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

Tracking Seasonal Movements of Adult Pacific Herring in Prince William Sound

Exxon Valdez Oil Spill Trustee Council Project 14120111-B

Final Report

Mary Anne Bishop*
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May 2018

*With contributions by: John Eiler, National Marine Fisheries Service, Alaska Fisheries Science Center, Auke Bay Lab, Juneau, AK 99574

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Study History: For this study a detailed project description was approved for funding by the *Exxon Valdez* Oil Spill Trustee Council in October 2011. Initially Sean Powers of University of South Alabama was a co-Principal Investigator but was unable to participate in the project, leaving Mary Anne Bishop as the sole Principal Investigator. Fieldwork for the project began in November 2011 when we refined our tagging methodology on a small sample of wild Pacific herring (*Clupea pallasii*) captured at Port Gravina. Based on the November 2011 results, efforts were redirected to tag herring in spring on the spawning grounds. In April 2012 and again in April 2013 we captured, acoustic-tagged, and released pre-spawning herring at Port Gravina. The Ocean Tracking Network, a series of six underwater acoustic arrays located at the major entrances between Prince William Sound and the Gulf of Alaska, were installed in March 2013. Data from the acoustic tags deployed at Port Gravina in April 2013 were uploaded from the Ocean Tracking Network in 2013 and 2014. This is the final report on activities conducted by this tagging project. Data from this project have been published in Eiler and Bishop (2016) and Bishop and Eiler (2018) and attached as Appendices in this report.

Abstract: One of the important knowledge gaps for the Pacific herring (*Clupea pallasii*) population in Prince William Sound is where adult herring disperse after spawning. Conservation concerns about this recovering population make it increasingly important to document migration patterns to inform our understanding of PWS adult herring survival. We acoustic-tagged pre-spawning Pacific herring in Port Gravina during April 2012 (n = 25) and April 2013 (n = 69). Post release, 23 of 25 (92%) tagged individuals in 2012 were detected by an acoustic receiver at the Port Gravina release site on one or more days with final detections coinciding with cessation of spawning in the immediate area. In March 2013 six acoustic arrays were installed at the major entrances to Prince William Sound from the Gulf of Alaska as part of the Ocean Tracking Network. These six arrays provided the first opportunity to detect herring outside of the Port Gravina release site. Of the fish tagged in April 2013, 64 of 69 were detected post release including 62% (43/69) at one or more of the tracking arrays. Movement was often rapid between Port Gravina to the arrays at Hinchinbrook Entrance and Montague Strait (2 and 3 d, respectively). Once fish arrived at the entrances, however, a large proportion remained in these areas until mid-June, most likely foraging on the seasonal bloom of *Neocalanus*, a copepod zooplankton. Pulses of tagged herring detected during September and October at Montague Strait suggest some herring returned from the Gulf of Alaska. Intermittent detections of individuals from September through early January at Montague Strait and at the arrays in the adjacent southwest passages indicated that herring schools are highly mobile and are overwintering in this area. The results of this pilot study demonstrate the exceptional opportunity provided by the tracking arrays to document migration patterns by Prince William Sound herring, and specifically the connectivity between the Gulf of Alaska and Prince William Sound.

Key Words: acoustic array, acoustic tags, *Clupea pallasii*, connectivity, Gulf of Alaska, migratory movements, nursery bays, Ocean Tracking Network, Pacific herring, prespawn, Prince William Sound .

Project Data:
Description of data – Data on acoustic-tagged fish were collected at Port Gravina in Prince William Sound, Alaska during April 2012 and April 2013 tagging efforts.
Detections of acoustic tagged fish were uploaded from acoustic arrays in Port Gravina as well as at the Ocean Tracking Network arrays located at the entrances to Prince William Sound.

Format –All detection data is available as csv files.

Data archive and custodians –
Carol Janzen
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https://portal.aoos.org/gulf-of-alaska.php#metadata/c1e401be-8d52-477b-a76b-acf5cd817686/project

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

Ocean Tracking Network data is available at http://oceantrackingnetwork.org/.

