tagged in 2018. However, 2018 fish mortality rates in the Sound were similar between the first and second half of the spring and summer season (Fig. 5).

The constrained model was used to investigate the relationship between tag burden and mortality. Tag-burden was not shown to have a significant effect on herring survival in the Sound or in the Gulf ($0 \in 90\%$ CIs for β_{2j}^4 and β_{2j}^8 for $j \in \{1, 2, 3, 4\}$).

Discussion

Our study shows how the AS modeling framework can be used to specify a likelihood that simultaneously models both seasonal migration between the Sound and the Gulf and survival. Existing software, such as Program MARK [44], could be used to estimate the survival and movement model parameters expressed in our likelihood (Equation 1) using the Expectation Maximization (EM) algorithm. However, with this approach, directional information recorded from the entrance arrays cannot be taken into consideration resulting in less precise parameter estimates. In the case of the Sound herring, when directional information is ignored, the AS model is unable to determine whether a fish moved into the Sound or into the Gulf. One solution would be to define temporally shorter detection events and to add additional model states so that there are separate states for the inner and outer receiver lines at each entrance. However, existing software is not equipped to handle large numbers of detection events, as would be the case here. The problem becomes increasingly complex when the direction of animal movement can be inferred for some but not all detections. With an empirical Bayesian modeling approach, incomplete directional information can be used to inform prior densities which can reduce the degree of state uncertainty to a level that allows researchers to answer questions related to fish survival and movement.

Success of the tagging procedure

When working with stationary receivers spread across geographically complex regions, it can be difficult to estimate the degree to which a capture and tagging

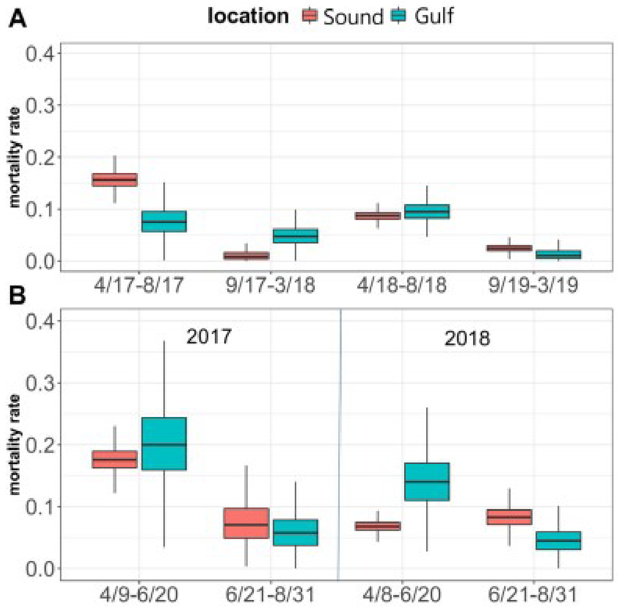

Fig. 5 a Seasonal mortality rates for Prince William Sound Pacific herring based on weekly time periods. Mortality rates in the Sound $(1 - S_j^A)$ are denoted in red. Mortality rates in the Gulf $(1 - S_j^B)$ are denoted in blue. Mortality was higher during the spring and summer season (April-August) than the fall and winter season (September-March) in both the Sound and the Gulf. **b** Mortality rates for Pacific herring tagged in 2017 and 2018 during the initial months following the tagging procedure

procedure influences fish survival. Numerous studies have used return rates to report varying degrees of success marking herring with external tags [4, 45, 46]. However, when there is a large degree of uncertainty regarding the location of fish, return rates may not reflect fish survival. The AS modeling framework allows researchers to separate movement from survival so that mortality can be estimated directly. Additionally, this framework allows survival to be modeled as a function of time as well as a function of features related to the capture and tagging process such as handling-related stress or tag burden. This is a useful modeling feature in that fish mortality can be attributed to the capture and tagging procedure itself.

We found that mortality rates of herring did not differ by tag-burden category. This does not mean that tag-burden had no influence on fish survival as our two tag-burden categories may not have expressed enough variation to show a significant effect given the power of our model. We did find evidence that the tagging procedure had a differential effect on herring survival over time. Our results suggest that mortality spikes in the initial weeks following the tagging procedure and this rate decays over time.

This result does not come as a surprise. Herring spawning aggregations attract large numbers of predators including seabirds, Steller sea lions (*Eumetopias jubatus*), and humpback whales (*Megaptera novaeangliae*)[47, 48]. In addition, laboratory studies have shown that the tagging procedure can lead to mortality rates as high as 4% in the first four weeks, and tag shedding rates of 4% between 6–8 weeks after surgery [49]. However, the quantification of mortality can yield insight that can be used to enhance sampling efforts. For example, fish mortality was estimated to be higher in the two months following the tagging campaign for fish tagged in 2017 compared to fish tagged in 2018. Environmental variability could explain these differences; nevertheless, our results suggest that the tagging campaign was more successful in 2018.

Migratory dynamics of sound herring

The lack of recovery by the Pacific herring population in the Sound more than 30 years after the *Exxon Valdez* oil spill, makes it increasingly important to document adult migration patterns and survival. However, determining how herring migrate between spawning, feeding, and wintering areas can be challenging because of technological, logistical, and financial constraints. In this paper we have demonstrated how Bayesian AS models can be used to analyze stationary acoustic telemetry data to gain insight into the movement and migration dynamics of fish. In the case of the Sound herring, the migration pattern found in the movement probabilities at Hinchinbrook show that a portion of the Sound herring population migrates seasonally between the Sound and the Gulf through Hinchinbrook. Our estimates show that these fish tended to enter the Gulf during the spring and summer after spawning and return to the Sound during the fall and winter. We suggest the movements into the Gulf are related to the differences between the Gulf and the Sound in the timing of the spring plankton bloom and the associated increase in large calanoid copepods (primarily *Neocalanus pluchrus* and *N. flemingeri*), which are important herring prey. Satellite imagery and in situ measurements indicated that the plankton bloom occurs earlier in the Sound than along the continental shelf [50].

A migratory pattern did not appear at the Strait or the Passages. A migratory pattern would not be present if herring were taking an indirect path of passing repeatedly back and forth through the Strait and the Passages in route to the wintering grounds. Results from the Passages suggest this is the case. Across both fall and winters of this study, herring were detected at the Passages only during September 2017. These fish were found to be equally likely to move from the Passages into the Sound as into the Gulf.

However, other explanations exist for why the migratory pattern did not appear at the Strait and the Passages. A migratory pattern would not appear if these entrances were located at the far end of the Sound herring population's migratory range. Additionally, this pattern would not appear if the seasonal definitions (April to August and September to March) were misaligned to capture herring's back and forth movement at these locations.

Evidence suggests that the Sound's herring are partial migrants [19]. That is, the Sound's Pacific herring population consists of both resident and migratory fish. Aerial forage fish surveys conducted during June and July throughout the Sound have noted the persistence of adult herring schools [51], suggesting that areas within the Sound may serve as summer feeding grounds. Furthermore, the major biomass of adult herring currently overwinters close to the spring spawning grounds [52]. However, commercial fishers have reported large schools of herring moving from the Gulf into the Sound during both fall and spring while others have observed herring during winter in nearby Gulf waters [53].

Given that both resident and migratory populations exist within the Sound, our model helps discern the factors that potentially distinguish the two groups. Lighter fish were shown to be more likely to move from the Sound to the spawning grounds arrays in the winter months (they were more likely to stay in the Sound and return to the spawning grounds) while heavier fish were more likely to move from the Sound to the Strait during the spring and summer season. Because weight is positively correlated with length and age, our results suggest that the heavier, longer, and older fish are more likely to migrate than smaller, younger fish. However, weight was not found to have a significant influence on the probability of movement from the Sound to Hinchinbrook during the spring and summer. Because the Strait is located further from the spawning grounds than Hinchinbrook, heavier herring may simply travel greater distances within their seasonal migration than lighter herring.

Similarly, results from field studies of migration in Atlantic herring (*C. harengus*) suggested that migration distance is a function of length, weight, and age, with the extent of migration increasing with increasing body length. In this same study, their model results predicted that for smaller (<20 cm) fish, long-distance migration costs may exceed energy intake, due to increased hydrodynamical drag with decreasing fish size [54].

Conclusion

As acoustic transmitters become increasingly small, stationary acoustic telemetry is expected to become more commonly used for studying the movement patterns of small fish. It can be challenging to analyze acoustic telemetry data using ordinary AS models if information related to the direction of fish travel is recorded by the receivers. Directional information is especially important when building models over geographically complex regions. We have shown how an empirical Bayesian modeling approach can be used to extend the AS modeling framework to incorporate directional information. Using this approach, we have demonstrated that some of the Sound's herring population migrate seasonally between the Sound and the Gulf and we documented the timing and direction of this movement. AS models have the added benefit that movement and survival are modeled simultaneously. This is useful as these models can be used to assess the efficacy of a tagging campaign. The modeling framework presented in this document is very general and can be applied to other systems and species.

Abbreviations

AS: Arnason-Schwarz; Gulf: Gulf of Alaska ; Sound: Prince William Sound; Hinchinbrook: Hinchinbrook Entrance; Strait: Montague Strait; Passages: Southwest Passages; MCMC: Markov Chain Monte Carlo

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Council. Reference to trade, firm, or product names is for descriptive purposes only, and does not imply endorsement by the Trustee Council or PWS Science Center.

Authors' contributions

MAB conceived of the project, secured funding, conducted fieldwork, manuscript preparation and revision. JWB developed models and conducted data analysis, manuscript preparation and revision. All authors approved of the final manuscript submission.

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Availability of data and materials

The datasets and computer code used during the current study are available from the corresponding author on reasonable request.

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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References

1. 2017 FAO yearbook. Fishery and Aquaculture Statistics. Rome: Food and Agricultural Organization of the United Nations; 2015.
2. Springer AM, Speckman SC. A forage fish is what? Summary of the symposium. In: Proceedings of the Symposium on the Role of Forage Fish in the Marine Ecosystem. Fairbanks: Alaska Sea Grant College Program AK-SG-9701; 1997.
3. Eiler JH, Bishop MA. Tagging response and postspawning movements of Pacific herring, a small pelagic forage fish sensitive to handling. Trans Am Fish Soc. 2016;145(2):427–39.
4. Krieger KJ. Tagging herring with coded-wire microtags. Mar Fish Rev. 1982;44:18–21.
5. Hay D, McKinnell S. Tagging along: association among individual Pacific herring (*Clupea pallasi*) revealed by tagging. Can J Fish Aquat Sci. 2002;59(12):1960–8.
6. Tojo N, Kruse GH, Funk FC. Migration dynamics of Pacific herring (*Clupea pallasii*) and response to spring environmental variability in the southeastern Bering Sea. Deep-Sea Res Pt II. 2007;54(23–26):2832–48.
7. Secor D. Migration Ecology of Marine Fishes. Baltimore: John Hopkins University Press; 2015.
8. Toresen R, Østvedt OJ. Variation in abundance of Norwegian spring-spawning herring (*Clupea harengus, Clupeidae*) throughout the 20th century and the influence of climatic fluctuations. Fish Fish. 2000;1(3):231–56.
9. Chavez F, Ryan J, Lluch-Cota S, Ñiquen M. From anchovies to sardines and back: multidecadal change in the Pacific Ocean. Science. 2003;299:217–21.
10. Petitgas P, Secor D, McQuinn I, Huse G, Lo N. Stock collapses and their recovery: mechanisms that establish and maintain life-cycle closure in space and time. ICES J of Mar Sci. 2010;67(9):1841–8.
11. Buren A, Murphy H, Adamack A, Davoren G, Koen-Alonso M, Montevecchi W. The collapse and continued low productivity of a keystone forage fish species. Mar Ecol Prog Ser. 2019;616:155–70.
12. Huse G, MacKenzie B, Trenkel V, Doray M, Nøttestad L, Óskarsson G. Spatially explicit estimates of stock sizes, structure and biomass of herring and blue whiting, and catch data of bluefin tuna. Earth Syst Sci Data. 2015;7(1):35–46.
13. Slotte A, Skaret G. Norwegian spring-spawning herring. In: Petitgas P, editor. Life-cycle spatial patterns of small pelagic fish in the Northeast Atlantic. ICES Coop. Res. Rep. No. 306. Copenhagen: International Council for Exploration of the Seas; 2013. p. 2–6.
14. Huse G, Fernö A, Holst J. Establishment of new wintering areas in herring co-occur with peaks in recruit to repeat spawner ratio. Mar Ecol Prog Ser. 2010;409:189–98.
15. Botz J, Sheridan T, Wiese A, Moffitt S, Brenner R. 2013 Prince William Sound area finfish management report. Alaska Dep Fish Game Fish Manage Rep. Anchorage: Alaska Department of Fish and Game; 2014. p. 14–43.
16. Hulson P-JF, Miller SE, Quinn TJ, Marty GD, Moffitt SD, Funk F. Data conflicts in fishery models: incorporating hydroacoustic data into the Prince William Sound Pacific herring assessment model. ICES J of Mar Sci. 2008;65(1):25–43.
17. Exxon Valdez Oil Spill Trustee Council. Exxon Valdez oil spill restoration plan: 2014 update of injured resources and services. Anchorage: Exxon Valdez Oil Spill Trustee Council; 2014.
18. Beacham T, Schweigert J, MacConnachie C, Le K, Flostrand L. Use of microsatellites to determine population structure and migration of Pacific herring in British Columbia and adjacent regions. Trans Am Fish Soc. 2008;137(6):1795–811.
19. Chapman B, Skov C, Hulthen K, Brodersen J, Nilsson PA, Hansson LA, et al. Partial migration in fishes: definitions, methodologies and taxonomic distribution. J Fish Biol. 2012;81(2):479–99.
20. Welch DW, Melnychuk MC, Rechisky ER, Porter AD, Jacobs MC, Ladouceur A, McKinley RS, Jackson GD. Freshwater and marine migration and survival of endangered cultus lake sockeye salmon (*Oncorhynchus nerka*) smolts using post, a large-scale acoustic telemetry array. Can J Fish Aquat Sci. 2009;66(5):736–50.
21. Welch DW, Melnychuk MC, Payne JC, Rechisky EL, Porter AD, Jackson GD, Ward BR, Vincent SP, Wood CC, Semmens J. In situ measurement of coastal ocean movements and survival of juvenile Pacific salmon. P Natl Acad Sci. 2011;108(21):8708–13.
22. Davoren GK. Divergent use of spawning habitat by male capelin (*Mallotus villosus*) in a warm and cold year. Behav Ecol. 2013;24(1):152–161.
23. Langård L, Skaret G, Jensen KH, Johannessen A, Slotte A, Nøttestad L, Fernö A. Tracking individual herring within a semi-enclosed coastal marine ecosystem: 3-dimensional dynamics from pre-to post-spawning. Mar Ecol Prog Ser. 2015;518:267–79.
24. Donaldson MR, Hinch SG, Suski CD, Fisk AT, Heupel MR, Cooke SJ. Making connections in aquatic ecosystems with acoustic telemetry monitoring. Front Ecol Env. 2014;12(10):565–73.
25. Simpfendorfer CA, Heupel MR, Hueter RE. Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movements. Can J Fish Aquat Sci. 2002;59(1):23–32.
26. Simpfendorfer CA, Heupel MR, Collins AB. Variation in the performance of acoustic receivers and its implication for positioning algorithms in a riverine setting. Can J Fish Aquat Sci. 2008;65(3):482–92.
27. Bishop MA, Eiler JH. Migration patterns of post-spawning Pacific herring in a subarctic sound. Deep-Sea Res Pt II. 2018;147:108–15.
28. Dorazio RM, Price M. State-space models to infer movements and behavior of fish detected in a spatial array of acoustic receivers. Can J Fish Aquat Sci. 2019;76(4):543–50.
29. Lewandoski S, Bishop MA. Distribution of juvenile Pacific herring relative to environmental and geospatial factors in Prince William Sound, Alaska. Deep-Sea Res Pt II. 2018;147:98–107.
30. Schwarz CJ, Arnason AN. A general methodology for the analysis of capture-recapture experiments in open populations. Biometrics. 1996;52(3):860–73.
31. Cormack R. Estimates of survival from the sighting of marked animals. Biometrika. 1964;51(3/4):429–38.
32. Jolly GM. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika. 1965;52(1/2):225–47.

33. Seber GA. A note on the multiple-recapture census. Biometrika. 1965;52(1/2):249–59.
34. Hestbeck JB, Nichols JD, Malecki RA. Estimates of movement and site fidelity using mark-resight data of wintering Canada geese. Ecology. 1991;72(2):523–33.
35. Brownie C, Hines J, Nichols J, Pollock K, Hestbeck J. Capture-recapture studies for multiple strata including non-Markovian transitions. Biometrics. 1993;49:1173–87.
36. Dupuis JA. Bayesian estimation of movement and survival probabilities from capture-recapture data. Biometrika. 1995;82(4):761–72.
37. Dupuis J, Badia J, Maublanc M-L, Bon R. Survival and spatial fidelity of mouflon (*Ovis gmelini*): A Bayesian analysis of an age-dependent capture-recapture model. J Agri Biol Envir St. 2002;7(2):277–98.
38. Amstrup SC, McDonald TL, Manly BF. Handbook of capture-recapture analysis. Princeton: Princeton University Press; 2010.
39. Hay D. Reproductive biology of Pacific herring (*Clupea harengus pallasi*). Can J Fish Aquat Sci. 1985;42(S1):111–26.
40. R Core Team. R: A Language and Environment for Statistical Computing. Vienna: R Foundation for Statistical Computing; 2014. http://www.R-project.org/.
41. Plummer M. Jags: A program for analysis of Bayesian graphical models using Gibbs sampling. In: Hornik K, Leisch F, Zeileis A, editors. Proceedings of the 3rd international workshop on distributed statistical computing. Vienna: Technische Universitat Wien; 2003. p. 10.
42. Plummer M. Rjags: Bayesian graphical models using MCMC. 2018. R package version 4–8. https://CRAN.R-project.org/package=rjags.
43. Brooks SP, Gelman A. General methods for monitoring convergence of iterative simulations. JCGS. 1998;7(4):434–55.
44. White GC, Burnham KP. Program mark: survival estimation from populations of marked animals. Bird Study. 1999;46(sup1):120–39.
45. Hay DE. Spawning habitat, continental shelf area and herring production in the North Pacific Ocean. In: Oceanic and anthropogenic controls of life in the Pacific Ocean. Dordrecht: Springer; 1992. p. 183–191.
46. Flostrand LA, Schweigert JF, Daniel KS, Cleary JS. Measuring and modelling Pacific herring spawning-site fidelity and dispersal using tag-recovery dispersal curves. ICES J of Mar Sci. 2009;66(8):1754–61.
47. Bishop MA, Watson JT, Kuletz K, Morgan T. Pacific herring (*Clupea pallasii*) consumption by marine birds during winter in Prince William Sound, Alaska. Fish Oceanogr. 2015;24(1):1–13.
48. Seitz AC, Norcross BL, Payne JC, Kagley AN, Meloy B, Gregg JL, Hershberger PK. Feasibility of surgically implanting acoustic tags into Pacific herring. Trans Am Fish Soc. 2010;139(5):1288–91.
49. Moran J, Heintz R, Straley J, Vollenweider J. Regional variation in the intensity of humpback whale predation on Pacific herring in the Gulf of Alaska. Deep-Sea Res Pt II. 2018;147:187–95.
50. Coyle KO, Pinchuk AI. Seasonal cross-shelf distribution of major zooplankton taxa on the northern Gulf of Alaska shelf relative to water mass properties, species depth preferences and vertical migration behavior. Deep-Sea Res Pt II. 2005;52(1-2):217–45.
51. Arimitsu ML, Piatt JF, Heflin B, von Biela V, Schoen SK. Monitoring long-term changes in forage fish distribution, abundance and body condition. (Restoration Project 16120114-O). Anchorage: Exxon Valdez Oil Spill Trustee Council; 2018.
52. Thorne RE. Trends in adult and juvenile herring distribution and abundance in Prince William Sound. (Restoration Project 070830). Anchorage: Exxon Valdez Oil Spill Trustee Council; 2010.
53. Brown ED, Seitz J, Norcross BL, Huntington HP. Ecology of herring and other forage fish as recorded by resource users of Prince William Sound and the outer Kenai Peninsula, Alaska. Alaska Fish Res Bull. 2002;9(2):75–101.
54. Nøttestad L, Giske J, Holst JC, Huse G. A length-based hypothesis for feeding migrations in pelagic fish. Can J Fish Aquat Sci. 1999;56(S1):26–34.

Publisher's Note

CHAPTER 2 POST-SPAWNING MOVEMENTS OF PACIFIC HERRING IN PRINCE WILLIAM SOUND

Mary Anne Bishop and Elaine Gallenberg

Introduction

Conservation concerns about the recovering Pacific herring (*Clupea pallasii*) population in Prince William Sound (PWS) make it increasingly important to document migration patterns to inform our understanding of PWS adult herring survival. Little is understood about adult Pacific herring annual migration movements between spawning, summer feeding, and overwintering areas within and between PWS and the Gulf of Alaska (GOA). Elsewhere, it is common for large herring populations to migrate from nearshore spawning areas to coastal shelf areas for summer feeding habitat (Hay and McCarter 1997, Hay et al. 2008). Corten (2002) suggested that observed herring migration patterns are not innate but are a learned behavior that initially happens when the recruiting year class follows older herring. In his review of migration in Atlantic herring (*C. harengus*) Corten observed that herring migration patterns tend to be stable over years, despite environmental variation.

In PWS, Brown et al. (2002) compiled local and traditional knowledge on adult herring movements. In that study, some fishers reported herring moving into PWS through Montague Strait (MS) prior to the fall bait fishery while others reported herring moving into PWS in spring through Hinchinbrook Entrance (HE), MS, and the southwest passages (SWP) of Elrington and LaTouche. These observations suggest that PWS herring are regularly migrating out of PWS and onto the shelf.

This study expands on an initial 2013 study of post-spawning movements by acoustic-tagged adult Pacific herring in PWS and established that after spawning, most fish moved from the spawning grounds to the Ocean Tracking Network acoustic arrays located at the entrances to the GOA (Eiler and Bishop 2016, Bishop and Eiler 2018). Our conclusions were limited in scope, however, because acoustic-tag life was < 9 months and because the Ocean Tracking Network acoustic arrays (hereafter referred to as the entrance arrays) consisted of single lines, precluding information on the direction of movements. With funding from the *Exxon Valdez* Oil Spill Trustee Council, in early 2017 we purchased and deployed additional receivers at the entrance arrays that would henceforth make possible determination of movement direction (i.e., back into PWS or out towards the GOA).

For this study we examined the spatial and temporal post-spawning migratory patterns of Pacific herring over a 5-year period (2017-2021). Of particular interest were migratory movements into the GOA. Here we provide detailed information on the migratory patterns of PWS herring, including the timing of departure from the spawning grounds, temporal, and spatial movements both within the Sound and into the GOA, and the biological and temporal variables influencing the likelihood of movements.