Citation:
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EXECUTIVE SUMMARY

Post-spawning movements by acoustic-tagged Pacific herring (*Clupea pallasii*) were studied at Port Gravina, Prince William Sound (PWS) during spring 2012 and 2013, and at the entrances from the Gulf of Alaska into Prince William Sound from April 2013 through early January 2014. Our study is a component of the integrated, multi-project PWS Herring Research and Management (HRM) program. This project was designed to inform the HRM program objective to: *Develop new approaches to monitoring herring.* Objectives specific to this study include:

1. Field test the application of recent advances in acoustic telemetry on wild adult herring.
2. Elucidate herring movement patterns between spawning and overwinter sites.
3. Utilize the Ocean Tracking Network acoustic arrays to monitor herring migration into and out of PWS.

We acoustic-tagged pre-spawning Pacific herring in Port Gravina during April 2012 and 2013. Post release, 23 of 25 (92%) tagged individuals in 2012 were detected by an acoustic receiver at the Port Gravina release site on one or more days with final detections coinciding with cessation of spawning in the immediate area. The 2013 deployment of the Ocean Tracking Network (OTN) arrays located at the entrances to the Gulf of Alaska from PWS allowed us to document post-spawn herring movements outside of the immediate release site. In April 2013 we acoustic-tagged 69 herring in spawning areas around Port Gravina. Tags had an expected life of 263 d. Post-release we detected all but 5 of the 69 tagged herring either at Port Gravina and/or the OTN arrays. Based on detections at the OTN arrays, some herring appeared to quickly move out into the Gulf of Alaska, while many remained in and around the entrances, most likely to feed on the *Neocalanus* copepod bloom through June.

Following the decline of the *Neocalanus* bloom, herring departed from Hinchinbrook Entrance and Montague Strait, with fish at Montague often shifting west and into to the Southwest Passages. Herring schools appeared to be actively moving throughout fall in and around Montague Strait and the Southwest Passages, although no equivalent movements were detected at Hinchinbrook Entrance. Arrays detected herring around Montague Strait and the Southwest Passages right up to when tags expired in early January 2014, indicating that not all herring winter in northeast PWS and that some herring may be moving back and forth into the Gulf even during winter months.

The results of this pilot study demonstrate the exceptional opportunity to document migration patterns by PWS herring, and specifically the connectivity between the Gulf of Alaska and PWS. The OTN is expected to last at least through early 2019. As currently configured, however, the OTN arrays do not permit determination of movement direction by tagged fish. With a relatively small investment, this could be remedied. We found that most detections occurred at the outermost receivers, therefore placement of receivers just above and below the outermost receivers would allow for determination of the movement direction for a large proportion of the detections. In addition, by using acoustic tag programmed at low power only, battery life on acoustic tags would be increased to of ~400 d days. This would allow us to monitor acoustic-tagged herring from one spawning season to the next.

INTRODUCTION

Adult Pacific herring (*Clupea pallasii*) along the eastern Pacific Ocean often overwinter close to spawning areas and in nearshore channels (Hay and McCarter 1997). This behavior has also been observed in Prince William Sound (PWS) herring populations, where historically large schools both overwintered and spawned around northern Montague and Green Islands. More recently however, the major biomass of adult herring during winter has shifted to the northeast and southwest areas of PWS. Currently the largest concentration of adult herring overwinters and spawns around Port Gravina and Port Fidalgo (www.aoos.org). Some spring spawning aggregations are not located near known overwintering areas suggesting that: (a) some adult herring populations are overwintering outside of PWS; (b) not all PWS overwintering populations are being detected; or, (c) overwintering schools such as those in northeast PWS break into smaller schools in spring with some schools moving away from their overwintering area to spawn.

Post-spawning behavior of adult PWS herring is poorly understood. 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). To date, our only information on adult PWS herring movements comes from a study by Brown et al. (2002) that compiled local and traditional knowledge. In that study, fishers reported herring moving north in fall through Montague Strait prior to the fall bait fishery while others reported herring moving into PWS in spring through Hinchinbrook Entrance, Montague Strait and the southwest passages of Elrington and LaTouche. In addition, some crab fishers operating during winter reported that some herring wintered in the Gulf of Alaska (Brown et al. 2002). These observations suggest that PWS herring are regularly migrating out of PWS and onto the shelf.

Acoustic transmitters make it possible to monitor fish movements both across large distances (Heupel et al. 2006) and in structurally complex habitats like those found in nearshore areas (Bishop et al. 2010). Acoustic tags offer many additional advantages, including: 1) the potential for multiple data points over time and space for each individual fish; 2) minimal handling - fish are captured and handled only once; 3) rapid surgery - transmitters can be implanted quickly, with low mortality and with low tag expulsion; 4) transmitters are programmed for individual identification; and, 5) the capability to use portable receivers to monitor spawning schools or large wintering schools of herring regardless of the location (Bishop 2008).

The Herring Marking Workshop sponsored by the *Exxon Valdez* Oil Spill Trustee Council (EVOSTC) in December 2008, reviewed all potential marking methods for herring and stated with regards to acoustic tagging:

A specific recommendation is the conditional endorsement of acoustic tagging, with the caveat that the initial involvement should be limited. Arrays of acoustic receivers have been installed in PWS and there may be opportunities to leverage costs with other organizations, so the present time is an excellent opportunity to pursue this approach…. It seems probable that useful information on herring ecology and migratory movements could be revealed by acoustic tagging (source: draft Integrated Herring Restoration Plan 2010, page 134).

This study encompasses field work conducted between November 2011 and May 2014. Our study objectives were to:

1. Field test the application of recent advances in acoustic telemetry on wild adult herring.
2. Elucidate herring movement patterns between spawning and overwinter sites.
3. Utilize the Ocean Tracking Network acoustic arrays to monitor herring migration into and out of PWS.

STUDY AREA AND METHODS

Study Area

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

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

Developing Methodology to Acoustic-tag Wild Herring

Our first field work was conducted from 18-22 November 2011 in collaboration with the Alaska Department of Fish and Game (ADFG) herring bait surveys. ADFG had difficulty catching herring due to fish being too deep for their seine net to catch, whales in proximity to the net, and bad weather conditions. Attempts to sample adult fish were made around Port Fidalgo, Port Gravina, and Simpson Bay. On the final sampling night (21 November), two sets yielded fish and we were provided a sample from the second (final) set. Except for two herring, fish were too small to hold a tag. Drawing on previous captive tagging work by Seitz and others (2010), we used this opportunity to refine our techniques, including the MS-222 dosages and recovery times, and surgery. Fish were held for >24h to determine their response to the anesthesia and the dummy tags. Upon completion, all fish were sacrificed.

In April 2012 and 2013 we jigged fish from pre-spawning aggregations in Port Gravina a large bay in northeast PWS that is used by herring for both overwintering and spawning (Fig. 1). Jigged herring were first transferred to a 40 gallon holding tank, later removed individually in a plastic container and anesthetized with MS-222, and then surgically implanted with an acoustic tag (Vemco model V9-2L/2 H, 69 kHz, 9 mm x 21 mm, 2.9 g in water) within the peritoneal cavity. Our post-surgery holding tank included non-tagged herring that served as control “buddies”. Acoustic-tagged and controls (untagged) herring were released simultaneously and near a herring school.

Acoustic Arrays & Analyses of Detections

Depending on the year we deployed one (2012) and 9 (2013) acoustic receivers in Port Gravina (Fig. 1). Receivers were recovered from Port Gravina on 19 May 2012 and 21 May 2013, respectively. In March 2013 the OTN was deployed across the six major entrances between PWS and the Gulf of Alaska (Fig. 1). Detections were uploaded in September 2013 (Montague Strait and Hinchinbrook Entrance), February 2014 (Montague Strait and the four southwest passages) and May 2014 (Hinchinbrook Entrance). A fish was considered present at an array on a day when at least 2 detections were recorded.