Methods

Study area

PWS is located on the coast of southcentral Alaska, primarily between 60° and 61°N. A number of marine passageways provide access to the Sound, including HE, MS, and four passageways in the southwest Sound (Fig. 2-1). The coastline is rugged and extensive, with many islands, fjords, and bays. Water depths in fjords and bays range from <50 M to > 400 m; outside of the bays and fjords are many basins and passages of varying depths up to 700 m.

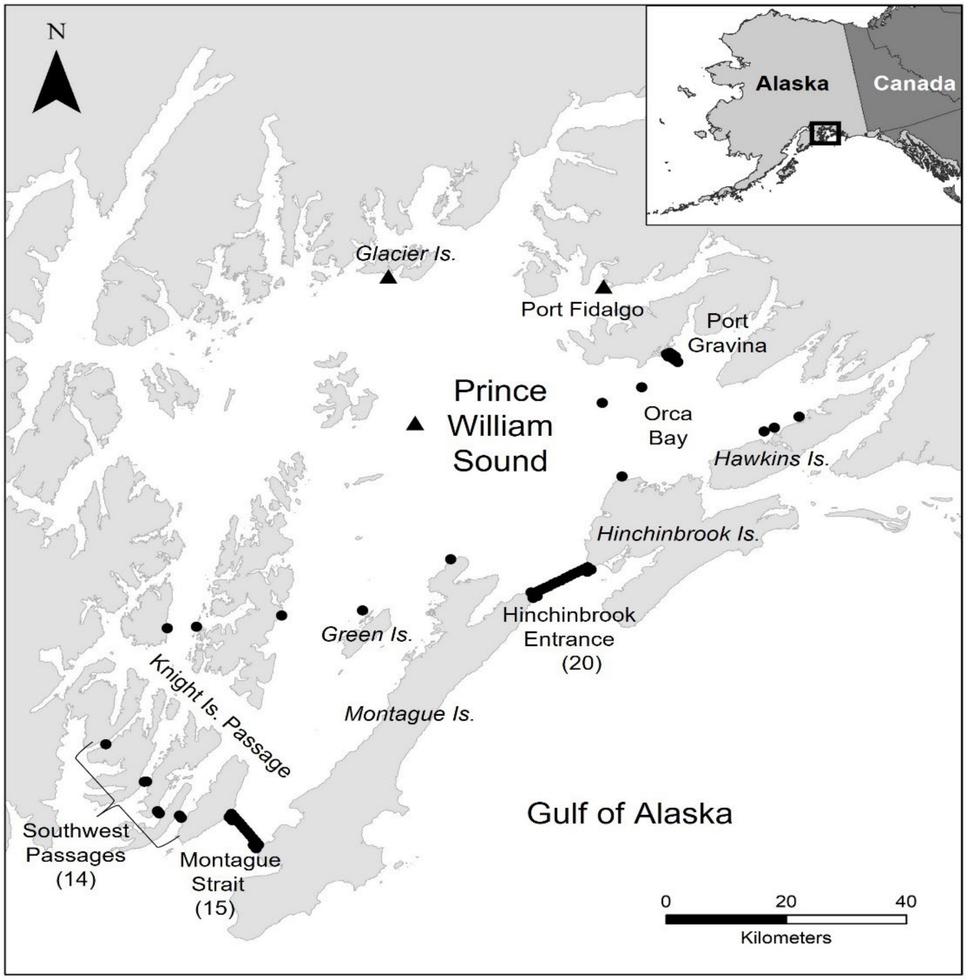


Figure 2-1. Map of Prince William Sound showing the locations of all submerged acoustic receivers (circles and triangles). Total number of acoustic receivers in the Ocean Tracking Network arrays at the principal entrances from the Gulf of Alaska are indicated in parentheses. Southwest Passages (southeast to northwest): LaTouche, Elrington, Prince of Wales, and Bainbridge. Receivers deployed for short (7-11 mo) or intermittent periods (5-7 mo) are denoted by triangles.

Fish capture and tagging

We captured and acoustic-tagged adult Pacific herring in PWS while in prespawning aggregations during April over a period of four years, 2017-2020 (Table 2-1). Except for 12 herring, all capture and tagging efforts took place in southeast PWS around Orca Bay and Port Gravina. Since 1999, southeast PWS has accounted for the highest annual proportion of total spawn in PWS (McGowan et al. 2021).

Table 2-1. Number of tags deployed on Pacific herring by year, tag type, first and last dates of tagging activities and spawning events and tagging locations. Except for 12 fish, all herring were tagged on the southeast Prince William Sound spawning grounds. Range of spawning dates is for all spawning events throughout the Sound.

	Tag Type		**Dates**[a]		
Year	**V9**	**V8**	**Tagging**	**Spawning**	**Tagging Locations**
2017	124		4/9-4/16	4/13-4/21	Port Gravina
2018	142	60	4/8-4/13	4/7-4/17	Port Gravina, Canoe Pass
2019	125[b]	40	4/2-4/10	3/26-5/3	Port Gravina, Canoe Pass, Double Bay, Rocky Bay
2020	185	50	4/1-4/8	4/2-5/2	Port Gravina, Canoe Pass
2021	-	-	-	3/28-4/29	

[a] Spawn dates from Vega et al. 2018, Russell et al. 2019, Morella et al. 2020, Botz et al. 2021

[b] Includes 12 herring tagged in Rocky Bay, Montague Island

Details describing herring capture, handling, and tagging methods have been described previously (Eiler and Bishop 2016). Briefly, fish were captured using barbed fishing jigs and then placed in a holding tank (770 L capacity). Individual fish were then transferred to a circular tub and anesthetized, weighed, measured (standard length), a single scale removed for aging (2019 and 2020 only) before being and placed in a tagging cradle. We made a small incision along the ventral midline to determine sex and to surgically implant an acoustic transmitter. Post-surgery, both tagged and untagged (i.e., not sedated, measured, or tagged) herring from the capture event were held together in a tank to ascertain when tagged herring had recovered from sedation and exhibited normal swimming and schooling behavior. Tagged and untagged herring were released together near a herring school. All capture procedures and protocols were approved by the PWS Science Center Institutional Animal Care and Use Committee.

We implanted into herring either a V9 or V8 transmitter (Models V9-2x, V9-2x-BLU-1, or V8-4x, 69 kHz; Innovasea, Halifax, Nova Scotia, Canada). The V9 transmitter weighed 4.7 g (2.9 g in water) and was programmed to randomly transmit an encoded signal every 70-150 s at 145 db (Model V9-2x) or 146 db (Model V9-2X-BLU). Manufacturer's projected battery life (d) ranged from 755-832 d for V9 tags. The V8 transmitter weighed 2.0 g (0.9 g in water) and was programmed to randomly transmit every 80-160 s at 144 db. Whenever possible, we implanted the V8 tags into herring weighing <100 g. Manufacturer's projected battery life (d) ranged from 231-246 d for V8 tags. However, a total of ten V8 tags deployed in 2020 were confirmed to have exceeded the maximum 231 d projected battery life (max = 307 d).

We aged herring tagged in spring 2019 and 2020 using scale-aging protocols developed by Alaska Department of Fish and Game (ADFG) specifically for PWS herring (unpubl. manual). Scales were mounted on microscope slides in the field then later placed under a microfiche reader (50X). An experienced technician then counted scale annuli and recorded either the age in years of the scale or, when that was not possible, recorded them as either regenerated or unreadable.

Acoustic arrays

We deployed 55-66 stationary acoustic receivers (Models VR2W, VR2AR, VR3, and VR4; Vemco Halifax, Nova Scotia, Canada) to monitor fish movements within PWS as well as movements both into and returning from the GOA. At the major entrances into the GOA from PWS, a total of six arrays comprising the entrance arrays were initially deployed in 2013 including at HE, MS, and the four SWPs. Receivers in the entrance arrays are moored approximately 0.7 km apart (SD = 0.1, range = 0.38–0.84 km) with depths ranging from 21 m to 359 m at HE, from 85 m to 232 m at MS, and from 20 m to 92 m at the SWP. A 2017 array expansion consisted of deploying a second, parallel receiver array at each site so that information related to the direction of fish movement could be recorded.

A 2013 study found that 96% –100% of the initial detections at the HE and MS arrays occurred at the receivers closest to the shoreline (Bishop and Eiler 2018). Therefore, at both the HE and MS arrays we deployed a partial, parallel array consisting of two receivers at each end. At the more constricted SWP arrays, each parallel array mirrored the original array and with the parallel array consisting of either one (Bainbridge Passage) or two receivers (LaTouche, Elrington, and Prince of Wales Passages).

On the southeast PWS spawning and tagging grounds, up to 10 receivers were deployed across six arrays at bottom depths ranging from 3 m -74 m throughout the study. During 2018, receivers were also deployed in the inside waters of northern MS (n = 3; July 2018) and southern Knight Island Passage (n = 2; August 2018). One to two other receivers were deployed intermittently at other locations in the Sound (Fig. 2-1).

Receiver data were downloaded 1-2 times a year through 9 May 2022. Previous range tests for the V9, 145 dB transmitters found that signals were regularly detected (>88% of the time) at distances between 200 m and 400 m from receivers (Eiler and Bishop 2016). We assumed that detection rates were similar, but slightly less with the V8, 144 dB transmitter.

Statistical analyses

All data analyses were performed in R (R Core Team 2021). Detection data from receivers were used to investigate herring spatial and temporal use of arrays. When a fish was detected, the date, time, and identity of the fish were recorded. We assumed that an acoustic-tagged fish was present at an array when two or more detections occurred with a 24 h period. Because V8 tags had a shorter estimated battery life compared to V9 tags (~8 mo versus 25+ mo), data from fish with V8 tags were only included where appropriate. An $\alpha = 0.05$ was used to determine significance.

Probability of detection at Gulf of Alaska entrance arrays. Logistic regression models were used to investigate whether certain biological and temporal variables influenced the probability of: 1) herring moving from the tagging grounds to a GOA entrance array (HE, MS, or SWP); and 2) herring initially moving to MS or SWP arrays after tagging. For the first analyses we excluded 28 fish never detected after their release and 12 fish tagged outside of the southeast PWS spawning grounds in 2019. Lastly, the dataset was limited to fish of known sex and encompassed the months of April through July after tagging. For the second analyses examining movements to MS/SWP, we used all first, post-tagging detections at an entrance array. For both analyses, the variables investigated were weight (g), standard length (mm), condition (based on Fulton's condition factor $k = \text{weight}/\text{length}^3$; Kvamme et al. 2003), sex, and tag year. Because of the high correlation of weight, standard length, and condition, these variables could not be included in the same model. Weight was used to find a best model and then standard length and condition were each substituted in to see how results compared to the model with weight. To find the best model to explain the probability of herring moving to an entrance array after tagging, a series of nested models were compared using likelihood ratio tests. For both analyses, age was investigated separately with the fish aged from 2019 and 2020 tag years. All models were fit using the glm command in R (R Core Team 2021).

Travel time to and residency at entrance arrays. One-way analyses of variance (ANOVAs) were used to test whether the average travel time (d) to entrance arrays varied significantly year to year. For these analyses, travel time was calculated as the number of days from release to the initial entrance array detection for fish arriving between April and July of the tag year. Models including year were compared to null models using likelihood ratio tests and Tukey's HSD was used to compare averages among all years.

Mean residency times were estimated at the entrance arrays and in the GOA from April 2017 through June 2021. Residency time (h) at the entrances were based on the time of first and last detection of the first post-tagging entrance where a fish was detected. Fish that went undetected for a period of >24 h were considered to have departed an entrance or spawning ground array. We used linear models to investigate what affected the time spent at a GOA entrance array during the first, post-tagging residency event. In addition to size, other variables considered were date of arrival since April 1, entrance array of first arrival, sex, and tag year, and size. Linear models were fit with different combinations of the variables and compared in R.

For each individual fish detected at an array (defined as two or more detections within a 24 h period), we also totaled detection days and residency or movement events over the entire tracking period of the fish. Once detected at an array, the "residency event" or "movement event" would end either 24 hours after the most recent detection or when the fish was detected at a different array. Therefore if 24 hours passed between consecutive detections at the same array, this was counted as two separate residency events.

Residency in the Gulf of Alaska. A GOA residency was defined as detection at an entrance array, followed by no detections for $\geq$ 14 d, and then detection at an entrance array. Additional rules based on direction were also considered for each analysis. Taking the most conservative approach, we designated a fish as having migrated out from and back into PWS when both the exit detection and return detection occurred along the outer line of receivers. At both the HE and MS arrays this was a partial, parallel array to the primary array, and consisted of two receivers at each end.

Residency length in days was modeled for fish with >14 d stays in the GOA. To maintain independence among observations, only the one residency (the maximum length) from each fish was used. Ordinary least squares (OLS) multiple linear regression was used to analyze how the variables of interest affected GOA residency length. The variables considered included size (weight, standard length, and condition; considered one at a time), sex, exit year (2017-2020), exit season (April-May, June-July, August-March), and exit region (HE or MS/SWP). Twenty candidate models were fit and compared. Interaction terms were considered for size and region and for size and sex. Because no analysis resulted in a heavily weighted, single best model, model averaging was used to reduce bias associated with model uncertainty. For each analysis, all models with 2 AICc of the top model were averaged.

Results

We implanted 726 herring with acoustic transmitters (V9 tags = 576, V8 tags = 150) between 1 and 16 April over a four-year period (2017-2020). Except for 12 fish tagged in 2019 at northern Montague Island, more than 98% (n = 714 of 726) of all fish were tagged within the southeast PWS spawning grounds (Table 2-1). We determined sex for 97% (n = 701) of the fish, while sex was not determined for 25, spawned-out herring. The sex ratio of tagged fish was slightly biased towards males (F:M = 0.9:1.0). Based on scale samples, we were able to estimate the age of 87% (144/165) of the 2019 tagged fish and 67% (157/235) of the 2020 tagged fish. In 2019, mean age was 3.6 ± 0.9 y (range = 3-6 y) for V8 tagged fish and 4.6 ± 1.2 y (range = 3-9 y) for V9 tagged fish. In 2020, our age results showed that 4+ y was the dominant age class for both V8 and V9 tagged fish (V8 = 4.1 ± 0.4 y; range = 4-6 y; V9 = 4.5 ± 0.8 y; range = 3-8 y).

Fish tagged with V8 tags averaged a standard length of 200.4 ± 5.2 mm (range 185-214 mm) and weight averaged 95.5 ± 7.6 g (range 79-117 g). In 2019 V8 tagged herring weighed significantly less on average than fish tagged in 2018 and 2020 (ANOVA; both p's < 0.001). For fish tagged with the larger, V9 transmitter, standard length averaged 214.0 ± 9.6 mm (SD; range 195-260 mm) and weight averaged 121.6 ± 18.4 g (range 94-216 g). In the ANOVA comparisons of V9 tags among years, it was found that the average weight of fish from 2018 (129 g) was significantly higher than any other tag year (p-values all less than 0.02). It was also found that the average length of fish from 2018 (216 mm) was significantly longer than fish from 2020 (212 mm), but not different than fish from 2017 or 2019.

Initial detections at entrances to the GOA

A total of 506 of the 714 herring (70.9%) tagged at the southeast PWS spawning grounds between 2017 and 2020, were detected at the GOA entrance arrays during their first tagging year, including >98% (498/506) between April and 16 July (Fig. 2-2). There was significant support that a model with weight and tag year influenced the probability of detection at a GOA entrance array and was significantly better than simpler models (Table 2-2). The best model estimated that as weight increased, the probability of detection at a GOA entrance array also increased. Depending on the tag year, the overall likelihood of detection was estimated to be slightly different with 2017 being lower overall than other tag years (Table 2-3, Fig. 2-3). Models with standard length and tag year as well as with condition and tag year were also fit and results were similar to the model with weight. There was no significant support that sex influenced the probability of detection at an entrance array. Similarly, when we included only known-age fish in the dataset (tag years 2019 and 2020) there was no significant support that age affected the likelihood of detection at a GOA entrance array. A univariate model including age was compared to the null model and no significant effect from age was found ($\chi_1^2 = 0.05$, $p = 0.80$). Additionally, a bivariate model including age and tag year was compared to the null model and no significant effect from either was found ($\chi_2^2 = 2.5$, $p = 0.28$).

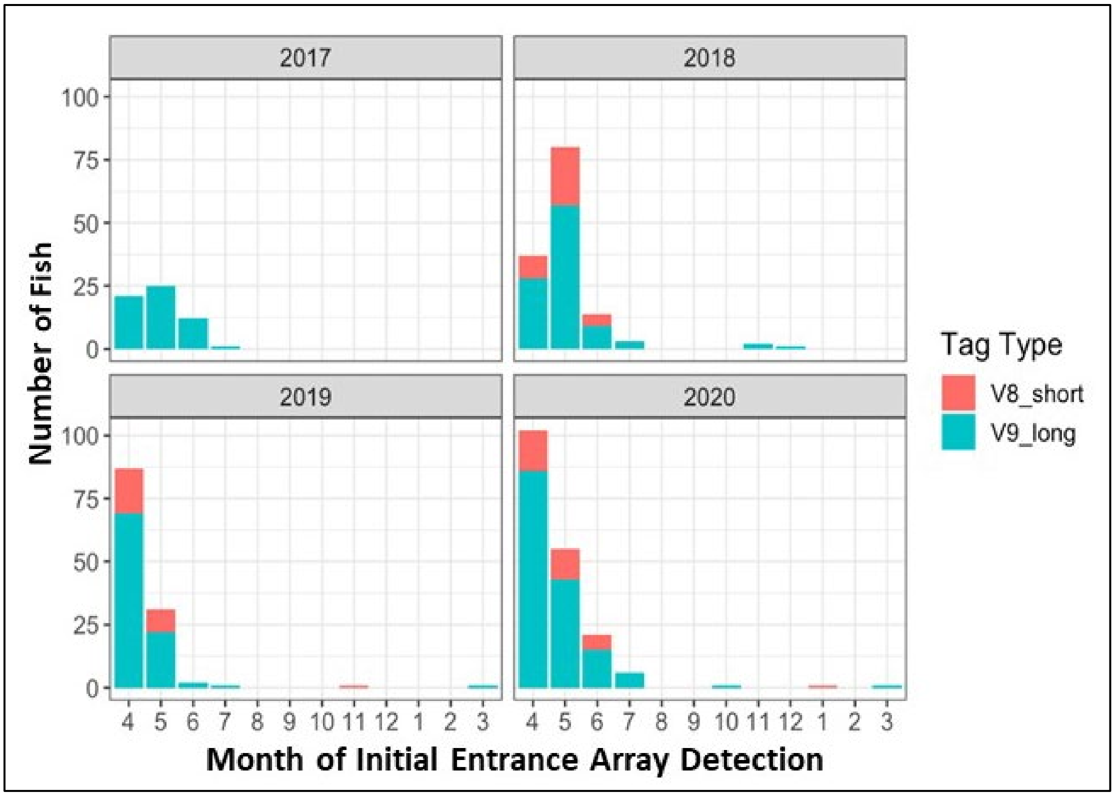


Figure 2-2. Month of initial detection by tag year and tag type for n = 506 fish tagged on the southeast Prince William Sound spawning grounds and detected at a Gulf of Alaska entrance array during their first year (April of tag year – March of following year).

Table 2-2. Summary of the likelihood ratio tests comparing the nested models fit. wt = weight in grams and ty = tag year. A low p-value indicates the more complex model (Model 2) resulted in a significant improvement to model fit compared to the simpler model (Model 1).

Model 1	**Model 2**	**Test Statistic**	**df**	**p-value**
null (intercept)	wt	5.42	1	0.02
wt	wt + ty	56.76	3	<0.001
wt + ty	wt + ty + sex	3.36	1	0.07
wt + ty	wt * ty	0.37	3	0.95
wt + ty	wt * ty + sex	3.63	4	0.46
wt + ty	wt * sex + ty	0.37	3	0.95

Table 2-3. Coefficient point estimates and 95% confidence intervals from the best model. Estimates are on the logit scale.

Variable	**Estimate**	**SE**	**Lower 95% CI**	**Upper 95% CI**
Intercept	-2.44	0.66	-3.75	-1.17
wt	0.019	0.005	0.009	0.029
2018	1.17	0.25	0.68	1.67
2019	2.02	0.31	1.43	2.65
2020	1.54	0.25	1.05	2.04

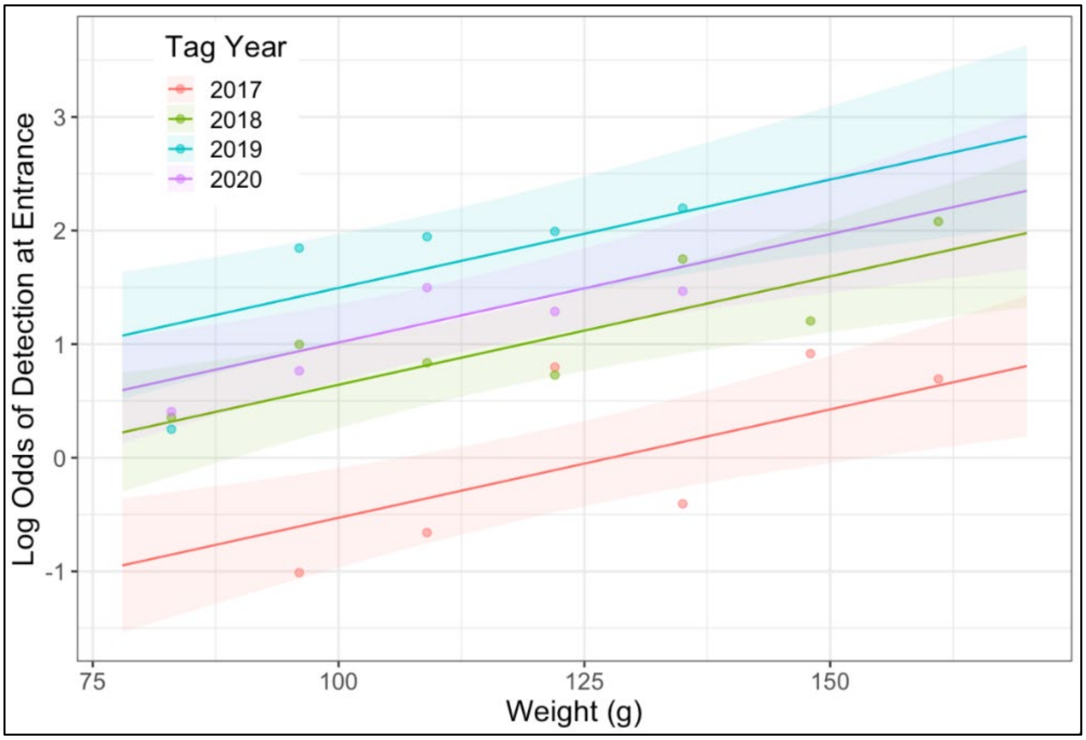


Figure 2-3. Predictions from the model with weight and tag year of the log odds of detection at a Gulf of Alaska entrance array with approximate 95% confidence intervals. Observed log odds were plotted as points by grouping observations into 10-15 g weight bins.

HE was the initial entrance array for 86% of the herring tagged on the southeast PWS spawning grounds (427/506), followed by MS (12%) and the SWP (2%) (Fig. 2-4). While only 12 fish were tagged at northern Montague Island's Rocky Bay, 11 of the 12 were detected at the GOA entrance arrays with initial entrance detections highest at MS (45%; 5 of 11) and equal percentages detected at SWP (Elrington Passage) and HE (both 27% and 3 of 11).

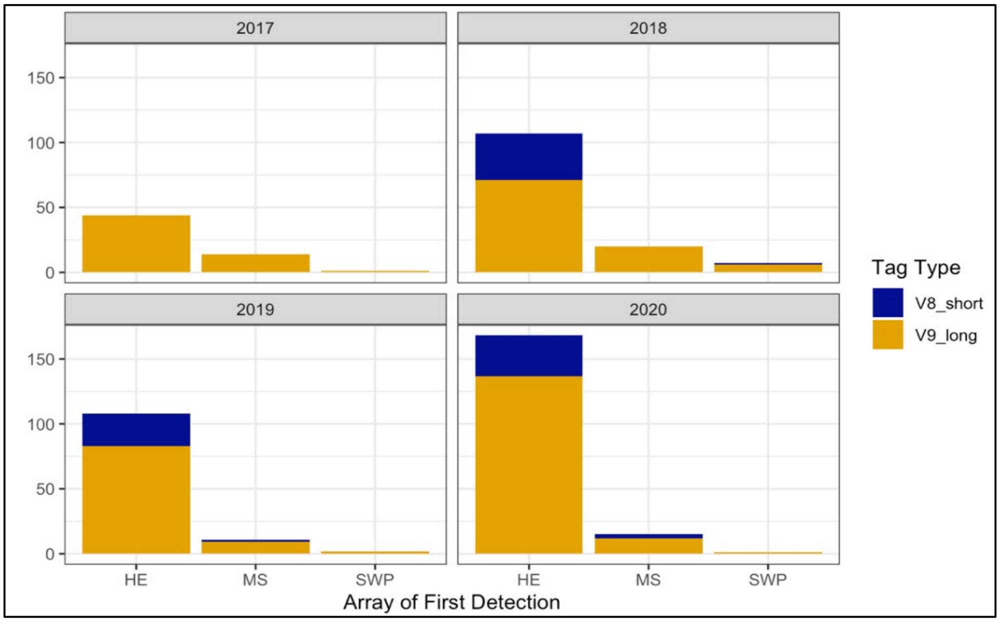


Figure 2-4. Array location by tag type and tag year of the initial detection at a Gulf of Alaska entrance array for 498 herring tagged on the southeast Prince William Sound spawning grounds. Array locations include Hinchinbrook Entrance (HE), Montague Strait (MS), and Southwest Passages (SWP).

We estimated the probability that the first detection at a GOA entrance array would occur at either MS or the nearby SWP. Initially, we used the data set comprised of the 235 known-age fish, however, no variable was found to be significant. Because age was not shown to significantly affect the probability compared to the null model ($\chi^2 = 0.47$ on 1 df, $p = 0.49$), analysis continued with all 517 fish detected at the entrance arrays. Both weight and standard length were found to significantly affect the probability of a first detection at MS/SW. Continuing the analyses using weight, a univariate model was found to be significantly better than the null model ($\chi^2 = 15.44$ on 1 df, $p < 0.001$) and a model with both weight and tag year was found to be marginally better than the model with weight alone ($\chi^2 = 6.7$ on 3 df, $p = 0.08$). Both models found that as weight increased, the probability of first detection at MS/SW over HE increased. The model with tag year additionally found that the overall probability varied somewhat year to year, with 2020 having the lowest overall probability of a first detection at MS/SW (Fig. 2-5).

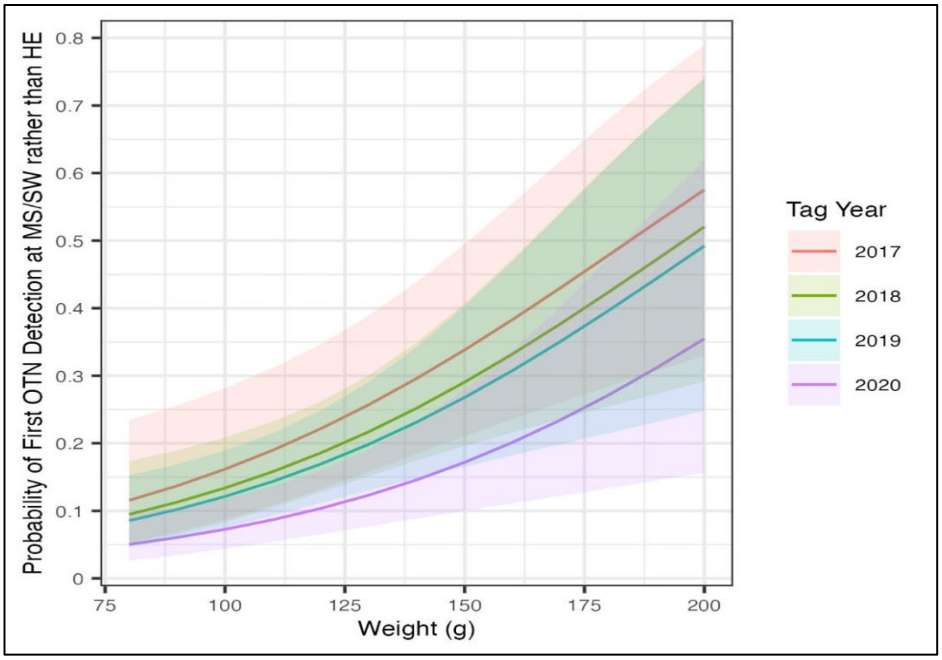


Figure 2-5. Using a model from 517 fish detected at a Gulf of Alaska Ocean Tracking Network (OTN) entrance arrays in the year after tagging, it was estimated that the probability of a first array detection at Montague Strait (MS) or Southwest Passages (SWP) rather than Hinchinbrook Entrance (HE) increased as weight increased, and that the overall probability varied based on the tag year with 2020 tag year fish having an overall lower probability of first detection. The relationship between weight and odds was estimated to be the same for each year.

Travel time to entrance arrays

Average travel time from the southeast PWS spawning grounds to HE (release to arrival) ranged from 14.3 d (2019) to 29.8 d (2018). Travel time to HE was significantly shorter in 2019 than all other years ($p < 0.001$ for each) and included five fish arriving within 24 h of release. Average travel time from release to arrival at MS ranged from 32 d (2018) to 69.1 d (2020), with the 2020 travel time significantly longer than all other years (comparison with 2019: $p = 0.007$, comparison with 2017 and 2018: $p < 0.001$). Travel time to SWP was excluded due to small sample sizes (Fig. 2-6).

Residency at entrance arrays

Residence time at GOA entrance arrays tended to be relatively short. Using data from the first entrance residency event, residencies averaged 10.22 h (range = 0.02 – 185.98 h; n = 487 fish). The best linear model had relatively high support (63.44%) and included the variables log(date), tag year (TY), and weight. In general, however, here was a large variation (SD = 20 h) in the model's estimates of residency time. The overall conclusions were that the average residency time increased over time and as the herring weight increased. In addition, average residency time

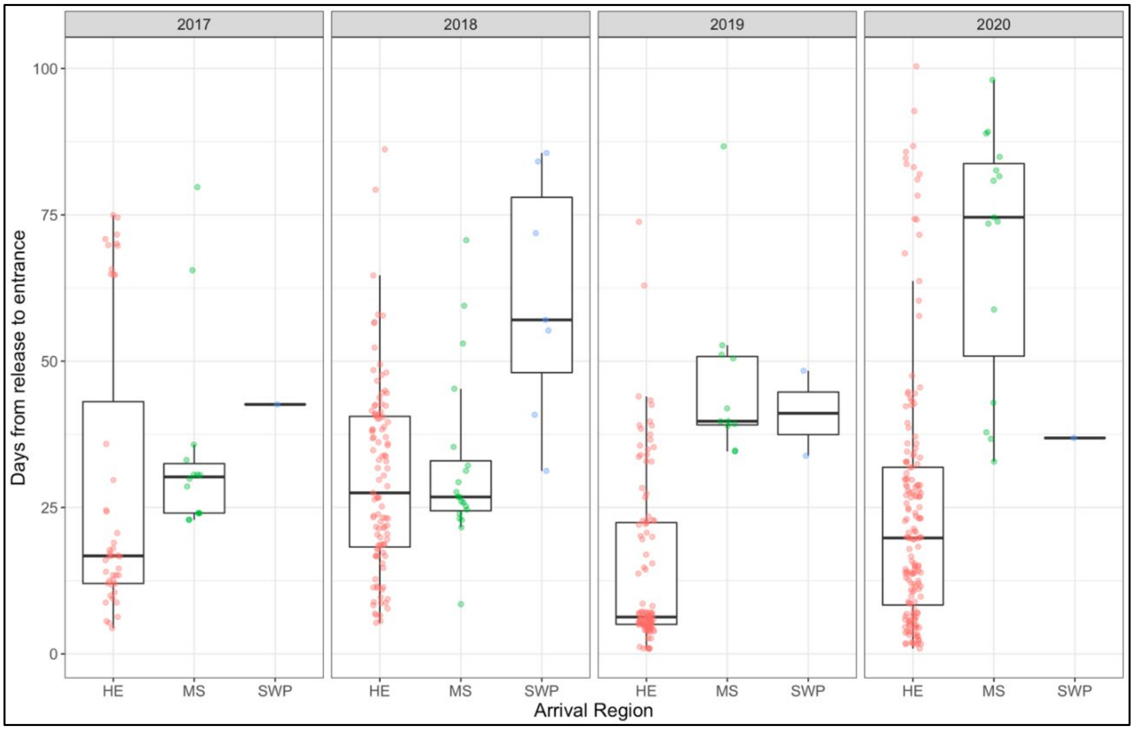


Figure 2-6. Number of days from release to Gulf of Alaska entrance array by tag year. HE = Hinchinbrook Entrance, MS = Montague Strait, and SWP = Southwest Passage arrays.

in 2018 and 2019 was shorter than in 2017 (Fig 2-7). There was no significant support that average residency time varied due to sex or entrance array.

Among the entrance arrays to the GOA, MS recorded the highest average number of detection days (nonconsecutive) as well as the highest number of residency/movement events per individual herring, followed by the nearby SWP arrays (Table 2-4). MS also had the most consistent use throughout this study. Over a 50-month period, April 2017 – June 2021, fish were detected at the MS array in all but one month (Fig. 2-8). By comparison, HE and SWP each had several months when no fish were recorded (Figs. 2-9, 2-10).

Movements immediately following initial residency at entrance arrays

Following their initial post-tagging residency at an entrance array, 6% (33/517) next moved out into the GOA followed by a return. Most of these fish (21 of 33) were considered migratory (residency in the GOA ≥ 14 d before returning to PWS). Of the remaining fish, 29% (148/517) were never again detected following their initial entrance array residency, 6% (33/517) were next detected back on the spawning grounds, while 59% of all fish (303/517) returned to the same entrance array or moved to another array.

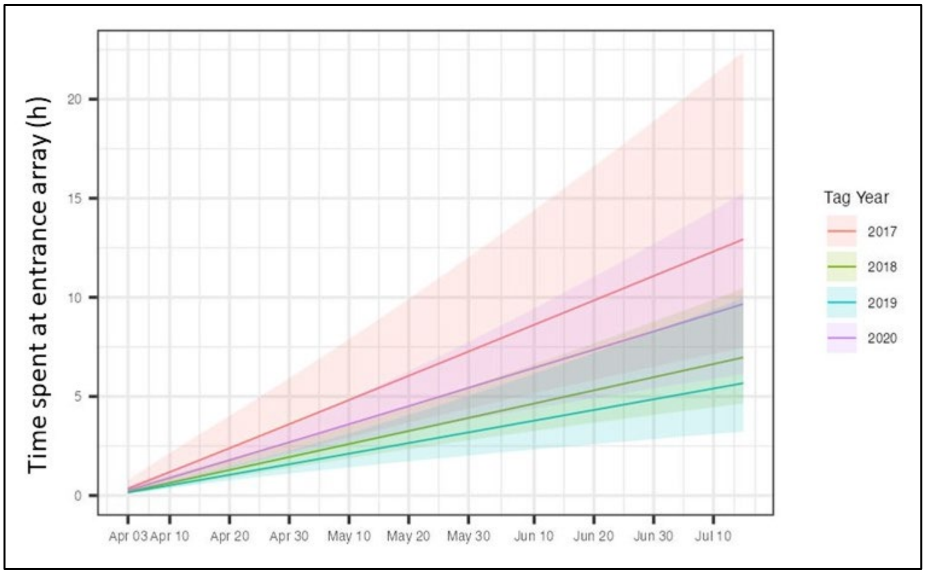


Figure 2-7. Results from the best fit model including log(date), weight, and tag year. Here, the average time spent at the Gulf of Alaska entrance array in hours was predicted with 95% confidence. Results were backtransformed to be shown on the original scale. Here, how results change over date and tag year is shown while weight was held at 115 g.

Table 2-4. Number of detection days and number of residency/movement events by array for tagged Pacific herring, April 2017-June 2021.

	Days Detected		**Residency/ Movement event**	
Gulf of Alaska Entrance Array	**Avg**	**Max**	**Avg**	**Max**
Hinchinbrook Entrance	4.2	37	2.6	15
Montague Strait	12.2	88	6.7	48
Southwest Passages (combined)	7.7	67	3.1	20
Elrington	6.3	64	2.4	17
Prince of Wales	5.9	46	1.9	8
Bainbridge	2.3	8	2.0	6
LaTouche	1.8	4	1.4	3

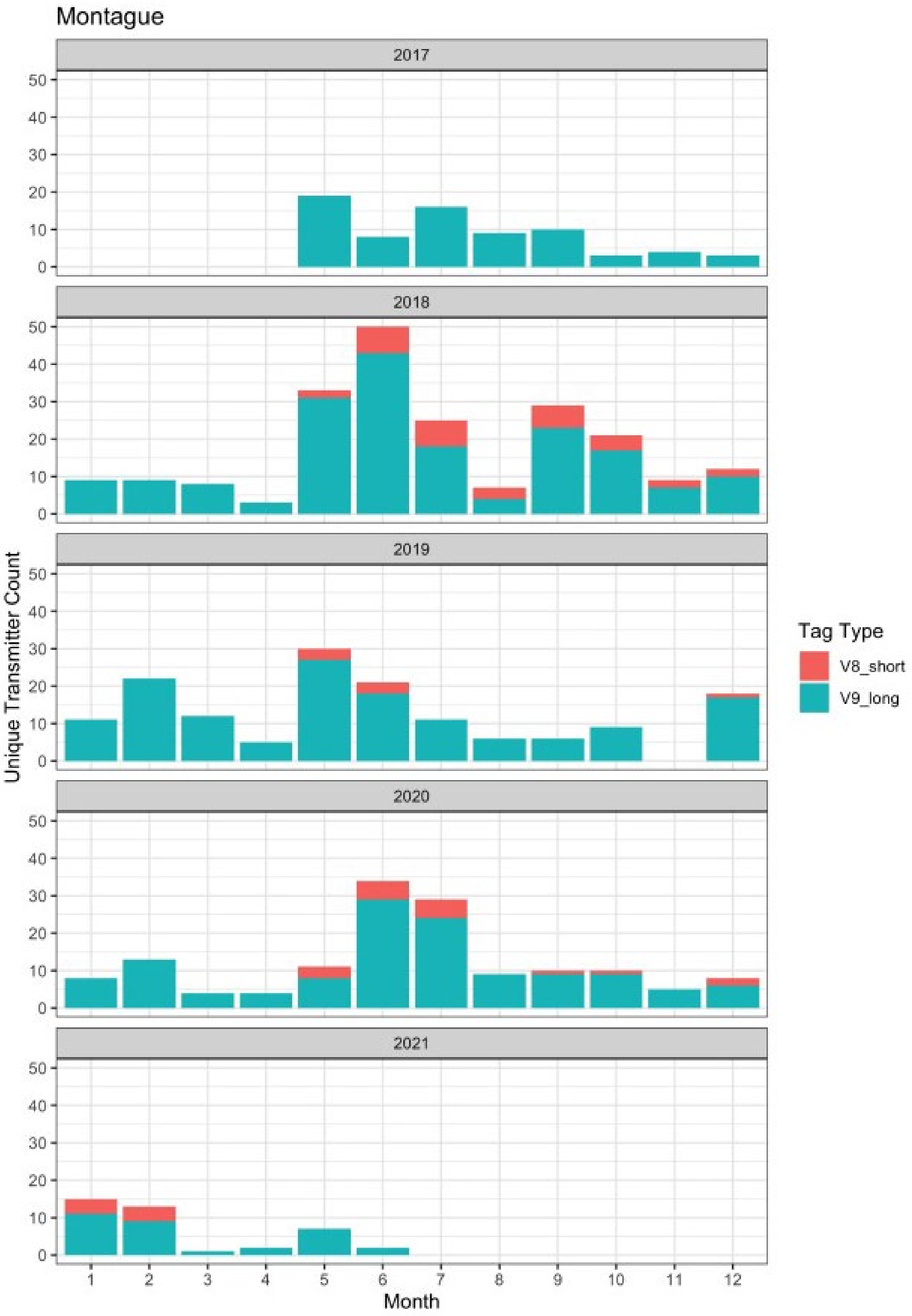


Figure 2-8. Number of acoustic tags detected by month, year, and tag type at Montague Strait entrance array, April 2017 – June 2021.

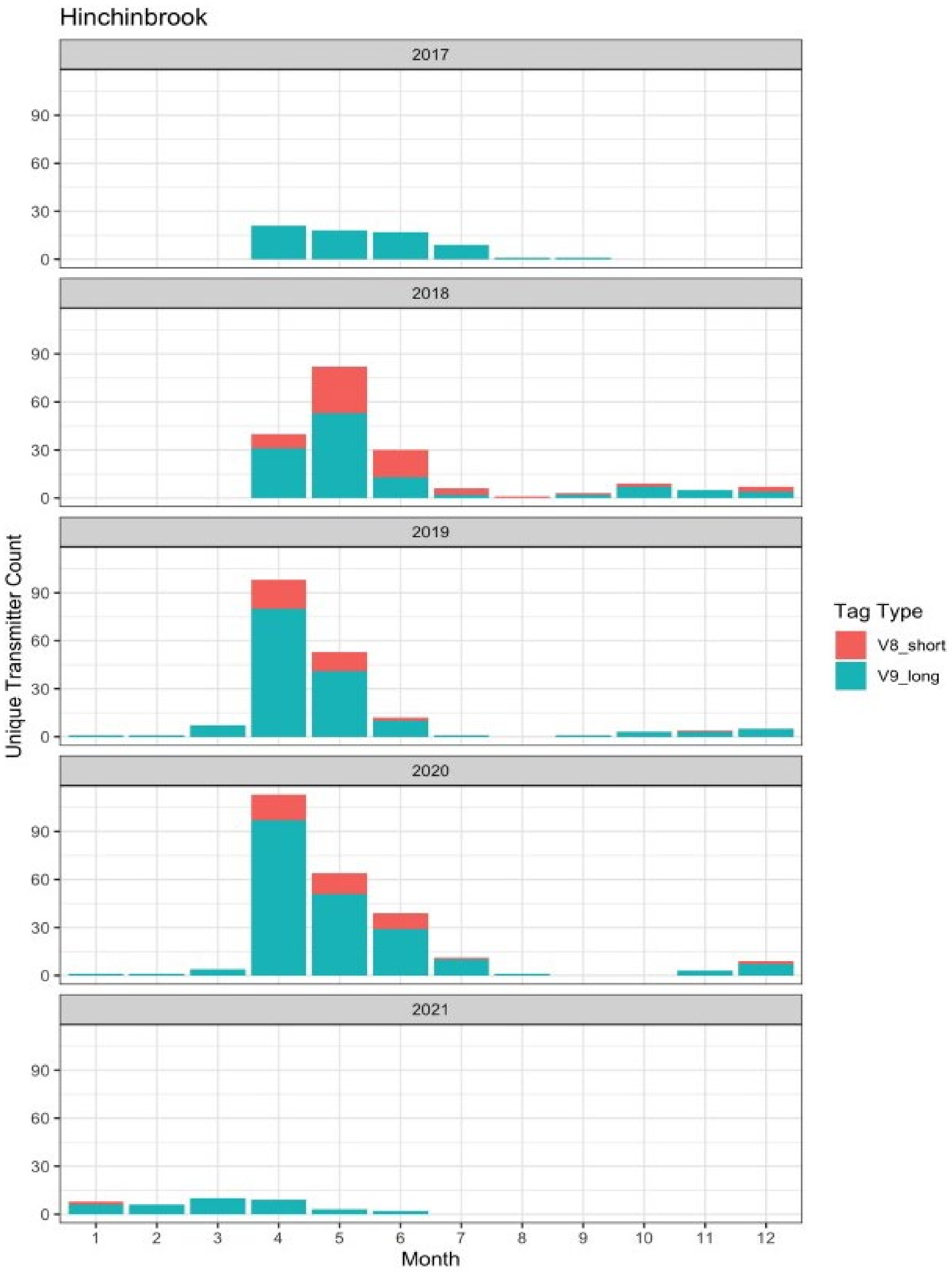


Figure 2-9. Number of acoustic tags detected by month, year, and tag type at Hinchinbrook Entrance array, April 2017 – June 2021.