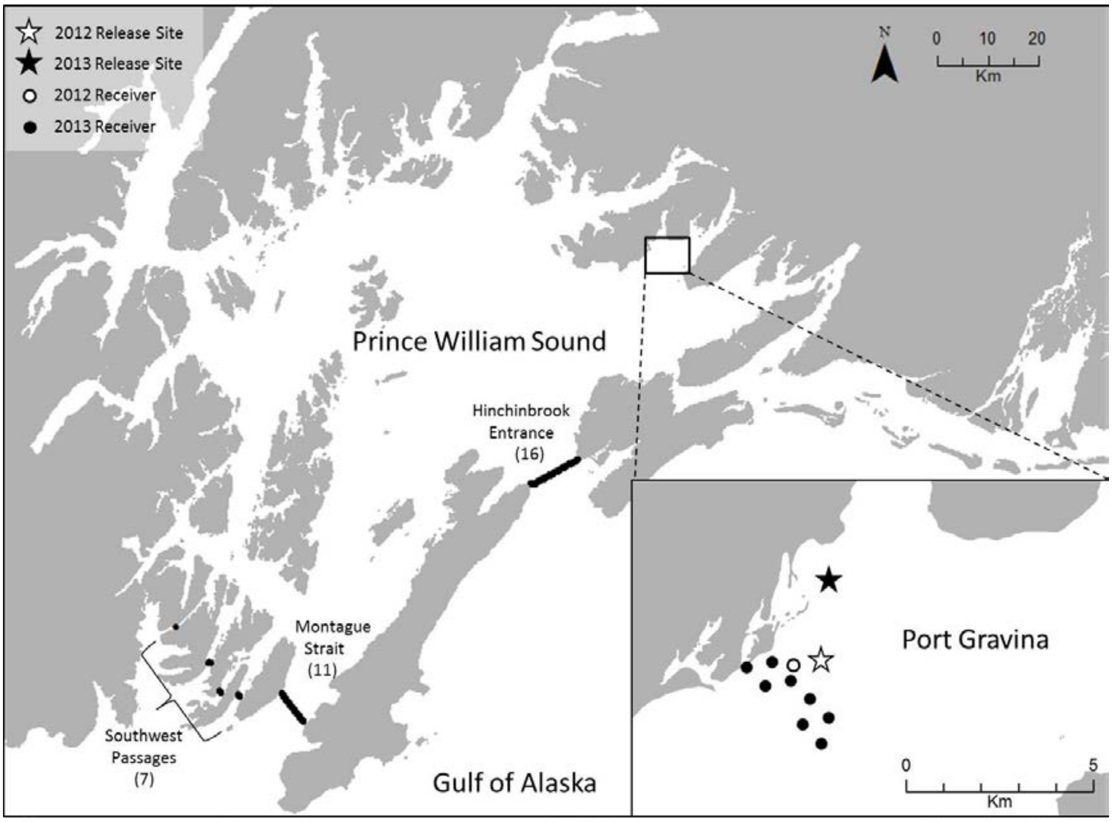

Figure 1. Location of herring tagging and acoustic monitoring areas in Prince William Sound. Pre-spawning herring were tagged during early April 2012 and 2013 in Port Gravina. The Ocean Tracking Network arrays at Hinchinbrook Entrance, Montague Strait, and Southwest Passages were deployed in March 2013.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

Range Tags

The acoustic tags that we deployed in herring (Vemco model V9-2L/2 H) were programmed to run on low power (146 db) for the first 120 d, followed by high power (151 db) for the estimated 143-158 d remaining tag life. Tags were programmed to randomly ping at intervals ranging between 90 and 150 sec while on low power and at intervals between 40 and 60 sec while on high power.

In order to determine the probability of detection at the OTN arrays, we deployed three range tags at Hinchinbrook Entrance in September 2013. Range tags were programmed to ping alternately on low power and high power, with fixed delays between pings set at 3600 sec and 3300 sec following a low and high ping, respectively. We examined the probability of detection for a range tag located at 315 and 400 m from the receiver. This mimicked the approximate distance between receivers. While detection probability was higher at high power (0.94 at 314 m, 0.98 at 400 m), detection probability at low power was also very high (0.88 at 314 m, 0.94 at 400 m).

RESULTS

Herring in Port Gravina

In 2012 we tagged 25 herring on 11 April. In 2013 we tagged 69 herring between 6 and 7 April. Mean standard length (± 1 sd) of tagged herring were similar both years (2012: 226.6 ± 11.8 mm, range 194-255; 2013: 230.1 ± 11.3 mm, range 197-250). Based on ADFG age-length-weight data (S. Moffitt, ADFG, unpubl. data), we estimated that 22/25 of fish tagged in 2012 and 62/69 of fish tagged in 2013 were 7 years or older (>216 mm).

In 2012, 23 of 25 (92%) tagged individuals were detected by a Vemco VR2W acoustic receiver in Port Gravina multiple times on one or more days with final detections recorded 5 d post release and coinciding with cessation of spawning in the immediate area (Fig. 2). Only one of the 25 herring was never detected, and one fish exhibited signs of post-tagging mortality (a significantly high number of detections through May). In 2013, 56 (81%) of the 69 tagged fish were detected at the Port Gravina array while 5 herring (7%) were never detected at Port Gravina or the OTN arrays.