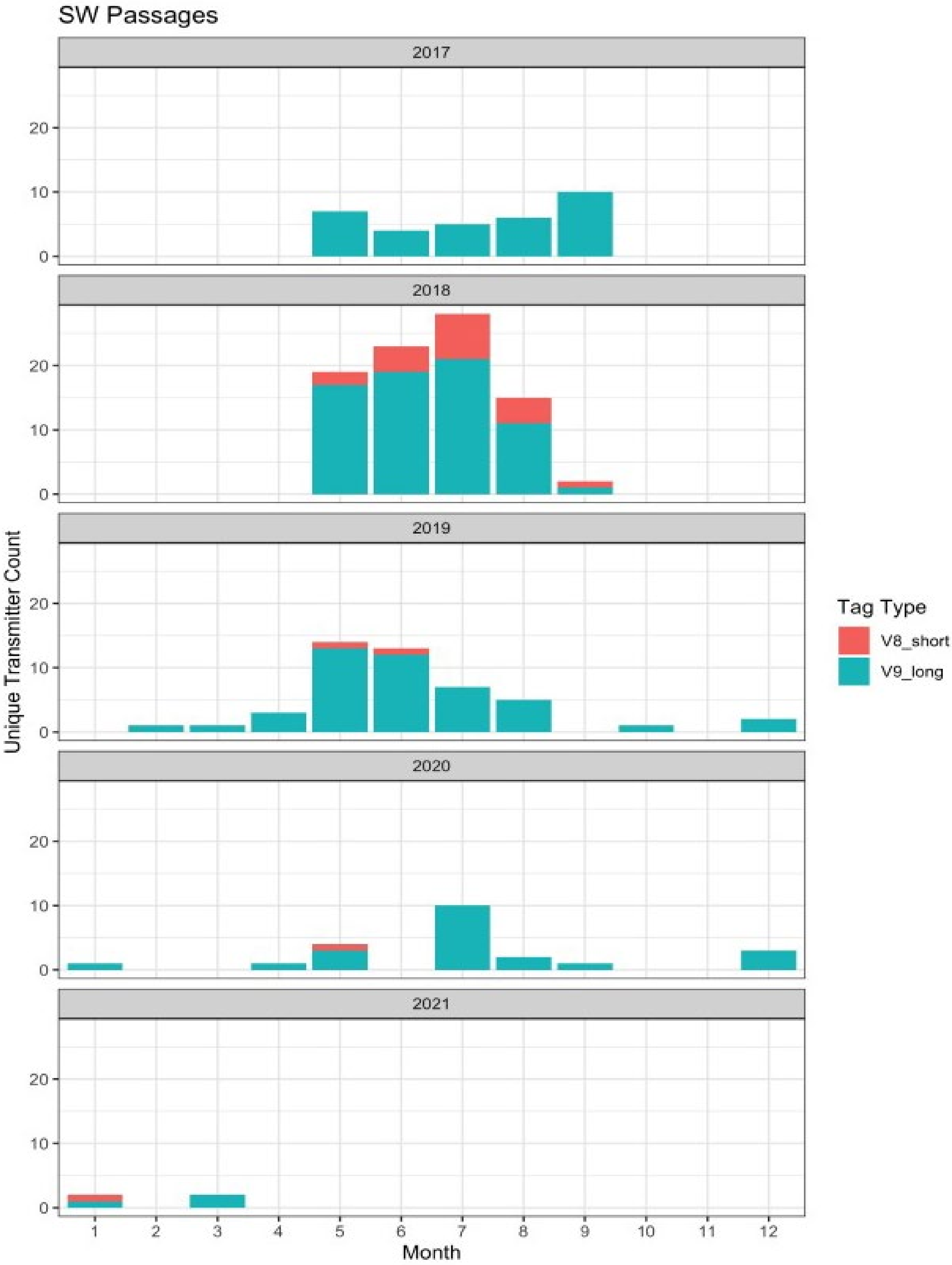


Figure 2-10. Number of acoustic tags detected by month, year, and tag type at the four Southwest Passages (Elrington, Prince of Wales, Bainbridge, and LaTouche, April 2017 – June 2021.

Timing of migratory movements

There were 162 migratory movements by 104 tagged herring over a 4-year period (April 2017-March 2021) based on exit and return detections at the outermost entrance arrays. Migratory movements out into the GOA from HE and SWP were highly seasonal, primarily April-mid-June at HE, and May-early July at SWP although there were no documented exits out of SWP during 2020. In contrast to HE and SWP, migratory movements out from MS into the GOA occurred regularly during the 9-10 months after spring spawning (Fig. 2-11).

Across the four years, herring were recorded returning from the GOA throughout the year except for March (n = 1) and April (n = 0). While returns from the GOA through HE occurred primarily from May through October, we did detect tagged fish returning between November and March. Fish returning through the SWP were detected almost exclusively June and July. While fish returned through MS typically from June through February, peak number of fish returning occurred during the winter months: January 2018, February 2019, and December 2019 (Fig. 2-12).

Residency in the GOA

Average residence time in the GOA was 66.9 ± 64.2 (SD), and maximum residency time in the GOA was 309 d (Fig. 2-12). MS was used most often as an exit into the GOA and as a return from the GOA from spring through winter (Fig. 2-13). Fish exiting through HE and returning to PWS via SWP had the longest GOA residency times (112.9 d, n = 6; Fig. 2-14). Over 40% (n = 66) of the GOA 162 residency events involved fish exiting from and returning along the western shoreline of MS. Of the 162 occurrences where we could estimate residency time, almost 25% (40/162) were in the GOA for >3 months (max = 309 d) and 53% (21/40) returned during either December or January (Fig. 2-13).

We used multiple linear regression to understand the factors influencing residency time in the GOA. After averaging the top 3 models, results indicated that the interaction of length and exit array had a significant effect on the GOA residency time (Table 2-5). Sex was also included in this averaged model but was not found to be significant. Standard length positively affected average GOA residency time for fish exiting from HE, but not for fish exiting from MS/SWP. For condition and weight models, no variables were found to significantly affect average residency time in the GOA.

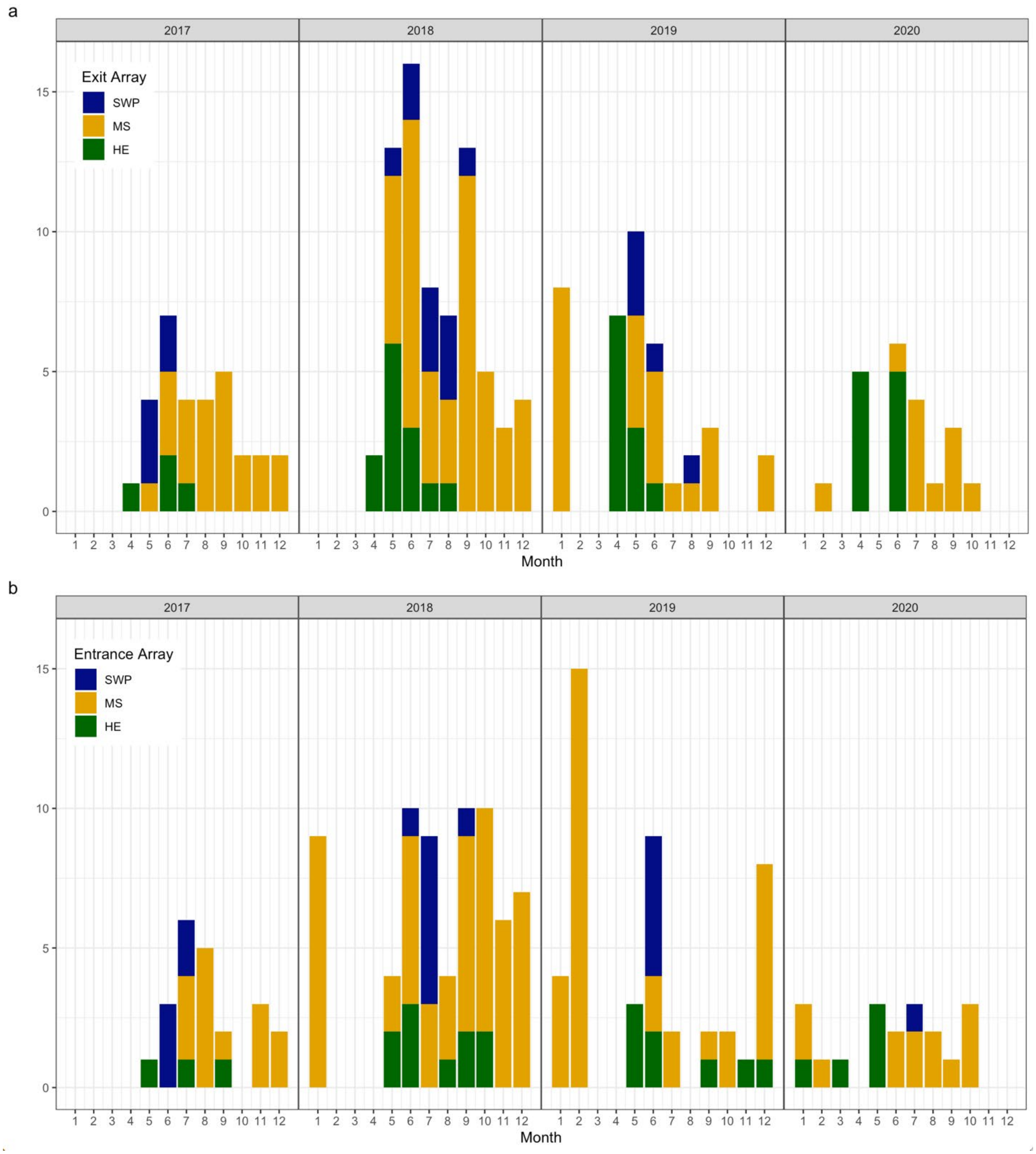


Figure 2-11. Number of fish exiting by month from Prince William Sound into the Gulf of Alaska (a, top) and returning to Prince William Sound from the Gulf of Alaska (b, bottom) by entrance array during years 2017 through 2020. SWP = Southwest Passages, MS = Montague Strait, HE = Hinchinbrook Entrance. Numbers reflect fish with residence time in Gulf of Alaska ≥ 14 d.

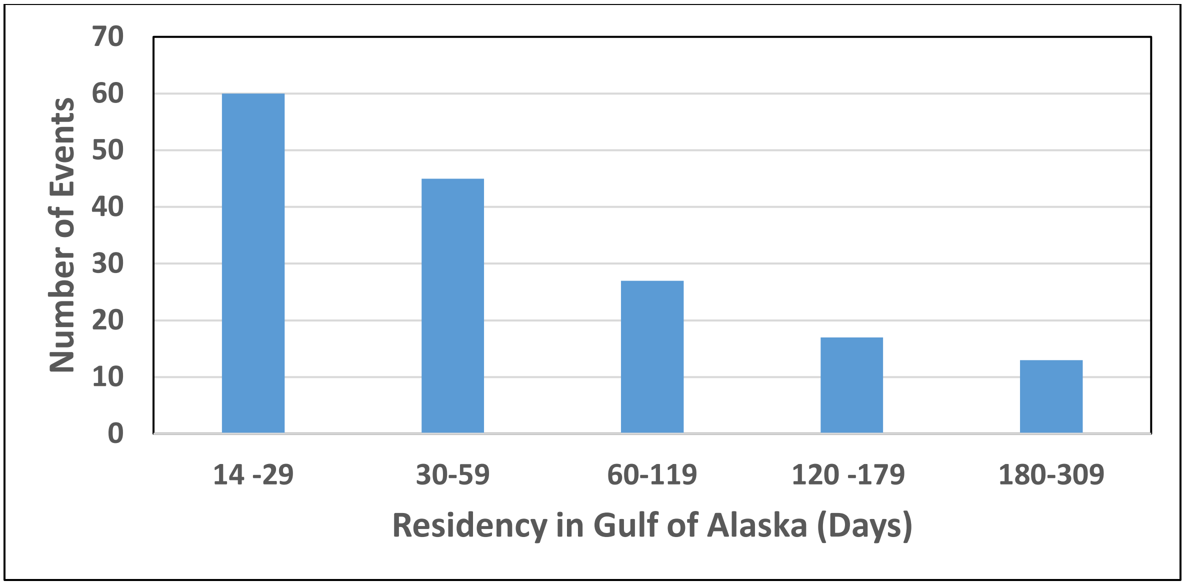


Figure 2-12. Residency (d) for fish exiting to and remaining in the Gulf of Alaska ≥ 14 d, followed by a return to Prince William Sound. N = 162 residency events representing 104 individual fish between April 2017 – March 2021.

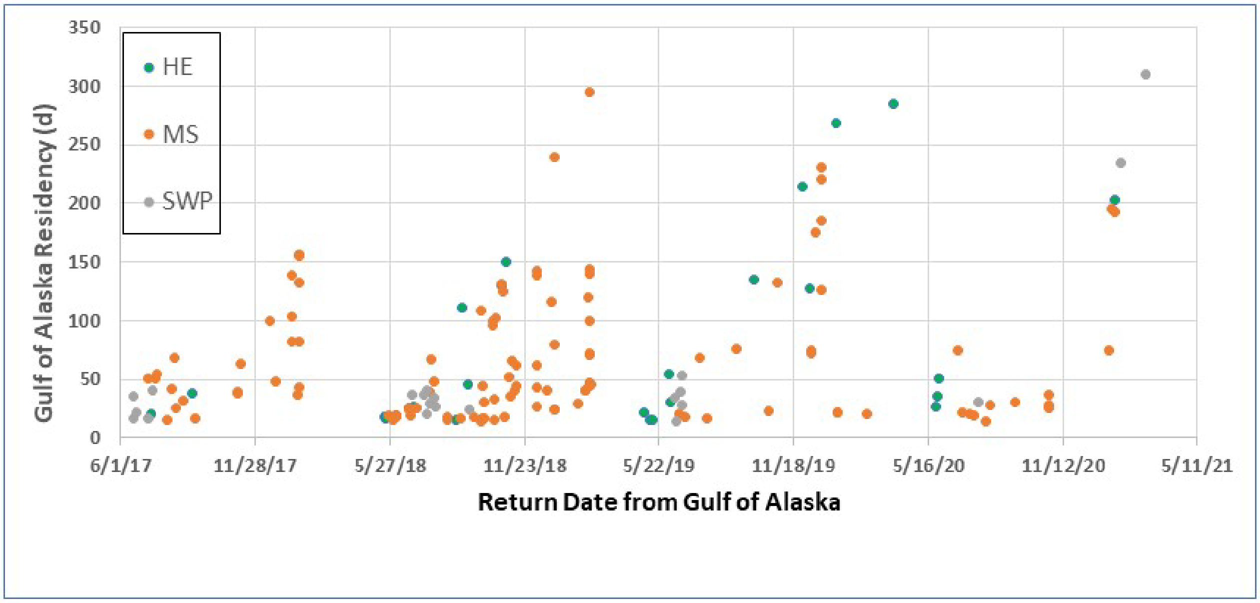


Figure 2-13. Residency time (d) in the Gulf of Alaska calculated as a function of their return date to Prince William Sound and their return entrance array. HE = Hinchinbrook Entrance, MS = Montague Strait, and SWP = Southwest Passages. Note the tendency of fish with longer stays to return to the Sound during winter months (December-February).

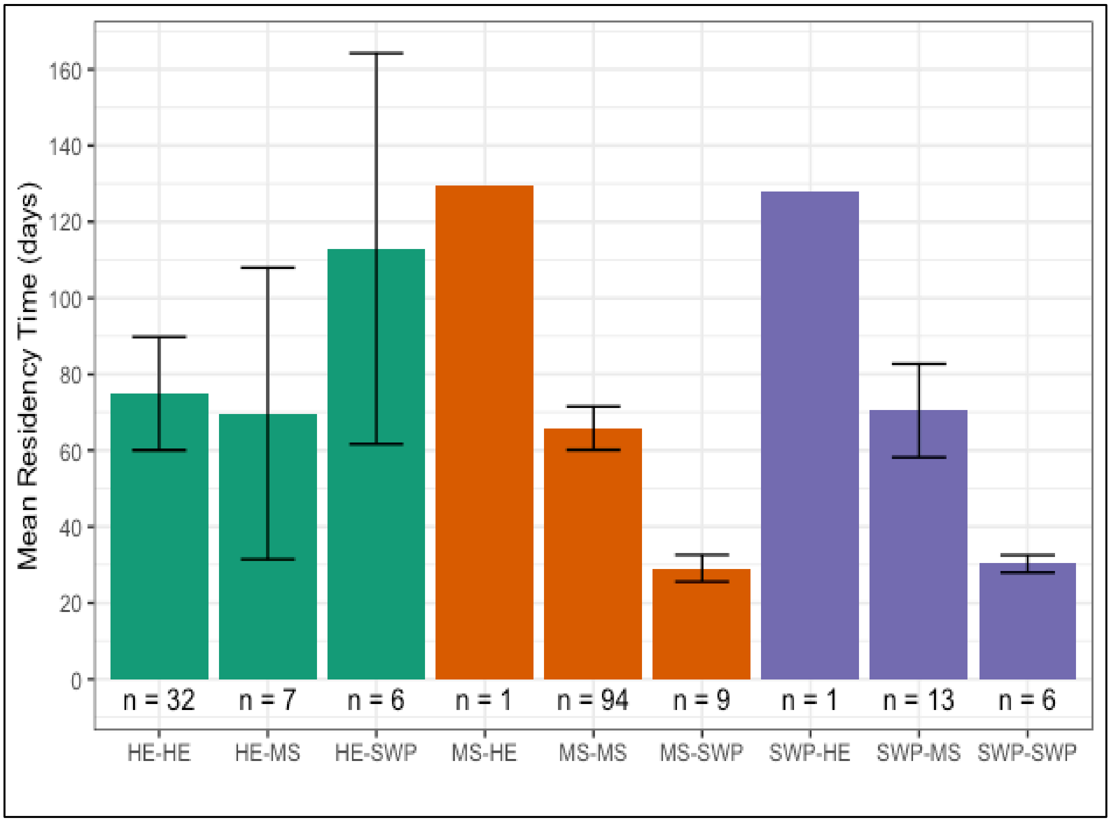


Figure 2-14. Mean (±SE) residency time (d) for fish exiting to and remaining in the Gulf of Alaska ≥ 14 d, followed by a return to Prince William Sound. Residency estimate shown by exit and return entrance arrays. Exit Arrays: HE = Hinchinbrook Entrance (red), MS = Montague Strait (green), SWP = Southwest Passages (blue). n = total exit/return where residency could be estimated for a total of 104 individual fish and 162 residency events between April 2017 and March 2021.

Table 2-5. Variables influencing residency time in the Gulf of Alaska. Estimates and 95% confidence intervals for the result of averaging all models within two AIC of the top model using the variable length. Note that these estimates are on the log scale.

Term	**Estimate**	**Lower 95% CI**	**Upper 95% CI**
(Intercept)	-5.856	-11.836	0.123
sl	0.047	0.018	0.075
exit_region_combMS/SWP	8.971	2.119	15.823
SexM	-0.181	-0.611	0.032
exit_region_combMS/SWP:sl	-0.041	-0.073	-0.009

Discussion

This project marks the first, long-term study of large-scale movements of individual Pacific herring. We were able to detect herring up to 25 months including three spring spawn events. In general, migration patterns from the spawning grounds were similar between years with most tagged fish moving south and arriving between April and May at the entrance arrays to the GOA. We detected both outmigration into the GOA (>14 d in the GOA) and return movements into PWS from April through February. Of the six entrance arrays, MS was used almost year-round, while HE and the four SWP were used almost exclusively spring through the end of August. This strongly suggests that the waters around HE and SWP arrays are summer foraging areas and are spring/summer migration corridors to the GOA whereas both southern MS and the GOA are used as summer foraging and overwintering areas.

Our analyses revealed that the likelihood of movement from the spawning grounds to the entrances increased with weight and depended on the tag year. Fish tagged in 2017 were less likely to move to the entrance arrays. While weights of 2017 herring were lower than 2018 tagged fish, they were not significantly different from 2019 and 2020 tagged herring. We suggest that high predation on the spawning grounds was the likely the cause of fewer herring at the entrances in 2017. ADF&G aerial surveys for herring spawn recorded one to three humpback whales and >175 sea lions in the area during our tagging activities (S. Shepard, ADF&G, unpubl. data).

We found no significant support for age affecting the likelihood of moving to the entrance arrays after spawning. We would expect that if the likelihood of moving increased with weight it would also increase with age, because on average, weight increases with age. However, only 278 fish of the 726 tagged herring were aged during this study, with tag years 2019 and 2020 comprising the age sample. And, of the fished aged, almost one-half were determined to be age 4+. Therefore, while our analyses did not show a relationship, another sample with a better spread and representation of ages might show that age does influence the likelihood of movement to the entrances.

HE is the closest array to the tagging grounds (22-55 km) and in this study was the initial, post-spawning entrance array used by 86% of the tagged fish. These results contrast with our 2013 pilot study results. During that study, MS had the highest number of initial detections (58%), followed by HE (30%) and SWP (12%) (Bishop and Eiler 2018). Corten (2002) suggested that observed herring migration patterns are not innate but are a learned behavior that initially happens when the recruiting year class follows older herring. We speculate that the change in initial movement patterns from MS observed in 2013 to almost exclusively HE by 2017 was associated with reduced numbers in older herring. This trend began in 2016 when ages 3+ and 4+ began to numerically dominate and continued until 2020 with ages 3+ and 4+ comprising 64% (2016) to 90% (2020) of the adult population each year. In contrast, during the 2013 study, only 26% of the adult population were ages 3+ and 4+ and we estimated that >80% of the fish we tagged were age ≥ 7+ and weighed on average 182.9 g compared to 121.6 g during the current study, and supports this study's model that weight, and standard length positively influence the probability of a first detection at MS.

Even though HE accounted for >85% of the first entrance array detections, it was used as an exit into the GOA exclusively during the spring and summer months and used by very low numbers of tagged herring outside of those seasons. In contrast, except for during spawning, MS was used by migrant herring throughout the year and was by far the most important exit and return entrance. This is similar to what Bishop and Eiler (2018) observed during the shorter, nine-month pilot study in 2013 when MS recorded almost 3x the number of individual tags as HE and recorded ≥2 fish per month during 8 of the 9 study months compared to only 3 of the 9 months at HE.

These similarities between 2013 and the 2017-2020 tagged fish migration patterns support Corten's observations of the congeneric Atlantic herring, that herring migration patterns tend to be stable over years, despite environmental variation. Furthermore, we suggest that the preference for MS is related to its circulation patterns in PWS. Both circulation in PWS and seasonal northeast winds are weak during spring (Wang et al. 2001), creating conditions that favor herring moving to either HE or MS. From June through October, circulation patterns shift in HE such that both inflow and outflow can occur simultaneously at HE while at MS outflow remains weak (Musgrave et al. 2013, Halverson et al. 2013).

The proportion of fish that we observed migrating out to the GOA and returning to PWS (14%; 104/726) should be considered a minimum. Our definition of migration was conservative as it was defined as a ≥14 d absence following a last (exit) and first (return) detection at the outermost parallel array. While the arrays at SWP had equal number of parallel receivers in both the inner and outer arrays, the innermost arrays consisted of 16 receivers at HE and 11 receivers at MS whereas the outermost arrays consisted of only 2 receivers at each end for a total of 4 receivers each. We did record several fish whose exit detection was at an inner array, but the return detection was at outer array, as well as fish whose exit detection was at an outer array but return detection was at the inner array. Given the distance between receivers and arrays, as well as the presence of only a partial, parallel outer array at HE and MS, migratory movements were undoubtedly underestimated.

CHAPTER 3 SPAWNING SITE FIDELITY BY PACIFIC HERRING IN PRINCE WILLIAM SOUND

Mary Anne Bishop and Elaine Gallenberg

Introduction

Spawn site fidelity, that is, the repeated return by an adult fish to the same breeding habitat, is common in iteroparous fish such has herring (Secor 2015). While many studies have related herring spawn site fidelity to spawning events (c.f. McQuinn 1997, McGowan et al. 2021) site fidelity in adults can also occur outside of the spawning season. During winter, adult Pacific herring along the eastern Pacific Ocean often return to coastal areas and remain close to spawning areas and in nearshore channels (Hay and McCarter 1997). This behavior has also been observed in PWS herring populations, where historically large schools both overwintered and spawned around northern Montague and Green Islands. Beginning in 2003, the distribution of overwintering and prespawning aggregations of herring has been more restricted, with herring only located consistently in the northeast and southeast areas of PWS, just outside of Port Fidalgo and Port Gravina, respectively (Thorne 2010; ADF&G herring portal http://data.aoos.org/maps/pwsherring/).

In this chapter we examine the year-round use of the southeast PWS spawning grounds. Based on detections of acoustic tagged fish, we examined movements out from and back to the spawning grounds where they were tagged. Here we provide detailed information on the timing of departure from the spawning grounds, temporal and spatial movements within the spawning grounds, and the biological and temporal variables influencing the likelihood of movements.

Methods

Study area

PWS is located on the coast of southcentral Alaska, primarily between 60° and 61°N. The Sound is separated from the adjacent GOA by large mountainous islands. The coastline is rugged and extensive, with many islands, fjords, and bays. Water depths in fjords and bays range from <50 M to > 400 m; outside of the bays and fjords are many basins and passages of varying depths up to 700 m. Tagging took place in southeast PWS around Orca Bay and Port Gravina. Since 1999, this area has accounted for the highest annual proportion of total spawn in PWS (McGowan et al. 2021).

Fish capture and tagging

We captured and acoustic-tagged adult Pacific herring in PWS while in prespawning aggregations during April over a period of four years, 2017-2020 (Table 3-1). All captures and tagging took place at the southeast PWS spawning grounds (Fig. 3-1), except for 2019 when a small number of fish (n = 12) were tagged at northern Montague Island. Details describing herring capture, handling, and tagging methods have been described previously (Eiler and Bishop 2016). Briefly, fish were captured using barbed fishing jigs and then placed in a holding tank (770 L capacity). Individual fish were then transferred to a circular tub and anesthetized, weighed, measured (standard length) and placed in a tagging cradle. We made a small incision along the ventral midline to determine sex and to surgically implant an acoustic transmitter. Post-surgery, both tagged and untagged (i.e., not sedated, measured, or tagged) herring from the capture event were held together in a tank to ascertain when tagged herring had recovered from sedation and exhibited normal swimming and schooling behavior. Tagged and untagged herring were released together near a herring school. All capture procedures and protocols were approved by the PWS Science Center Institutional Animal Care and Use Committee.

We implanted into herring either a V9 or V8 transmitter (Models V9-2x, V9-2x-BLU-1, or V8-4x, 69 kHz; Innovasea, Halifax, Nova Scotia, Canada). The V9 transmitter weighed 4.7 g (2.9 g in water) and was programmed to randomly transmit an encoded signal every 70-150 s at 145 db (Model V9-2x) or 146 db (Model V9-2X-BLU). Manufacturer's projected battery life (d) ranged from 755-832 d for V9 tags. The V8 transmitter weighed 2.0 g (0.9 g in water) and was programmed to randomly transmit every 80-160 s at 144 db. Whenever possible, we implanted the V8 tags into herring weighing <100 g. Manufacturer's projected battery life (d) ranged from 231-246 d for V8 tags. However, a total of ten V8 tags deployed in 2020 were confirmed to have exceeded the maximum 231 d projected battery life (max = 307 d).

Table 3-1. Number of tags deployed on Pacific herring by tag type, first and last dates of tagging activities, and of spawning events in Prince William Sound, 2017-2022. Except for 12 fish, all herring were tagged on the southeast Prince William Sound spawning grounds. Range of spawning dates is for all spawning events throughout the Sound.

	Tag Type		**Dates**[a]	
Year	**V9**	**V8**	**Tagging**	**Spawning**
2017	124		4/9-4/16	4/13-4/21
2018	142	60	4/8-4/13	4/7-4/17
2019	125[b]	40	4/2-4/10	3/26-5/3
2020	185	50	4/1-4/8	4/2-5/2
2021	-	-	-	3/28-4/29
2022	-	-	-	4/2-4/27

[a] Spawning dates from Vega et al. 2018, Russell et al. 2019, Morella et al. 2020, Botz et al. 2021., Alaska Department of Fish & Game unpubl. data.

[b] Includes 12 herring tagged in Rocky Bay, Montague Island

Acoustic arrays

A series of receivers (Models VR2W, VR2AR, and VR3; Vemco, Halifax, Nova Scotia, Canada) were deployed in the southeast PWS spawning grounds to monitor the movements of acoustic-tagged herring (Fig. 3-1). Depending on the year and season, from 8 April 2017 through 9 May 2022, a total of 6 to 10 receivers were deployed across six arrays (Fig. 3-2; Appendix Table A-1). One array (Port Gravina) was deployed throughout the duration of the study. Four arrays (Cedar, Canoe Pass, Redhead 1, and Redhead 2) were initially deployed mid-September 2018, while the Johnstone Point array was deployed September 2019. While most array receivers were deployed within 2 km of the shoreline (min = 368 m), Redhead 1 and Redhead 2 in Orca Bay were 7.3 km and 3.8 km from shore, respectively. Bottom depths of receiver moorings ranged from 3-74 m. Receiver data were downloaded 1-2 times a year through 9 May 2022. Previous range tests for the V9, 145 dB transmitters found that signals were regularly detected (>88% of the time) at distances between 200 and 400 m from receivers (Eiler and Bishop 2016). We assumed that detection rates were similar, but slightly less with the V8, 144 dB transmitter. Fish swimming within reception range of a receiver were detected and the date, time, and individual identity of the fish recorded.

Depending on the year, a total of 49 to 56 receivers (Models VR2W, VR2AR, VR3, and VR4; Vemco Halifax, Nova Scotia, Canada) were deployed in other areas of PWS (Fig. 3-1). These receivers were used to determine survival status for fish not detected on the southeast PWS spawning grounds. Six arrays (n = 49 receivers), initially deployed in 2013 and expanded in February 2017, are part of the Ocean Tracking Network (Dalhousie University, Halifax, Newfoundland, Canada) and are located at the entrances into the GOA from PWS. In 2018, an additional five receivers were deployed in the inside waters of northern Montague Strait (n = 3; July 2018) and southern Knight Island Passage (n = 2; August 2018). One to two other receivers were deployed intermittently at other locations in the Sound throughout the study (Fig 3-1). Data from receivers outside of the spawning grounds study area were downloaded every 6 or 12 mo through 7 April 2022.

Statistical analyses

Detection data from receivers were used to investigate herring spatial and temporal use of the southeast PWS spawning grounds. We assumed that an acoustic-tagged fish was present at an array when two or more detections occurred with a 24 h period. Due to the presence of only one receiver array on the southeast PWS spawning grounds between September 2017 through March 2018, data from fish tagged in 2017 are excluded from some analyses. In addition, because V8 tags had a shorter estimated battery life compared to V9 tags (~8 mo versus 25+ mo), data from fish with V8 tags were only included where appropriate. We also excluded data from 12 herring implanted with V9 tags at northern Montague Island in 2019. All data analyses were performed in R (R Core Team 2021). Significance was evaluated using an α value of 0.05.

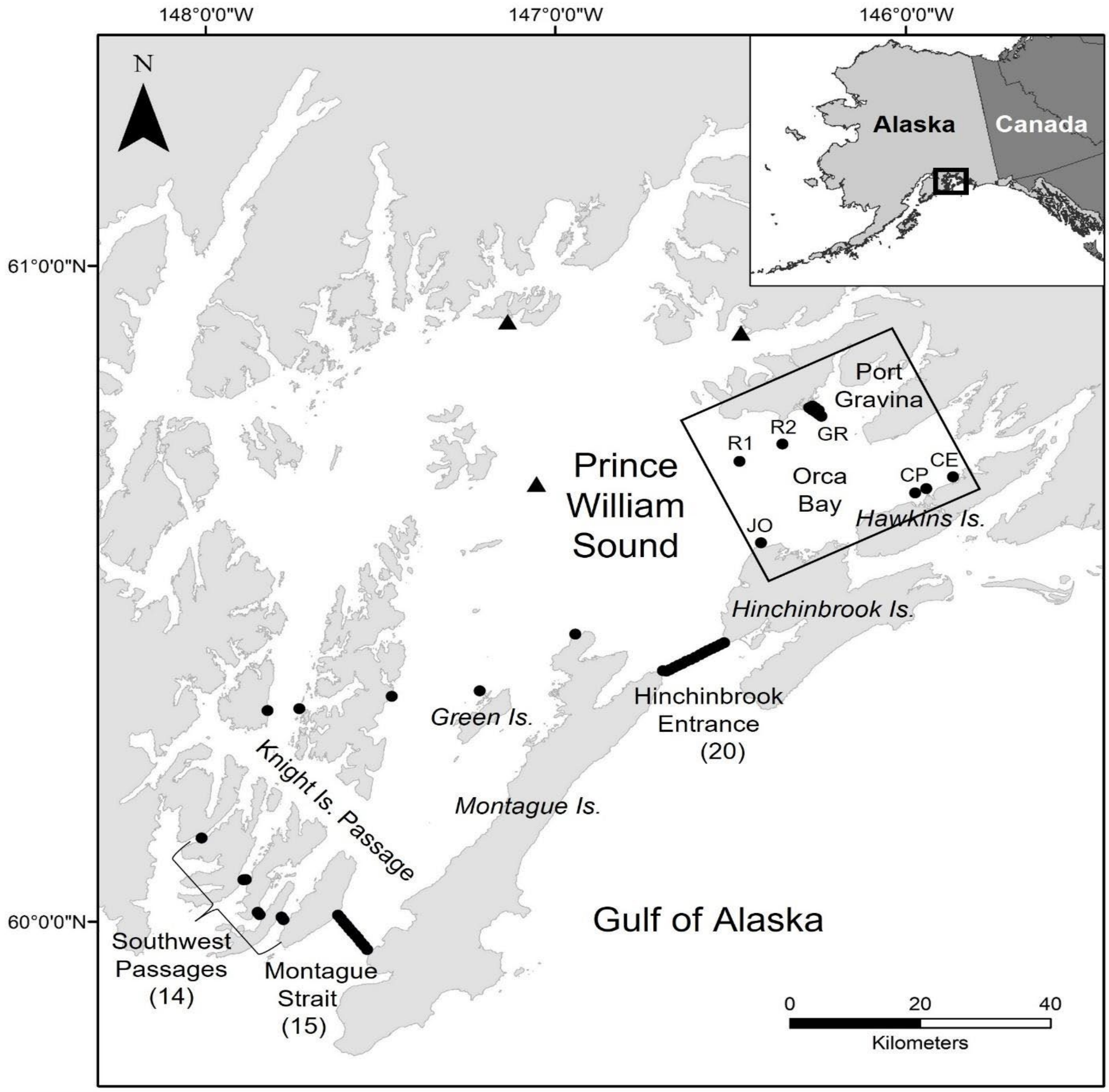


Figure 3-1. Map of Prince William Sound showing a) the southeast Prince William Sound spawning grounds study area (square) where prespawning Pacific herring were initially captured, acoustic-tagged, and released; and b) locations of all submerged acoustic receivers (circles and triangles) in the Sound. Total numbers of acoustic receivers in the Ocean Tracking Network arrays at the principal entrances from the Gulf of Alaska into the Sound are indicated in parentheses. Receivers deployed for short (7-11 mo) or intermittent periods (5-7 mo) are denoted by triangles. Acoustic receiver arrays in the study area include JO = Johnstone Point, CP=Canoe Pass, CE = Cedar Bay, GR = Gravina, R1 and R2 = Redhead 1 and Redhead 2.

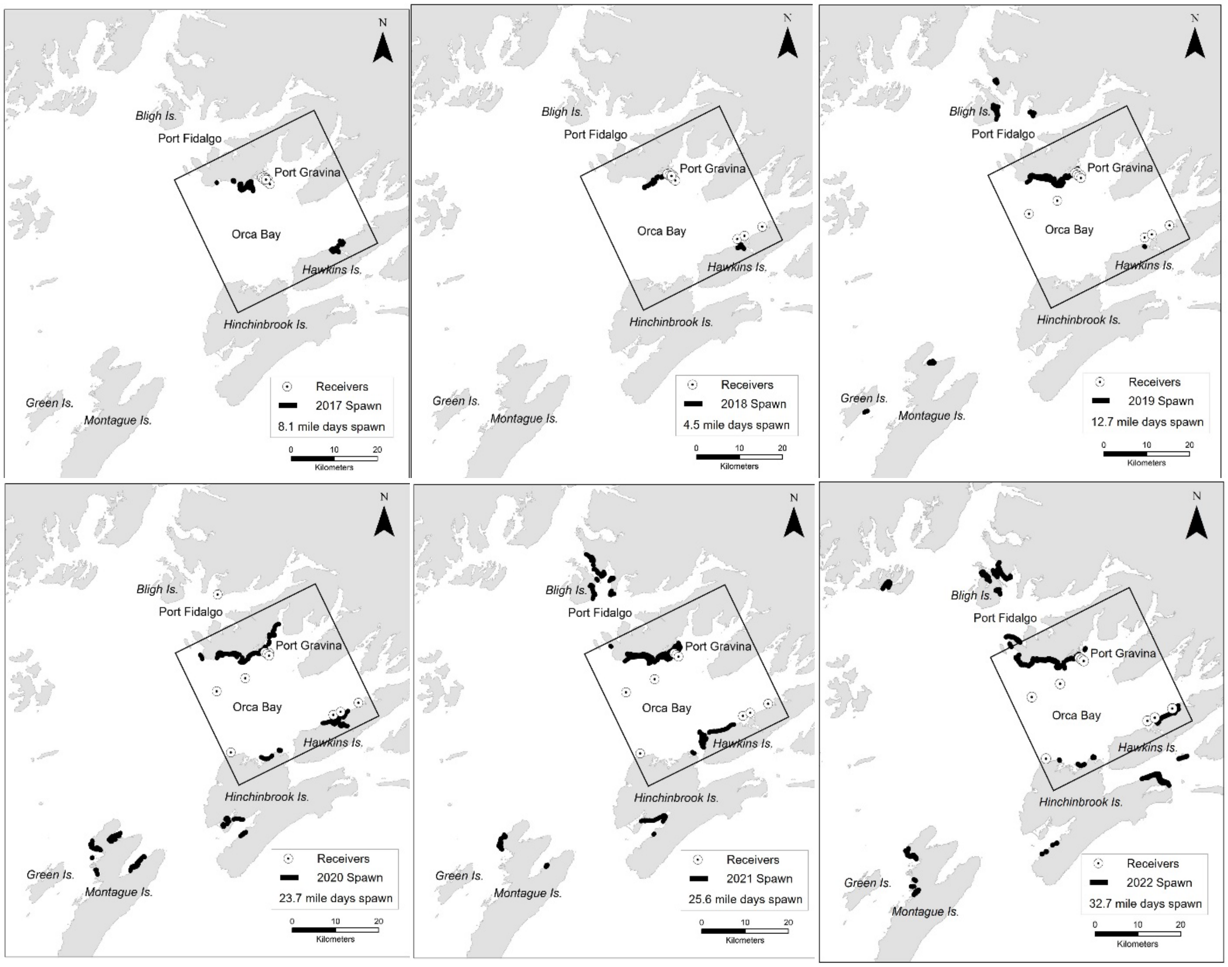


Figure 3-2. Location of Southeast Prince William Sound study area (square), herring spawn (black lines), and acoustic receivers (circles) during April and May by year (2017 – 2022). Mile days of spawn refers to observed active spawn.

Influence of tag year, herring size and previous movement to Gulf of Alaska entrances. Logistic regression models were used to investigate annual differences in the proportion of herring never detected post release or detected only at the southeast PWS spawning grounds. In addition, logistic regression models were used to investigate variables influencing herring returns to the southeast PWS spawning grounds. Using detections from fish tagged between April 2018-2020, we tested whether biological characteristics of herring influenced the probability of an "early" return (September through November). Univariate models separately considering weight, length, and condition (based on Fulton's condition factor k = weight/length^3; Kvamme et al. 2003) of the fish upon capture were compared to the null model using likelihood ratio tests. We then tested whether herring return rates to the southeast PWS spawning grounds varied by entrance arrays utilized prior to their return. For V9-tagged fish detected between September and April at the GOA entrance arrays, return rates were compared between fish detected solely at HE and fish detected at combinations of MS, SWP, and HE. The univariate model considering region was compared to the null model using a likelihood ratio test. All models were fit using the glm command in R (R Core Team 2021).

Factors influencing survival and return rate. To determine the seasonal return rate of fish to the southeast PWS spawning grounds while accounting for imperfect detection and apparent mortality, a multistate mark-recapture framework was used. Multistate models are an extension of Cormack-Jolly-Seber models (Pollock and Alpizar-Jara 2005) where, in addition to the detection (p) and apparent survival (S) parameters normally estimated, parameters related to movement or transitions between states (Ψ) can also be estimated (Schwarz 2005). Transitioning between states from one detection (or capture) period to the next is conditional on survival to the following period.

We defined two seasons, winter (November-January) and spring (March-April) for a total of 11 capture/recapture periods beginning spring 2017 through spring 2022. For each period we used acoustic receiver array detections to assign fish to one of two geographic states: 1) the southeast PWS spawning grounds ("T") where herring were tagged and released or 2) elsewhere ("E"), which encompassed all other PWS acoustic receiver arrays (Fig. 3-1). Because transmitter life was ~25 months, the probability of detection after two years was fixed to zero. Additionally, the model was defined such that all survival estimates were converted to monthly estimates assuming constant monthly survival between periods. This allowed direct comparison of monthly survival between the spring and winter periods even though there was more time from spring to winter than from winter to spring. Mortality could not be distinguished from permanent emigration or tag loss/premature tag failure; therefore, survival is referred to as apparent survival.

Using the package RMark (Laake 2013) which constructs models for program MARK (White and Burnham 1999) in program R, a total of 10 models were developed and compared using Akaike's Information Criterion with a correction for potentially small sample sizes (AICc; Burnham and Anderson 2002). In the models, monthly apparent survival, S, was defined to be different each period (time), constant (.), or vary between spring and winter (season), due to the fish's location (state), and/or by weight of the fish upon capture (weight). Probability of detection, p, was defined be different each period, constant, or varied due to state, season, number of different regions with receiver arrays (arrays), and/or length of the period in months (effort). Probability of transitions between states, ψ, was defined to be different each period, constant, or vary due to state and/or season.

Goodness-of-fit testing was done with the package R2ucare (Gimenez et al. 2018) as well as with the median-c test in MARK. Tests with R2ucare showed no indication of lack of fit, although the composite test "M.LTEC" could not be fit. Median-c tests on the most complex models performed in MARK indicated that c was either less than or equal to 1. Therefore, no adjustments to AICc were made based on lack of fit.

Seasonal residency and spatial use. To describe seasonal residency on the southeast PWS spawning grounds, we calculated the total number of days a V9-tagged individual was detected within a season. For this analysis we defined two seasons: winter (October – February) and spring (March – April) and utilized data from October 2018 through April 2022. Within each season, ANOVA was used to determine whether the mean number of days fish were detected at the spawning grounds varied among years. Models were fit with the aov function and pairwise-comparisons between years were made with the TukeyHSD function in R (R Core Team 2021). The number of days in winter was log-transformed to meet the necessary assumptions of an ANOVA.

To describe spatial use patterns within each season we calculated the proportion of total days at each array for all herring with ≥ 5 detection days at the southeast PWS spawning grounds. To make array coverage as equal as possible, we excluded data from Winter 2017/2018 and Spring 2018 when only one receiver array (Port Gravina) was deployed. Additionally, the Johnstone Point array was only included in calculations beginning Winter 2019/20.

Results

We implanted 726 herring with acoustic transmitters (V9 tags = 576, V8 tags = 150) between 1 and 16 April over a four-year period (2017-2020; Table 3-1). More than 98% (n = 714) of all fish were tagged within the southeast PWS spawning grounds. We determined sex for 97% (n = 701) of the fish, while sex was not determined for 25, spawned-out herring. The sex ratio of tagged fish was slightly biased towards males (F:M = 0.9:1.0).

For fish tagged with the larger, V9 transmitter, standard length averaged 214.0 ± 9.6 mm (SD; range 195-260 mm) and weight averaged 121.6 ± 18.4 g (range 94-216 g). Fish tagged with V8 tags averaged a standard length of 200.4 ± 5.2 mm (range 185-214 mm) and weight averaged 95.5 ± 7.6 g (range 79-117 g). Between tag years, fish with V9 tags weighed significantly more on average in 2018 than the other 3 tag years (ANOVA; all p-values <0.02) and fish with V8 tags weighed significantly less on average in 2019 than fish tagged in 2018 and 2020 (both p-values < 0.001) (Fig. 3-3). Based on age-length-weight relationships for herring in the Sound, spawning aggregations in 2017 and 2019 were dominated by age 3+ (Botz et al. 2021).

Spawning grounds detections post release

Following release, 3.9% of all tagged fish (28/714) were never detected (Table 3-2). An additional 24.6% (176/714) were detected only at the southeast PWS spawning grounds, including 155 fish with a final detection occurring within 1 month of release. Only 5 fish detected only on the spawning grounds had final detections after July (November = 1, December = 2, January =1, March = 3; Fig. 3-4). Examining by tag year, a logistic regression found that the proportion of tagged fish with no detections or only spawning ground detections in 2017 and 2018 were significantly higher than during 2019 and 2020 (Fig. 3-5).