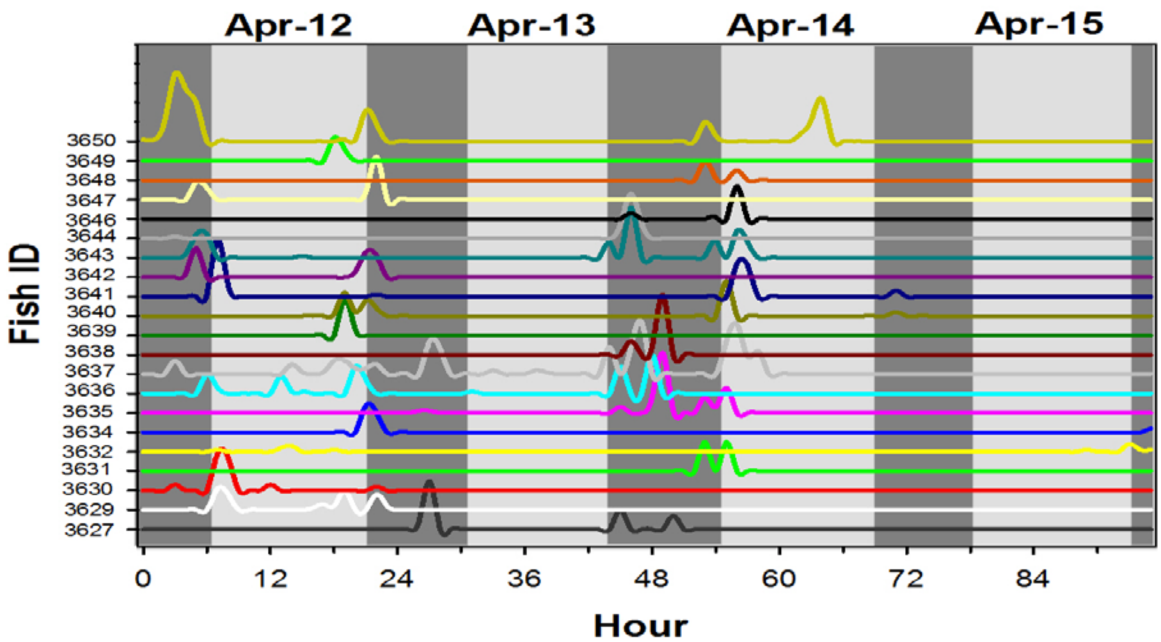

Figure 2. Detections of acoustic-tagged herring by hour of day. Port Gravina, April 2012. All detections are from one receiver located near the point of release.

Post-spawning Movements to Gulf of Alaska Entrances

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

December 2013. Sixty-two percent (43/69) of the herring tagged in Port Gravina during April 2013, were detected at one or more of the OTN arrays between 11 April 2013 and 2 January 2014 (Table 1). Total detection days for an individual fish ranged from 1 – 42 d.

Table 1. Detections of acoustic-tagged herring by array location. Herring were tagged at Port Gravina in April 2013. Tags expired early January 2014. * = Array removed.

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

Departure from the Port Gravina release site was concentrated during two time periods: 6-10 April and 22-26 April (Fig. 3) and coincided with spawning activity in the area. First detections of individual fish at the OTN arrays occurred primarily at Montague Strait (58% of 43 fish) and Hinchinbrook Entrance (30% of 43 fish). At both these arrays, >90% of the first detections occurred at the outermost receivers, with herring favoring the westernmost receivers.

Movement to Gulf of Alaska entrances was often rapid with herring recorded at Hinchinbrook Entrance within 2 d (n = 3) and 3 d (n = 2) and at Montague Strait within 3 d (n = 2) and 4 d (n = 3; Table 2, Fig. 3) of departure from Port Gravina. Based on the number of days since herring were released or last detected at Port Gravina, migration time was 6.5 $\pm$ 4.3 d (n = 13; range = 2-15d) to Hinchinbrook Entrance (~50 km from the Port Gravina array) and 19.04$\pm$21.9 d (n = 25; range = 3-80 d) to Montague Strait (~115 km), and 50.2 $\pm$39.4 d (n = 5, range = 13-107 d) to the Southwest Passages (130+ km).