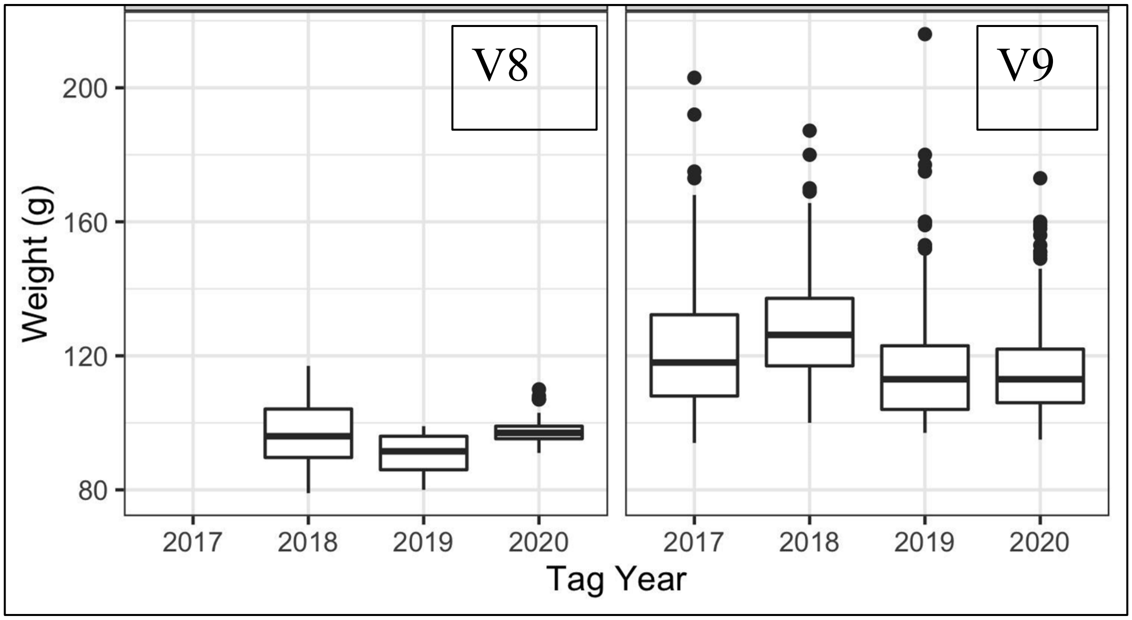


Figure 3-3. Box plots showing the weights of Pacific herring tagged with V8 (tag weight = 2.0 g) and V9 (tag weight = 4.7 g) acoustic transmitters in Prince William Sound, 2017-2020.

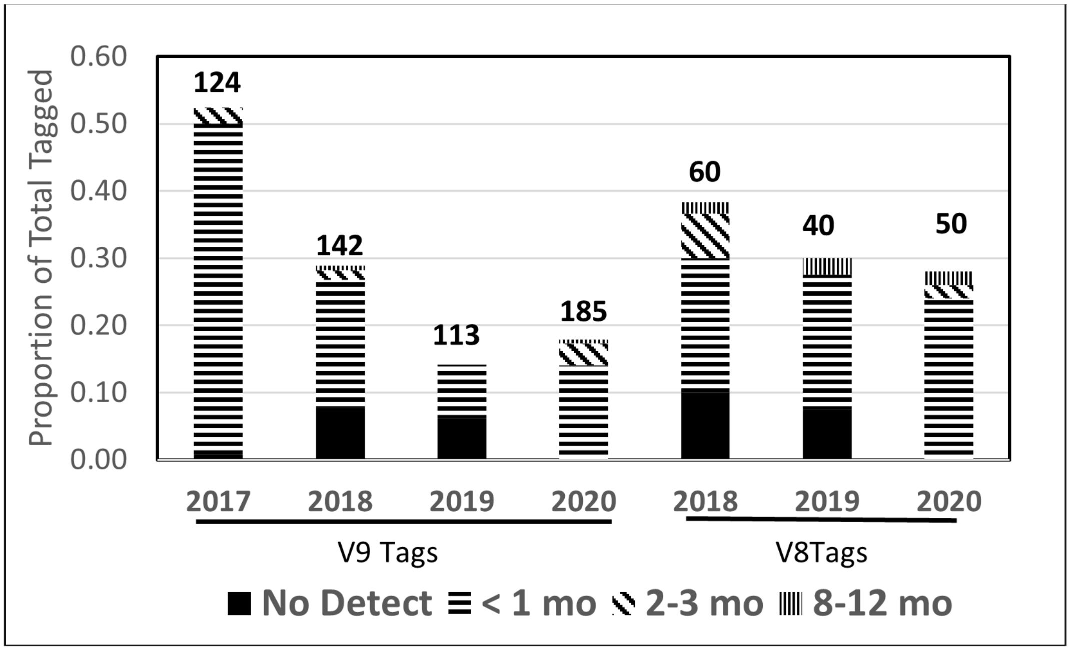


Figure 3-4. Proportion of fish by tag year and tag type that were either never detected post release (No Detect) or detected only on the spawning grounds. Final detection categories on the spawning grounds (<1 mo, 2-3 mo, and 8-12 mo) refer to months since release.

Table 3-2. Number and percentage by tag type and tag year of acoustic-tagged Pacific herring remaining at or returning to southeast Prince William Sound spawning grounds where they were tagged, April 2017-April 2021.

	Tag Year			
	2017[a]	**2018**	**2019**	**2020**
V9 Acoustic Tags				
Total fish acoustic-tagged	124	142	113[b]	185
Zero detections post tagging release	1	11	7	0
% Total	<1.0	7.7	6.2	0
Detected only on spawning grounds April through July Year 1	64	29	9	32
% Total	51.6	20.4	8.0	17.3
Detected returning to spawning grounds September Year 1 through April Year 2	9	27	14	37
% Total	7.2	19.0	12.4	20.0
Detected returning to spawning grounds September Year 2 through April Year 3	4	7	5	21
% Total	3.2	4.9	4.4	11.4
V8 Acoustic Tags				
Total fish acoustic-tagged		60	40	50
Zero detections post-tagging release		6	3	0
% Total		10.0	7.5	0
Detected only on spawning grounds April through July Year 1		16	8	13
% Total		26.7	20.0	26.0
Detected returning to spawning grounds September-February[a] Year 1		9	4	5[c]
% Total		15.0	10.0	10.0

[a] From April 2017 through March 2018 only one acoustic array was deployed on the southeast Prince William Sound spawning grounds.

[b] Does not include 12 fish tagged at Montague Island.

[c] Several V8 tags deployed in 2020 exceeded the expected December battery expiration. Three fish were recorded on the spawning grounds during 2021 January (n = 2) and February (n =1).

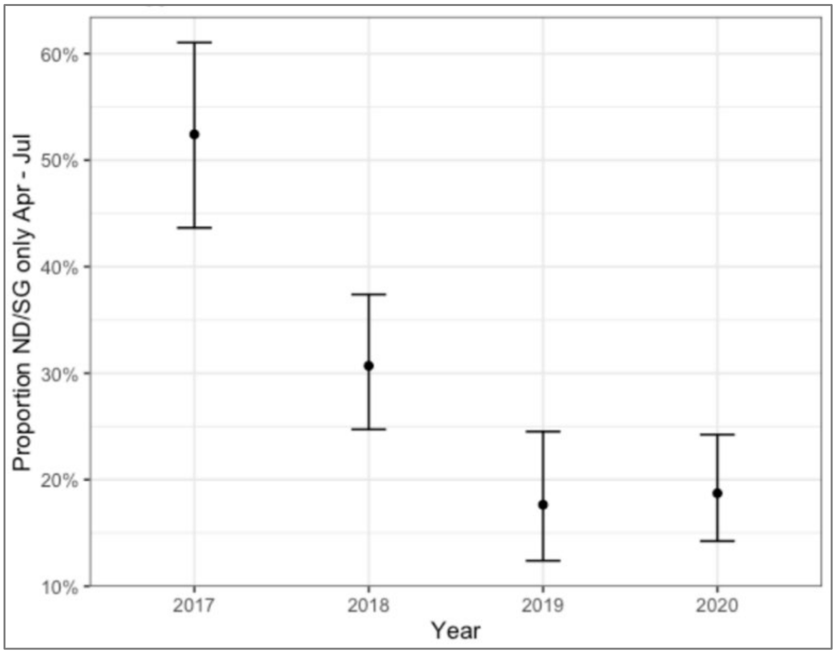


Figure 3-5. Point estimates and 95% confidence intervals from the logistic regression for the proportion of tagged fish with either no detections or spawning grounds detections only during April – July post-release.

Return phenology

Herring were detected on the southeast PWS tagging grounds during every month of the year. While herring generally began to return from the entrance arrays in September and October, a small percentage (range = 0.8% - 2.3%/tag year) returned between April and July. Overall, depending on the tag year, 10.0% -15% of all V8 tagged herring were detected on the spawning grounds with numbers generally increasing from September until December (2018 and 2019) when transmitter batteries expired (Table 3-2; Appendix Fig. A-1). For the V9-tagged fish, generally numbers increased steadily across the winter with the largest numbers arriving during the March-April spawning season (Fig. 3-6). The percentage of V9-tagged herring detected returning to the southeast PWS spawning grounds between September and April following tagging ranged from 7.8% - 20% while the percentage detected returning a second year during these same months ranged from 3.2% -11.4% (Table 3-2). Among fish returning the second year, we recorded 1 to 2 "skip-spawners" from each tag year that entered and remained in the GOA for 15.5 – 23 months before re-entering PWS and moving quickly to the spawning grounds. While 3 of the 6 skip spawners returned during November (n = 1) and December (n =2), all 6 skip spawners were recorded on the southeast PWS spawning grounds during March and/or April following their return.

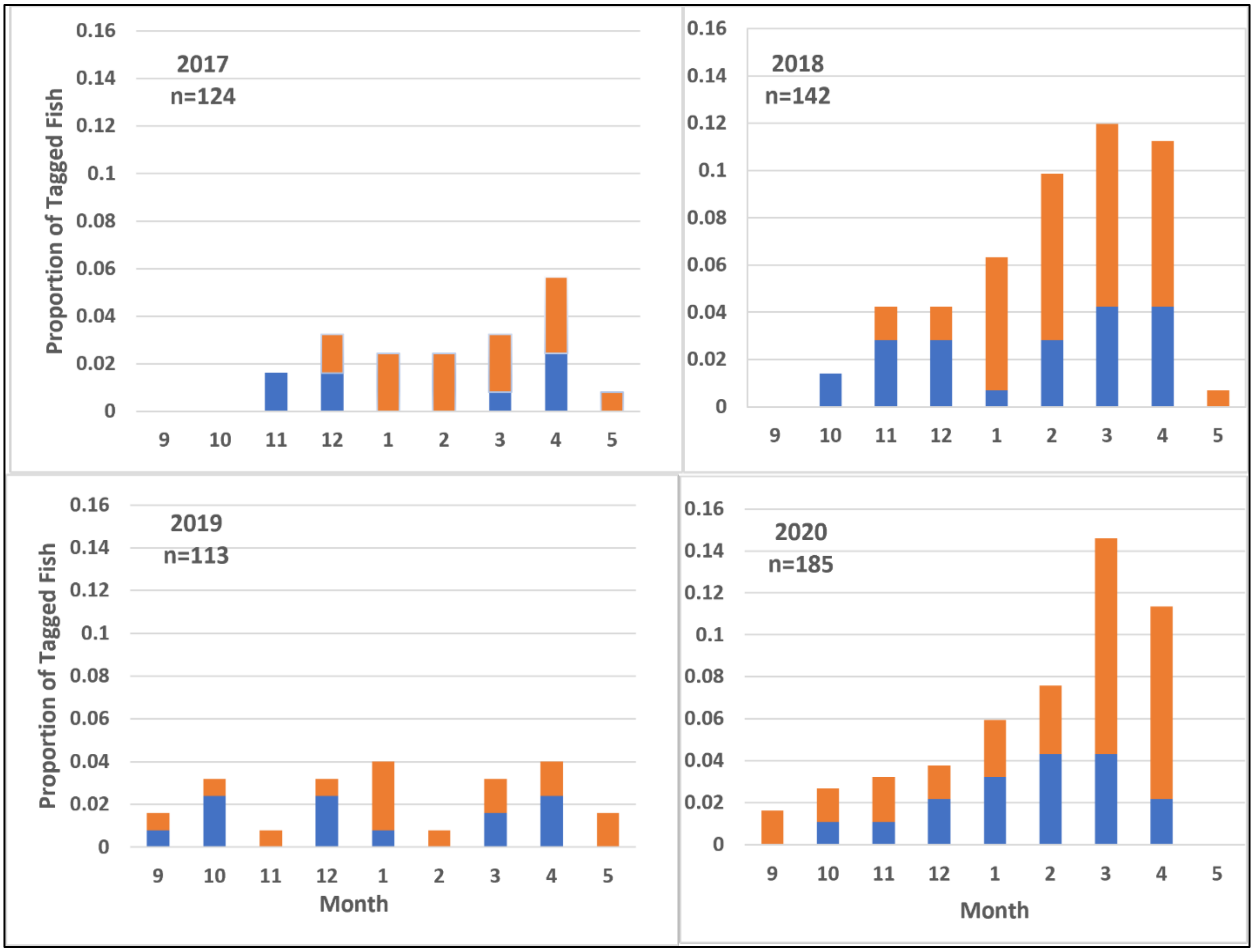


Figure 3-6. Proportion of V9 acoustic-tagged herring returning to and detected on the southeast Prince William Sound spawning and tagging grounds by month (September through May) and tag year (2017-2020). Fish were tagged during April of their respective tag year. Blue = initial detection; Orange = herring previously detected. Fish detected during both August and September (2019: n = 1, 2020: n = 3) are shown as previously detected in September.

Influence of herring size and previous entrance array utilized on spawning ground returns
Based on detection data from all PWS arrays (Fig. 3-1), 32 of a possible 164 herring (19%) returned early (between September and November) to the southeast PWS spawning grounds. There was compelling evidence that the probability of an early return was related to fish weight (χ_1^2= 6.5, p = 0.011; Fig. 3-7) and length (χ_1^2= 6.86, p = 0.009) with smaller herring significantly more likely to return than larger herring. Conversely, there was little evidence that condition was associated with the probability of an early return (χ_1^2= 0.44, p = 0.51). It was estimated that an increase in weight of 10 g was associated with a 25% decrease (95% CI: 4% – 40%) in the odds of being detected at the southeast PWS spawning grounds between September and November. Similarly, an increase of 10 mm in length was associated with a 43% decrease in

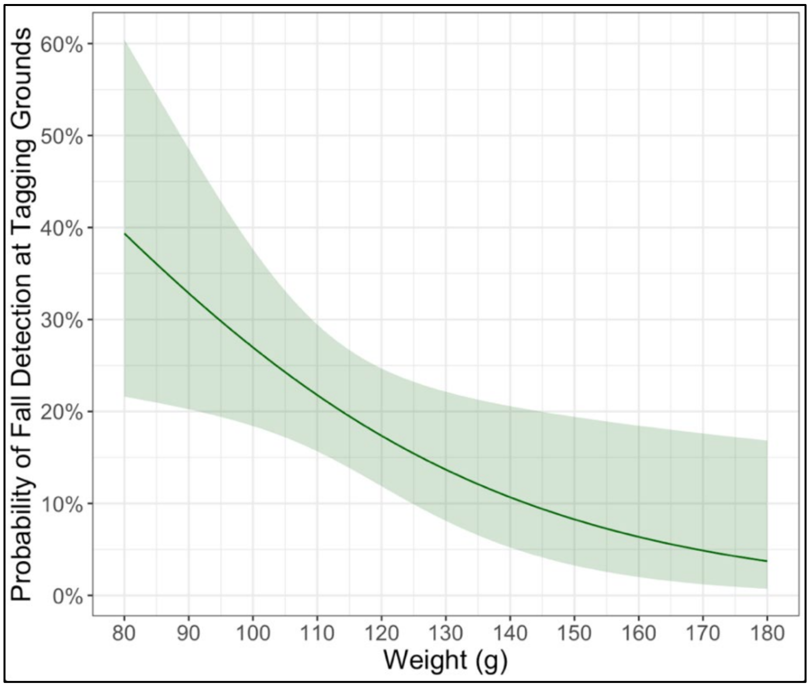


Figure 3-7. Logistic regression model showing a strong association between Pacific herring weight and the probability of a fish tagged in April returning between the months of September and November to the southeast Prince William Sound tagging and spawning grounds, 2018-2020. The solid line represents the mean estimate from the model and the shaded area represents the 95% confidence interval.

the odds of being detected (95% CI: 11% – 63%). On a probabilistic scale, an 80 g herring would have a 0.39 probability of being detected (95% CI: 0.22 – 0.60) compared to 0.04 for 175 g herring (95% CI: 0.01 – 0.17) while a 190 mm herring would have a detection probability of 0.43 (95% CI: 0.23 – 0.66) compared to 0.05 for a 240 mm herring (95% CI: 0.01 – 0.16).

Post-tagging movements to the GOA entrance arrays (HE, MS, and/or SWP) also influenced return rates to the southeast PWS spawning grounds. Between September and April and across four seasons (2017/18 – 2021/22), 141 V9-tagged fish were detected at the GOA entrance arrays including some fish during multiple years for a total of 180 occurrences. Herring with detections solely at the HE array (65/77 = 84%; 95% CI: 73% – 92%) had a significantly higher return rate to the southeast PWS spawning grounds (χ_1^2= 26.5, p < 0.001; Fig. 3-8) than fish that returning from MS/SWP arrays (39/103 = 38%; 95% CI: 29% – 47%).

Factors influencing survival and return rates

A total of 564 herring were implanted with V9 transmitters of which 135 (23.9%) were detected during a subsequent period (November – January and/or March – April). Model selection showed strong support for two models within 1.0 AICc units of one another (Table 3-3). The two models included different apparent monthly survival (*S*) between each period, effects for state of

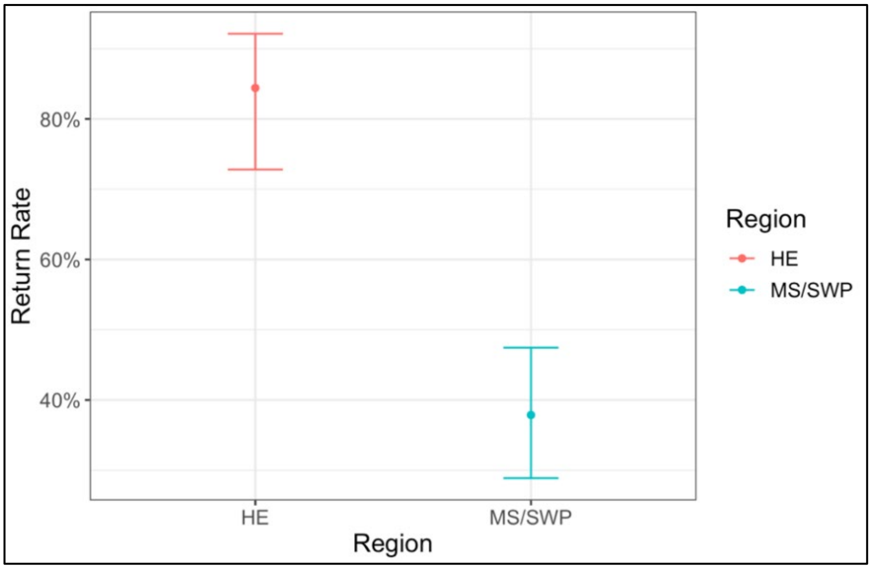


Figure 3-8. Estimated September to April return rate to the southeast Prince William Sound spawning grounds for acoustic-tagged Pacific herring previously detected at Ocean Tracking Network acoustic arrays located at the entrances into the Gulf of Alaska from Prince William Sound. HE = fish detected solely at Hinchinbrook Entrance. MS/SWP = fish detected at Montague Strait and/or Southwest Passage arrays or in combination with the Hinchinbrook Entrance array.

the fish on detection probabilities (p), and effects for state and season on transition probabilities (ψ). The difference between the top two models was the inclusion of the explanatory variable arrays (receiver coverage) for detection probabilities in the second-best model. Because receiver coverage was not found to be significant at the 95% level and results from the two models were similar, the results presented below are based on the AICc-preferred model.

Monthly survival estimates from spring to winter were either lower than or similar to estimates from winter to spring, depending on the year (Fig. 3-9). The lowest monthly apparent survival, (95% CI: 75% - 84%) occurred between spring 2017 and winter 2017/18. Herring were more likely to be detected at the southeast PWS spawning ground receiver arrays (95% CI: 71% – 100%) than at the other receiver arrays located throughout the Sound (95% CI: 39% – 60%).

The best model for the probability of transition ψ estimated that it varied due to state and season. For fish at the spawning grounds T in spring, the probability of moving elsewhere E in winter was greater than the probability of returning to the spawning grounds T during winter (Fig. 3-10; from spring to winter, T to E greater than T to T). For fish elsewhere in spring, the probability of being elsewhere in winter was higher than the probability of being at the spawning grounds in winter (from spring to winter, E to E greater than E to T). For fish on the spawning grounds in

Table 3-3. Comparison of AICc for the 10 multistate models considered.

	Model	**Num. Param.**	**AICc**	**ΔAICc**	**Weight**	**Cumulative Weight**
1	S(time) p(state) ψ(state * season)	16	1522.54	0.00	50.08%	50.08%
2	S(time) p(state + arrays) ψ(state * season)	17	1523.24	0.70	35.25%	85.33%
3	S(time + state) p(state + time) ψ(state * time)	41	1525.07	2.53	14.16%	99.49%
4	S(season) p(state + effort) ψ(state * season)	9	1532.52	9.98	0.34%	99.83%
5	S(weight + season) p(state) ψ(state * season)	9	1534.87	12.33	0.11%	99.94%
6	S(season) p(state) ψ(state * season)	8	1536.21	13.67	0.05%	99.99%
7	S(weight) p(state + season) ψ(state * season)	9	1539.58	17.04	0.01%	100.00%
8	S(season) p(state) ψ(state)	6	1593.13	70.59	0.00%	100.00%
9	S(.) p(.) ψ(state)	4	1637.01	114.47	0.00%	100.00%
10	S(.) p(.) ψ(.)	3	1640.06	117.52	0.00%	100.00%

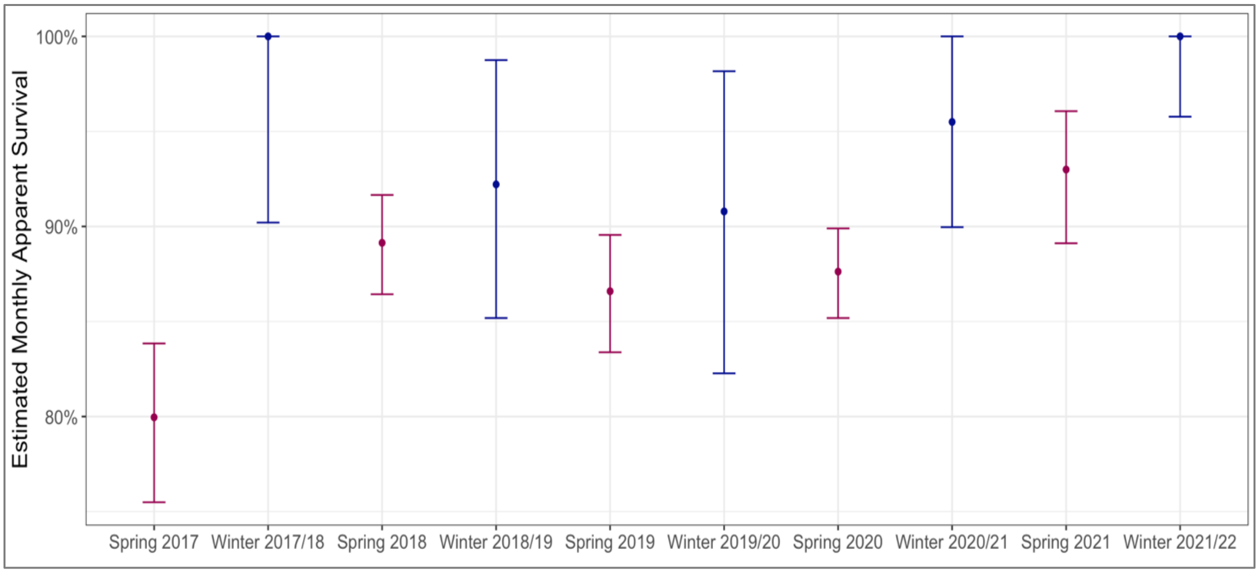


Figure 3-9. Monthly apparent survival between each capture/recapture period with 95% confidence intervals, estimated from the top model. Spring refers to the period between spring (March-April) of the year denoted and the following winter (November-January) while winter refers to the period between winter of the years denoted and the following spring.

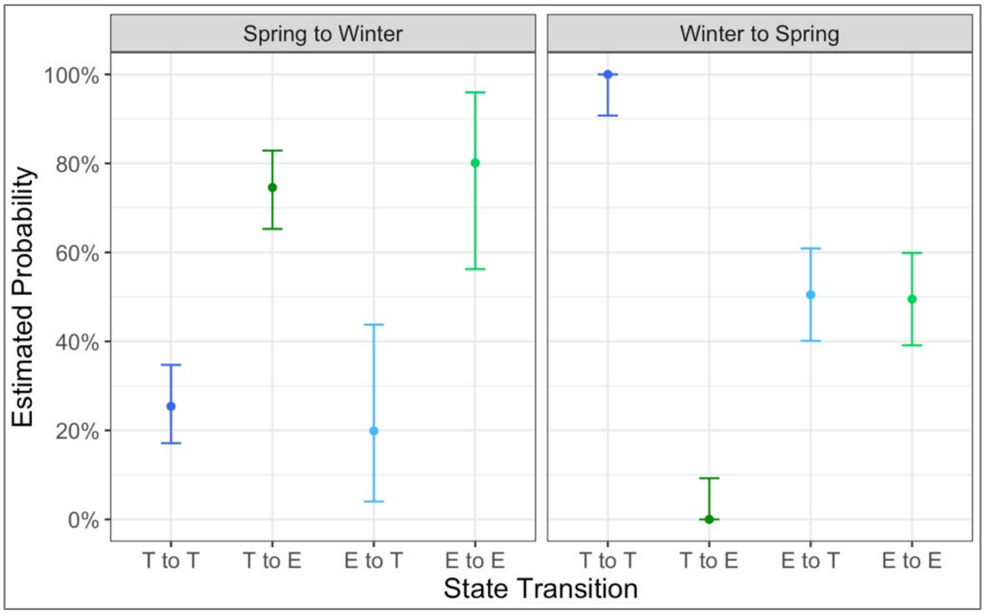


Figure 3-10. Estimated probability of transition based on state and season with 95% confidence intervals, estimated from the top model. T = Southeast Prince William Sound spawning grounds; E = elsewhere in Prince William Sound with receiver arrays.

winter, the probability of being present during spring on the spawning grounds was almost certain compared to the probability of moving elsewhere (Fig. 3-10; from winter to spring, T to T greater than T to E). For fish elsewhere in winter, the probability of moving to the spawning grounds in spring was similar to the probability of moving elsewhere in spring (from winter to spring, E to T similar to E to E).

Seasonal residency

Across the winter (October-February, 151 d) the proportion of total days herring were detected on the spawning grounds ranged from 0.70 in 2019/20 to 0.92 in 2018/19. Spatial patterns of detections on the southeast PWS spawning grounds shifted between winter and spring seasons. Herring returning during winter months were detected most often on the south side of Orca Bay around the Cedar Bay and Canoe Pass arrays. During spring (March-April, 61 d), tagged fish were detected most often at Port Gravina array followed by Canoe Pass and Cedar arrays in Orca Bay (Fig. 3-11).

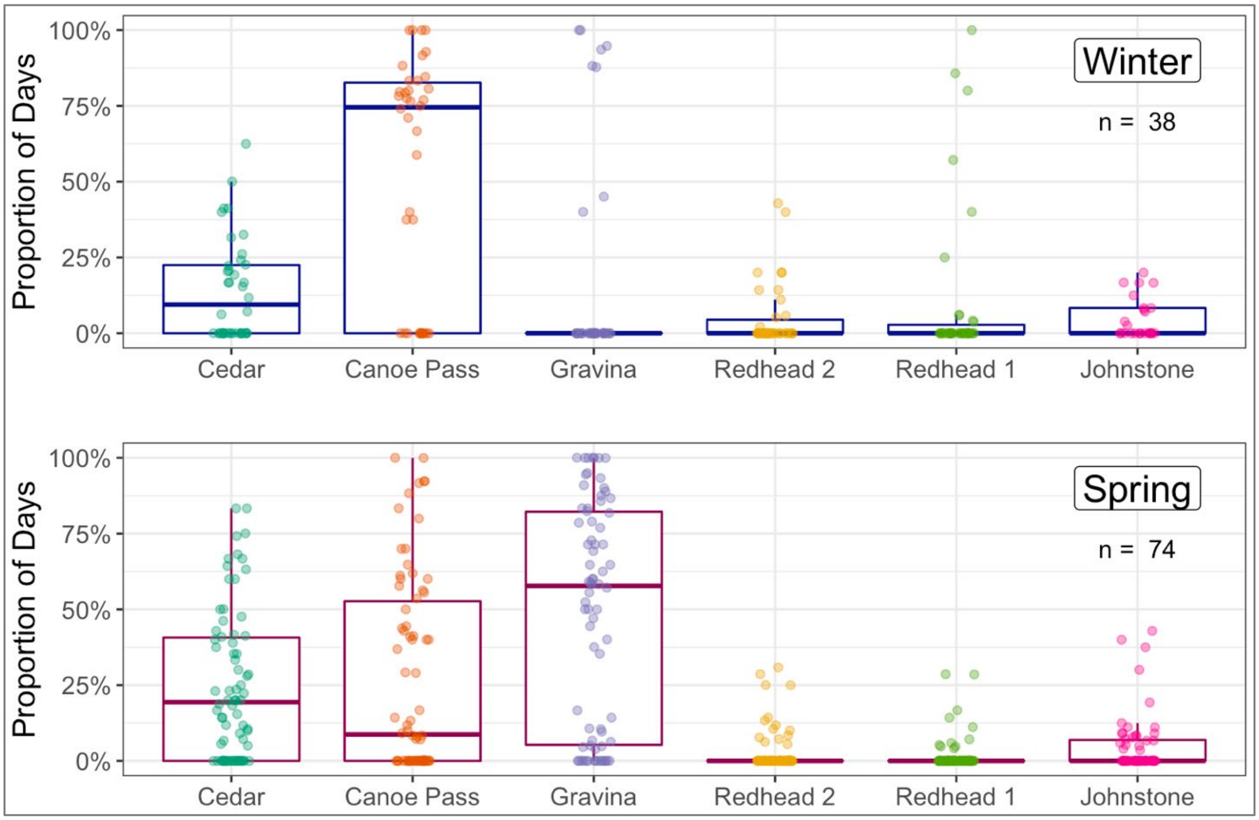


Figure 3-11. The proportion of total days that fish were detected per array on the southeast PWS spawning grounds by winter (n = 38) and spring (n = 74) seasons. Proportions are only shown for V9-tagged fish with ≥ 5 d with detections. A proportion of 100% = each day a fish was detected it was at that array; 0% = the fish was never detected at that array.

For herring returning during winter months, the mean number of days detected was 13.7 ± 15.8 d (V9 tags; n = 68, SD) while during spring the mean was 12.1 ± 7.7 d (n = 93; Table 3-4). Comparing among years within each season, the mean number of days detected across winter (log transformed) during the 2018/19 winter (26.7 d) was significantly higher than the 2021/22 winter (6.46 d; $p = 0.01$) and marginally higher than the 2020/21 winter (8.85 d; $p = 0.07$). Among spring seasons, there was strong support that the mean number of days detected at the tagging grounds during spring 2021 (16.5 d) was significantly higher than both spring 2019 and spring 2020 (8.13 d, 6.85 d, respectively; both $p < 0.001$; Table 3-4). Across four winters, only 2 (2.9%) returning fish departed and were detected at a receiver array outside of the spawning grounds, including one that subsequently returned. For most of the tagged herring returning in spring, once a fish departed from the spawning grounds it did not return within that same season and year. We recorded only 5 (5.4%) occurrences of fish departing, being subsequently detected at an array outside the spawning grounds, and then returning to the spawning grounds within the same March-April period.

Table 3-4. Number of days ($\bar{x}$, SD) by season V9 acoustic-tagged Pacific herring were detected on the southeast Prince William Sound tagging grounds. Winter = October-February, 151d; Spring = March-April, 61d.

	Winter		Spring	
Year	n	$\bar{x}$ (SD)	n	$\bar{x}$ (SD)
2018/19	18	26.7 (20.9)	23	8.1 (5.6)
2019/20	10	12.8 (14.0)	13	6.9 (4.6)
2020/21	27	8.9 (9.3)	37	16.5 (8.7)
2021/22	13	6.5 (8.3)	20	12.1 (4.3)

Discussion

To our knowledge, this study is the first to document spawning site fidelity of individual herring using acoustic arrays to record their movements out from and back to the spawning grounds where they were tagged. Returning herring occupied the southeast PWS spawning grounds continuously from September through the subsequent April spawning. Except for post-spawning migratory movements to the GOA entrances, once a herring returned it was rare for a herring to move and be detected at arrays away from the spawning grounds. While all arrays had detections during both seasons, during winter, fish were detected primarily along southern Orca Bay at Canoe Pass and Cedar (Fig. 3-1) arrays. Waters in Orca Bay are typically <200 m, with the deepest waters (up to 250 m) occurring near the Cedar acoustic array. In spring, herring shifted their spatial patterns and were detected most often around Port Gravina, the area with the most mile-days of spawn during this study (Fig. 3-2).

Previously, adult Pacific herring populations along the eastern Pacific Ocean have been documented overwintering in nearshore channels (100-200 m) including often in the general area where spawning occurs (Hay and McCarter 1997). However, overwintering habitats in other areas are typically occupied for 3-4 months (Hay and McCarter 1997), whereas in PWS the southeast PWS spawning grounds were occupied regularly by returning fish beginning 7 months prior to April spawning. The extensive use by adult herring of the southeast PWS spawning grounds as well as its importance as a juvenile herring rearing area (Pegau 2022) suggests that this area is critical year-round habitat for the PWS herring population.

Factors influencing returning fish

Our results showed that both fish size and post-spawning migratory movements influenced herring returns to the southeast PWS spawning grounds. Overall, herring were less likely to be detected on the spawning grounds through the fall months. However, the probability of returning between September and November was related to weight and length with smaller fish more likely to return between September and November than larger fish. We also confirmed that there were differences in the likelihood of returning to the spawning grounds, based on movements to the GOA entrances. Spawning grounds arrays are 20-55 km from HE array compared to ~110-155 km from the MS/SWP arrays. Across the two seasons (September – April) fish that were only detected at HE were more likely to return to the spawning grounds than fish detected at MS and/or the SWP. The lower return rate from fish detected at MS/SWP versus those detected solely at HE suggests that fish using MS/SWP were subsequently more likely to spawn somewhere other than the southeast PWS spawning grounds or had a higher mortality.

Spatial shifts in PWS spawning grounds

Interestingly, during years 2016-2018, spring spawning only occurred in southeast PWS (McGowan et al. 2021) and provided an opportunity to determine if herring from those hatch years displayed natal homing. Of the 3 hatch years, 2016 resulted in a numerically dominant cohort. By ages 3+ (spring 2019) and 4+ (spring 2020) the 2016 cohort comprised 71% and 82%, respectively, of the adult herring population (ADF&G, unpubl. data). Furthermore, although the 2016 cohort only hatched from the southeast PWS spawning grounds, by 2019 when the cohort was age 3+ spawning abruptly began to expand to areas outside of the southeast PWS spawning grounds, including at areas in the northeast shore and Montague Island management areas (Fig. 3-2).

The sudden spatial expansion in 2019 confirmed that natal homing is not a dominant behavioral trait in the PWS herring population and suggests straying by the young 2016 herring cohort. While the expansion of the spawning grounds may have been a density-dependence response to the increased adult herring biomass, it may also be due to social behavior. The previous 2018 spawning biomass was the lowest on record, suggesting that there were potentially few older fish with knowledge of migration routes to the spawning grounds. Nevertheless, the spawning areas occupied beginning in 2019, are typically within 45-75 km of the historically important Port Gravina spawning area at Hells Hole. Given the relatively small distances from the southeast PWS spawning grounds, this expansion to other areas suggests that while not natal spawners, PWS herring do show spawning site fidelity at a regional scale, in this case to an area of approximately 2000 km^2.

Depredation on the spawning grounds

Almost one-fourth of all tagged fish were detected only on the southeast PWS spawning grounds, with the final detection for most of these fish occurring within the 30 days of their release. Possible explanations for such a high proportion could be any combination of higher mortality, higher tag failure, and/or higher tag loss. In a laboratory study of Pacific herring response to acoustic tagging, mortalities occurred between days 9 and 25 after tag insertion (2 of 50) while tag shedding occurred later, between days 39 and 53 after surgery (4 of 100; Seitz et al. 2010). The predominance of final detections within 30 days of release during our study suggests that mortality and not tag shedding was the primary cause of spawning grounds only detections.

Comparing between tag years, fish tagged in 2017 and 2018 had a significantly higher proportion of combined post-release zero detections and spawning-grounds-only detections (2017 = 0.52; 2018 = 0.31; Fig. 3-5). For 2017 tagged fish, these results are analogous to the lower survival estimates (Fig. 3-9) for the spring to winter period estimated by our mark-recapture model, as well as a higher mortality estimated for the first half of spring and summer 2017 (April – 20 June) compared to the second half of the season (21 June – 30 August; Bishop and Bernard 2021).

We suggest that mortality during spring 2017 and 2018 may have been higher compared to the other two tag years due to the presence of humpback whales and relatively large numbers of Stellar sea lions at Port Gravina during tagging activities. In spring 2017 during tagging, one to three humpback whales and >175 sea lions were observed during ADFG aerial spawn surveys. Similarly, during 2018 one to two humpback whales and >200 sea lions were observed at Port Gravina during tagging and/or the aerial spawn surveys (S. Shepard, ADF&G, unpubl. data). In addition, record-setting-low mile-days of spawn were recorded in 2017 (8.1 mile-days over 9 d) and 2018 (4.5 mile-days over 11 d) (Table 3-1, Fig. 3-2; Botz et al. 2021), reflecting a reduced and highly contracted spawning population (McGowan et al. 2021).

In contrast during 2019 and 2020 when tagging activities took place at northern Hinchinbrook Island (2019), Port Gravina (2020), and Canoe Pass (2019 and 2020) the proportions of fish with spawning grounds only detections or with no post-release detections were 0.18 (2019) and 0.19 (2020). Both years, mile-days of spawn were larger and over a prolonged period of time compared to the two previous years, 12.7 mile-days over a period of 39 days in 2019 and 23.7 mile-days over a 30-day period in 2020 (Table 3-1, Fig. 3-2). No whales were observed in the tagging areas during or immediately after tagging activities (this study; S. Shepard, ADF&G,

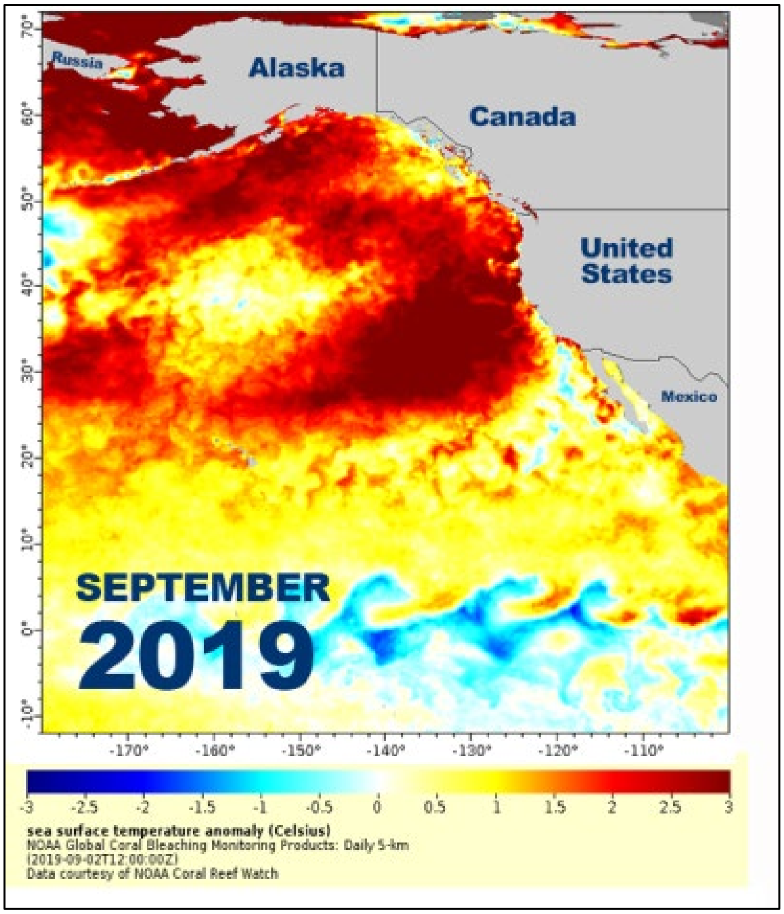
unpubl. data) suggesting that a combination of a protracted spawning season and spawning across multiple geographic areas can function to reduce marine mammal predation on adult herring.

2019 marine heatwave

The relatively lower proportion of 2019 tagged fish returning to the spawning grounds compared to 2018 and 2020, (0.12 vs 0.19 and 0.20, respectively) as well as the lower apparent survival rates (spring 2019 and winter 2019/20; Fig. 3-9) may have been a result of: a) tagged fish spawning outside of the southeast PWS spawning grounds; and b) reduced food availability due to a marine heatwave. In 2019, almost ¾ of the acoustic-tagged fish were captured and tagged around northern Hinchinbrook Island, an area that did not have spawn deposition that year. Tagging ended around 8 April 2019 and the next spawn event did not take place until 18 April and was at Port Fidalgo (Fig. 3-2), outside of the southeast PWS spawning grounds. More spawning occurred between 28 April and 3 May but was scattered at locations both within (Port Gravina) and outside of the study area (Port Fidalgo/Bligh Island and northern Montague Island; Fig. 3-2).

At the same time, returns and lower survival may have been a result of the June 2019-January 2020 marine heatwave that occurred across much of the GOA (Amaya et al. 2020; Fig. 3-11). Warming ocean conditions can be a source of large-scale, major ecosystem perturbations to the marine food web. Previously, the massive 2013-2016 marine heatwave in the GOA (referred to as "The Blob") was shown to reduce the availability of cold-water associated calanoid copepods (primarily *Neocalanus plumchrus and N. flemingeri*; McKinstry and Campbell 2018; Ashlock et al. 2022) and euphausiids (Arimitsu et al. 2021). Importantly, post-spawning herring primarily feed on *Neocalanus* copepods before shifting to euphausiids, amphipods, pteropods, and fish (Willette et al. 1999) when *Neocalanus* begin their ontogenetic migration to deeper waters.

The 2019 heatwave resulted in above average sea surface temperatures (SST) and record-high surface air temperature anomalies over Alaska (Amaya et al. 2020; von Biela et al. 2022). HE and MS, the two major passages to the GOA used by post-spawning herring, are dotted with rain and snow-fed rivers and streams. The high air temperatures combined with the lack of glacially influenced cooler waters resulted in higher than normal SST) at both passages (R. Campbell, pers. comm.). In May 2019, a period when herring are headed to the entrances and into the GOA to forage, SST at both HE (11.8 ºC) and MS (10.8 ºC; Du et al. 2022) exceeded the upper thermal threshold for *Neocalanus plumchrus* abundance (10.5 ºC) and occurrence (11.5 ºC; HE only) (Ashlock et al. 2022). By August 2019, a record-breaking SST of 17.5 ºC was recorded at MS (Du et al. 2022; R. Campbell, pers. comm.), the most important passage for PWS migratory herring into and out of the GOA from June through winter (Bishop and Eiler 2018).



NOAA Global Coral Bleaching Monitoring Products: Daily 5-km
(2019-09-02T12:00:00Z)
Data courtesy of NOAA Coral Reef Watch

Figure 3-12. Sea surface temperature anomaly map. Temperatures above normal are in orange and red. Courtesy of National Oceanic and Atmospheric Administration Coral Reef Watch. Source: www.noaa.fisheries.gov.

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LITERATURE CITED

Amaya, D. J., A. J. Miller, S. P. Xie, and Y. Kosaka. 2020. Physical drivers of the summer 2019 North Pacific marine heatwave. Nature Communications 11:1-9.

Arimitsu, M. L., J. F. Piatt, B. Heflin, V. von Biela, and S. K. Schoen. 2018. Monitoring long-term changes in forage fish distribution, abundance and body condition. *Exxon Valdez* Oil Spill Restoration Project Final Report (Restoration Project 16120114-O), *Exxon Valdez* Oil Spill Trustee Council, Anchorage, Alaska.

Arimitsu, M., J. Piatt, S. Hatch, R. M. Suryan, S. Batten, M. A. Bishop, R. W. Campbell, H. Coletti, D. Cushing, K. Gorman, R. R. Hopcroft, K. J. Kuletz, C. Marsteller, C. McKinstry, D. McGowan. J. Moran, W. S. Pegau, A. Schaefer, S. Schoen, J. Straley, and V. R. von Biela. 2021. Heatwave-induced synchrony within forage fish portfolio disrupts energy flow to top pelagic predators. Global Change Biology 27:1859-1878. doi: 10.111/gcb.15556.

Amstrup, S. C., T. L. McDonald, and B. F. Manly. 2010. Handbook of capture-recapture analysis. Princeton University Press, Princeton, New Jersey, USA.

Ashlock, L., M. García-Reyes, C. Gentemann, S. Batten, and W. Sydeman. 2021. Temperature and patterns of occurrence and abundance of key copepod taxa in the northeast Pacific. Frontiers in Marine Science 8:670795. doi:10.3389/fmars.2021.670795.

Beacham, T., J. Schweigert, C. MacConnachie, K. Le, and L. Flostrand. 2008. Use of microsatellites to determine population structure and migration of Pacific herring in British Columbia and adjacent regions. Transactions of the American Fisheries Society 137:1795–1811.

Bishop, M. A., J. T. Watson, K. Kuletz, and T. Morgan. 2015. Pacific herring (*Clupea pallasii*) by marine birds during winter in Prince William Sound, Alaska. Fisheries Oceanography 24:1–13.

Bishop, M. A., and J. H. Eiler. 2018. Migration patterns of post-spawning Pacific herring in a subarctic sound. Deep Sea Research Part II: Topical Studies in Oceanography 147:108-115.

Bishop, M. A., and J.W. Bernard. 2021. An empirical Bayesian approach to incorporate directional movement information from a forage fish into the Arnason-Schwarz mark-recapture model. Movement Ecology 9(8). https://doi.org/10.1186/s40462-021-00241-1.

Botz, J., T. Sheridan, A. Wiese, S. Moffitt, and R. Brenner. 2014. 2013 Prince William Sound area finfish management report. Alaska Department of Fish and Game Fish Management Report 2014/43 ii + 224 pp.

Botz, J., C. W. Russell, J. Morella, and S. Haught. 2021. 2020 Prince William Sound area finfish management report. Alaska Department of Fish and Game, Fishery Management Report No. 21-18, Anchorage.

Brooks, S. P., and A. Gelman. 1998. General methods for monitoring convergence of iterative simulations. Journal of Computational and Graphical Statistics 7:434-455.

Brown, E. D., J. Seitz, B. L. Norcross, and H. P. Huntington. 2002. Ecology of herring and other forage fish as recorded by resource users of Prince William Sound and the outer Kenai Peninsula, Alaska. Alaska Fisheries Research Bulletin 9:75-101.

Brownie, C., J. Hines, J. Nichols, K. Pollock, and J. Hestbeck. 1993. Capture-recapture studies for multiple strata including non-Markovian transitions. Biometrics 49:1173–87.

Buren, A., H. Murphy, A. Adamack, G. Davoren, M. Koen-Alonso, and W. Montevecchi. 2019. The collapse and continued low productivity of a keystone forage fish species. Marine Ecology Progress Series 616:155–170.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York, New York, USA. https://doi.org/10.1007/b97636.

Chapman, B., C. Skov, K. Hulthen, J. Brodersen, P. A. Nilsson, L. A. Hansson, and C. Brönmark. 2012. Partial migration in fishes: definitions, methodologies and taxonomic distribution. Journal of Fish Biology 81:479–499.

Chavez, F. P., J. Ryan, S. E. Lluch-Cota, and C. M. Ñiquen. 2003. From anchovies to sardines and back: multidecadal change in the Pacific Ocean. Science 299(5604):217-221.

Cormack, R. M. 1964. Estimates of survival from the sighting of marked animals. Biometrika 51(3/4):429-438.

Coyle, K. O., and A. I. Pinchuk. 2005. Seasonal cross-shelf distribution of major zooplankton taxa on the northern Gulf of Alaska shelf relative to water mass properties, species depth preferences and vertical migration behavior. Deep Sea Research Part II: Topical Studies in Oceanography 52(1-2):217–45.

Davoren, G. K. 2013. Divergent use of spawning habitat by male capelin (*Mallotus villosus*) in a warm and cold year. Behavioral Ecology 24:152-161.

Donaldson, M. R., S. G. Hinch, C. D. Suski, A. T. Fisk, M. R. Heupel, and S. J. Cooke. 2014. Making connections in aquatic ecosystems with acoustic telemetry monitoring. Frontiers in Ecology and the Environment 12:565-573.

Dorazio, R. M., and M. Price. 2019. State-space models to infer movements and behavior of fish detected in a spatial array of acoustic receivers. Canadian Journal of Fisheries and Aquatic Sciences 76:543-550.

Du, X., R. Campbell, and S. Kibler. 2022. Seasonal changes of microphytoplankton community in Prince William Sound, Alaska in 2019. Estuaries and Coasts. https://doi.org/10.1007/s12237-022-01144-z.

Dupuis, J. A. 1995. Bayesian estimation of movement and survival probabilities from capture-recapture data. Biometrika 82:761–772.

Dupuis, J., J. Badia, M. I. Maublanc, and R. Bon. 2002. Survival and spatial fidelity of mouflon (*Ovis gmelini*): A Bayesian analysis of an age-dependent capture-recapture model. Journal of Agricultural, Biological, and Environmental Statistics 7:277-298.

Eiler, J. H., and M. A. Bishop. 2016. Tagging response and postspawning movements of Pacific Herring, a small pelagic forage fish sensitive to handling. Transactions of the American Fisheries Society 145:427–439.

Exxon Valdez Oil Spill Trustee Council. 2014. *Exxon Valdez* oil spill restoration plan: 2014 update of injured resources and services. *Exxon Valdez* Oil Spill Trustee Council. 44 pp.

Flostrand, L. A., J. F. Schweigert, K. S. Daniel, and J. S. Cleary. 2009. Measuring and modelling Pacific herring spawning-site fidelity and dispersal using tag-recovery dispersal curves. ICES Journal of Marine Science 66:1754–1761.

Gimenez, O., J. Lebreton, R. Choquet, and R. Pradel. 2018. R2ucare: An R package to perform goodness-of-fit tests for capture–recapture models. Methods in Ecology and Evolution 9:1749-1754. https://oliviergimenez.github.io/R2ucare/.

Halverson, M. J., C. Bélanger, and S. M. Gay III. 2013. Seasonal transport variations in the straits connecting Prince William Sound to the Gulf of Alaska. Continental Shelf Research 63:S63-S78.

Hay, D. E. 1985. Reproductive biology of Pacific herring (*Clupea harengus pallasi*). Canadian Journal of Fisheries and Aquatic Sciences 42(S1):111–26.

Hay, D. E. 1992. Spawning habitat, continental shelf area and herring production in the North Pacific Ocean. Pages 183-191 *in* Ilyichev, V. I., and V. V. Anikiev, editors. Oceanic and Anthropogenic Controls of Life in the Pacific Ocean. Springer Dordrecht, Dordrecht, Netherlands.

Hay, D. E., and P. B. McCarter. 1997. Continental shelf area, distribution, abundance and habitat of herring in the North Pacific. Wakefield Fisheries Symposium. Alaska Sea Grant College Program 97-01:559–572.

Hay, D. E., and S. M. McKinnell. 2002. Tagging along: association among individual Pacific herring (*Clupea pallasi*) revealed by tagging. Canadian Journal of Fisheries and Aquatic Sciences 59:1960–1968.

Hay, D. E., K. A. Rose, J. Schweigert, and B. A. Megrey. 2008. Geographic variation in North Pacific herring populations: Pan-Pacific comparisons and implications for climate change impacts. Progress in Oceanography 77:233–240.

Hestbeck, J. B., J. D. Nichols, and R. A. Malecki. 1991. Estimates of movement and site fidelity using mark-resight data of wintering Canada geese. Ecology 72:523–33.

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

Huse, G, A. Ferno, and J. Holst. 2010. Establishment of new wintering areas in herring co-occur with peaks in recruit to repeat spawner ratio. Marine Ecology Progress Series 409:189–198.

Huse, G., B. MacKenzie, V. Trenkel, M. Doray, L. Nottestad, and G. Oskarsson. 2015. Spatially explicit estimates of stock sizes, structure and biomass of herring and blue whiting, and catch data of bluefin tuna. Earth System Science Data 7:35–46.

Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika 52(1/2):225–247.

Krieger, K. J. 1982. Tagging herring with coded-wire microtags. Marine Fisheries Review 44:18–21.

Laake, J. L. 2013. RMark: An R interface for analysis of capture-recapture data with MARK. AFSC Processed Rep 2013-01, 25p. Alaska Fisheries Science Center, NOAA, Natl. March. Fish. Serv., Seattle WA, USA.

Langård, L., G. Skaret, K. H. Jensen, A. Johannessen, A. Slotte, A., L. Nøttestad, and A. Fernö. 2015. Tracking individual herring within a semi-enclosed coastal marine ecosystem: 3-dimensional dynamics from pre-to post-spawning. Marine Ecology Progress Series 518:267-279.

Lewandoski, S. and M. A. Bishop. 2018. Distribution of juvenile Pacific herring relative to environmental and geospatial factors in Prince William Sound, Alaska. Deep Sea Research Part II: Topical Studies in Oceanography 147:98-107.

McKinstry, C. A., and R. W. Campbell. 2018. Seasonal variation of zooplankton abundance and community structure in Prince William Sound, Alaska, 2009–2016. Deep Sea Research Part II: Topical Studies in Oceanography 147:69-78.

Moran J., R. Heintz, J. Straley, and J. Vollenweider. 2018. Regional variation in the intensity of humpback whale predation on Pacific herring in the Gulf of Alaska. Deep Sea Research Part II: Topical Studies in Oceanography 147:187–95.

Musgrave, D. L., M. J. Halverson, and W. S. Pegau. 2013. Seasonal surface circulation, temperature, and salinity in Prince William Sound, Alaska. Continental Shelf Research 53: 20-29.

Nøttestad, L., J. Giske, J. C. Holst, and G. Huse. 1999. A length-based hypothesis for feeding migrations in pelagic fish. Canadian Journal of Fisheries and Aquatic Sciences 56(S1):26–34.

Pegau, W. S. 2022. 2022 Prince William Sound forage fish observations. (Contract 9511.22.01). Valdez: Prince William Sound Regional Citizens Advisory Council.

Petitgas, P., D. Secor, I. McQuinn, G. Huse, and N. Lo. 2010. Stock collapses and their recovery: mechanisms that establish and maintain life-cycle closure in space and time. ICES Journal of Marine Science. 67:1841–1848.

Plummer, M. 2003. Jags: A program for analysis of Bayesian graphical models using Gibbs sampling. Pages 1-10 *in* Proceedings of the 3rd international workshop on distributed statistical computing. Vol. 124 no. 125.10.

Plummer, M. 2018. Rjags: Bayesian graphical models using MCMC. R package version 4–8. https://CRAN.R-project.org/package=rjags.

Pollock, K. H., and R. Alpizar-Jara. 2005. Classical open-population capture-recapture models. Pages 36-55 *in* S. C. Amstrup, T. L. McDonald, and B. F. J. Manly, editors. Handbook of capture-recapture analysis. Princeton University Press, Princeton, New Jersey, USA.

R Core Team. 2014. R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. Vienna, Austria. http://www.R-project.org/.

R Core Team 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Schwarz, C. J. 2005. Multistate Models. Pages 165-195 *in* S. C. Amstrup, T. L. McDonald, and B. F. J. Manly, editors, Handbook of capture-recapture analysis. Princeton University Press, Princeton, New Jersey, USA.

Schwarz, C. J., and A. N. Arnason. 1996. A general methodology for the analysis of capture-recapture experiments in open populations. Biometrics 52:860-873.

Seber, G. A. 1965. A note on the multiple-recapture census. Biometrika 52(1/2):249–59.

Secor, D. 2015. Migration Ecology of Marine Fishes. John Hopkins University Press, Baltimore, Maryland, USA.

Seitz, A. C., B. L. Norcoss, J. C. Payne, A. N. Kagley, B. Meloy, J. L. Gregg, and P. K. Hershberger. 2010. Feasibility of surgically implanting acoustic tags into Pacific herring. Transactions of the American Fisheries Society 139:1288-1291.

Simpfendorfer, C. A., M. R. Heupel, and R. E. Hueter. 2002. Estimation of short-term centers of activity from an array of omnidirectional hydrophones and its use in studying animal movements. Canadian Journal of Fisheries and Aquatic Sciences 59:23-32.

Simpfendorfer, C.A., M. R. Heupel, and A. B. Collins. 2008. Variation in the performance of acoustic receivers and its implication for positioning algorithms in a riverine setting. Canadian Journal of Fisheries and Aquatic Sciences 65:482-492.

Slotte A, and G. Skaret. Norwegian spring-spawning herring. 2013. Pages 2-6 *in* P. Petitgas, editor. Life-cycle spatial patterns of small pelagic fish in the Northeast Atlantic. ICES Coop. Res. Rep. No. 306. Copenhagen: International Council for Exploration of the Seas.

Springer, A. M., and S. C. Speckman. 1997. A forage fish is what? Summary of the symposium. In Proceedings of the Symposium on the Role of Forage Fish in the Marine Ecosystem. Alaska Sea Grant College Program AK-SG-9701.

Thorne, R. E. 2010. Trends in adult and juvenile herring distribution and abundance in Prince William Sound. (Restoration Project 070830). *Exxon Valdez* Oil Spill Trustee Council, Anchorage, Alaska.

Tojo, N., G. H. Kruse, and F. C. Funk. 2007. Migration dynamics of Pacific herring (*Clupea pallasii*) and response to spring environmental variability in the southeastern Bering Sea. Deep Sea Research Part II: Topical Studies in Oceanography 54(23–26):2832–2848.

Toresen, R, and O. J. Østvedt. 2000. Variation in abundance of Norwegian spring-spawning herring (*Clupea harengus*, Clupeidae) throughout the 20th century and the influence of climatic fluctuations. Fish and Fisheries 1:231–256.

von Biela, V. R., C. J. Sergeant, M. P. Carey, Z. Liller, C. Russell, S. Quinn-Davidson, P. S. Rand, P. A. Westley, and C. E. Zimmerman. 2022. Premature mortality observations among Alaska's Pacific salmon during record heat and drought in 2019. Fisheries 47:157-168. https://doi.org/10.1002/fsh.10705.

Welch, D. W., M. C. Melnychuk, E. R. Rechisky, A. D. Porter, M. C. Jacobs, A. Ladouceur, R. S. McKinley, and G. D. Jackson. 2009. Freshwater and marine migration and survival of endangered Cultus Lake sockeye salmon (*Oncorhynchus nerka*) smolts using POST, a large-scale acoustic telemetry array. Canadian Journal of Fisheries and Aquatic Sciences 66:736–750.

Welch, D. W., M. C. Melnychuk, J. C. Payne, E. L. Rechisky, A. D. Porter, G. D. Jackson, B. R. Ward, S. P. Vincent, C. C. Wood, and J. Semmens. 2011. In situ measurement of coastal ocean movements and survival of juvenile Pacific salmon. Proceedings of the National Academy of Sciences 108:8708–8713.

White, G. C. and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46(s1):120-139. https://doi.org/10.1080/00063659909477239.

Willette, T. M., R. T. Cooney, and K. Hyer. 1999. Predator foraging mode shifts affecting mortality of juvenile fishes during the subarctic spring bloom. Canadian Journal of Fisheries and Aquatic Sciences 56:364-376

OTHER REFERENCES

This section includes peer reviewed publications, *Exxon Valdez* Oil Spill Trustee Council reports and other significant report contributions, publicly available datasets, scientific presentations, and outreach associated with the project.

Peer-reviewed publications

Bishop, M. A., and J. H. Eiler. 2018. Migration patterns of post-spawning Pacific herring in a subarctic sound. Deep Sea Research Part II: Topical Studies in Oceanography 147:108-115. https://doi.org/10.1016/j.dsr2.2017.04.016.

Bishop, M. A., and J. W. Bernard. 2021. An empirical Bayesian approach to incorporate directional movement information from a forage fish into the Arnason-Schwarz mark-recapture model. Movement Ecology 9(8). https://doi.org/10.1186/s40462-021-00241-1.

Cypher, A. D., H. Statscewich, R. Campbell, S. Danielson, J. Eiler, and M. A. Bishop. 2023. Detection efficiency of an autonomous underwater glider carrying an integrated acoustic receiver for acoustically tagged Pacific herring. ICES Journal of Marine Science. 80: 329-341. https://doi.org/10.1093/icesjms/fsac241.

Gray, B., M. A. Bishop, and S. P. Powers. 2019. Structure of winter groundfish feeding guilds in Pacific herring *Clupea pallasii* and walleye pollock *Gadus chalcogrammus* nursery fjords Journal of Fish Biology 95:527-539. https://doi.org/10.1111/jfb.13984.

Gray, B. P., M. A. Bishop, and S. Powers. 2021. Winter variability in the diets of groundfish inhabiting a subarctic sound with a focus on Pacific herring and walleye pollock piscivory. Deep Sea Research Part II: Topical Studies in Oceanography 194:104984. https://doi.org/10.1016/j.dsr2.2021.104984.

Lewandoski, S., and M. A. Bishop. 2018. Distribution of juvenile Pacific herring relative to environmental and geospatial factors in Prince William Sound, Alaska. Deep Sea Research Part II: Topical Studies in Oceanography 147:98-107. http://dx.doi.org/10.1016/j.dsr2.2017.08.002 .

Reports

Bishop, M. A. 2018. Tracking seasonal movements of adult Pacific herring in Prince William Sound. *Exxon Valdez* Oil Spill Long-Term Herring Research and Monitoring Program Final Report (*Exxon Valdez* Oil Spill Trustee Council Project 14120111-B). *Exxon Valdez* Oil Spill Trustee Council, Anchorage, Alaska.

Bishop, M. A. 2018. Annual herring migration cycle: expanding acoustic array infrastructure. *Exxon Valdez* Oil Spill Long-Term Herring Research and Monitoring Program Final

Report *(Exxon Valdez* Oil Spill Trustee Council Project 16160111-S). *Exxon Valdez* Oil Spill Trustee Council, Anchorage, Alaska.

Bishop, M. A., and J. W. Bernard. 2020. Annual Herring Migration Cycle. Pages 4-1 – 4-10 *in* W. S. Pegau and D. R. Aderhold, editors. Herring Research and Monitoring Science Synthesis. Herring Research and Monitoring Synthesis Report, (*Exxon Valdez* Oil Spill Trustee Council Program 20120111). *Exxon Valdez* Oil Spill Trustee Council, Anchorage, Alaska.

Publicly available datasets

Bishop, M. A., and E. Gallenberg. Annual herring migration cycle, Prince William Sound Alaska, April 2017 – April 2022. Gulf of Alaska data portal: https://gulf-of-alaska.portal.aoos.org/#metadata/c1e401be-8d52-477b-a76b-acf5cd817686/project/folder_metadata/41882394.

Bishop, M.A., and E. Gallenberg. Annual herring migration cycle, Prince William Sound Alaska, April 2017 – April 2022**.** DataONE: https://search.dataone.org/view/10.24431/rw1k7d0.

Scientific presentations

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

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

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

Outreach

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

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

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

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

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

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

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

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

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

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

Pearson, A. 2020. Sound Science: Where are the herring going? The Cordova Times. April 4.

APPENDIX A: SUPPLEMENTARY MATERIAL

Table A-1. Location and number of acoustic receivers around southeast Prince William Sound spawning grounds during months of September-March by year.

Array Location & Name	**2017-18**	**2018-19**	**2019-20**	**2020-21**	**2021-22**
Port Gravina	6	2	4	3	2
Orca Bay					
Redhead 1		1	1	1	1
Redhead 2		1	1	1	1
Hawkins Island					
Canoe Pass		2	2	2	2
Cedar Bay		1	1	1	1
Hinchinbrook Island					
Johnstone Point			1	1	1
Total Receivers	6	7	10	9	8

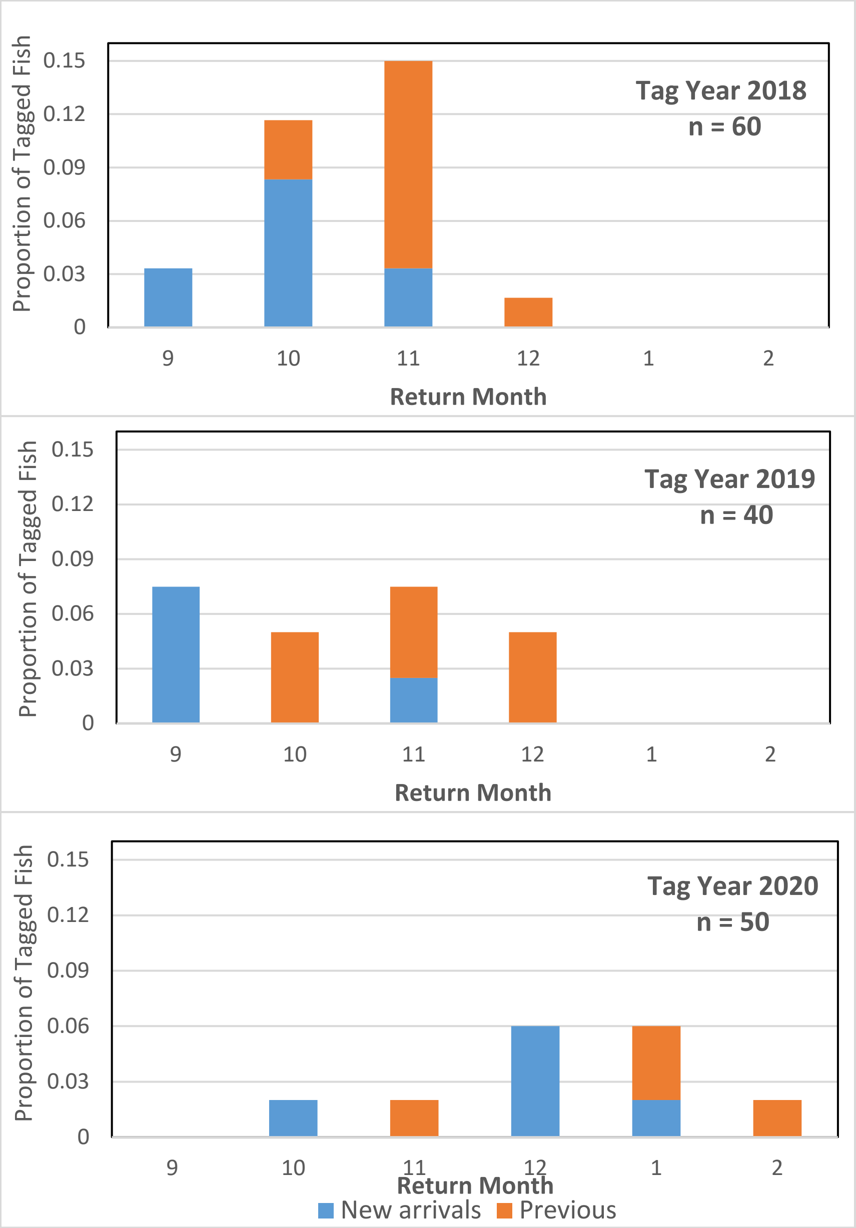

Figure A-1. Proportion of V8 acoustic-tagged herring returning to and detected on the southeast Prince William Sound spawning and tagging grounds by month (September through February) and tag year (2018-2020). Fish were tagged during April of their respective tag year on the southeast Prince William Sound spawning grounds. Blue = initial detection of individual tagged herring between September and February on spawning grounds; Orange = herring previously detected during September through February period on the spawning grounds. Estimated tag life ranged from 231-246 d, expiring early to mid-December. However, 10 of 50 V8 tags deployed in April 2020 exceeded the estimated tag life (max = 307 d).