Phenology, Movements, and Length of Stay at Entrances

April through August. Phenology of herring use was similar from April through August at both Hinchinbrook Entrance and Montague Strait. Detection numbers peaked in early May and remained relatively high throughout the month. Detections were much lower in June and by 9 and 24 July detections ceased until fall for Hinchinbrook and Montague, respectively (Figs. 4 and 5). The average length of stay, defined as first day detected to last day detected was shorter at Hinchinbrook Entrance (x = 17.6 $\pm$15.1 d) compared to Montague Strait (x = 29.5 $\pm$ 29.9 d) although the difference was not significant. We did observe movements

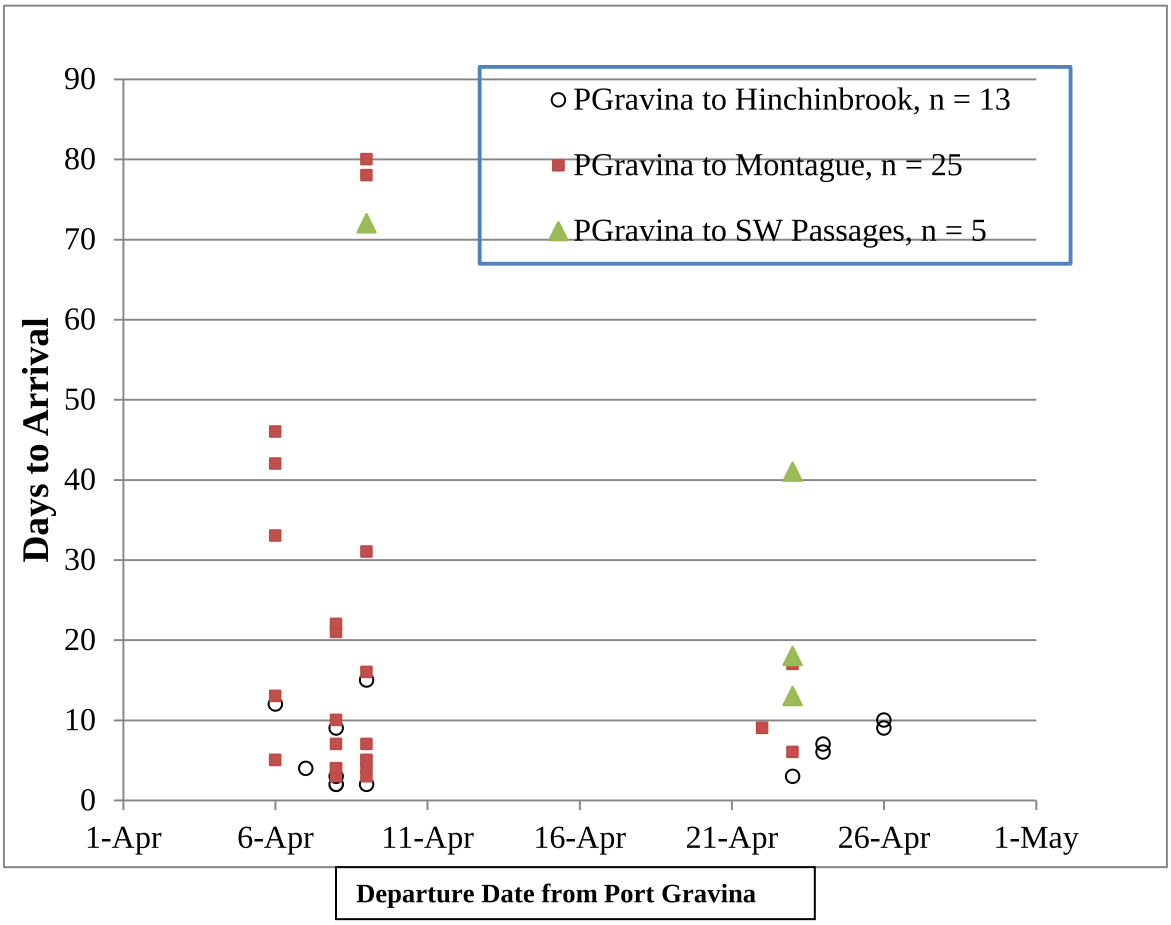

Figure 3. Number of days since release at Port Gravina (n = 8 fish) or since final detection at Port Gravina array (n = 35 fish) to first detection at Ocean Tracking Network arrays. Herring tagged at Port Gravina on 6 and 7 April 2013. Not shown is one herring arriving at the SW Passages 107 d (22 July) after its final Port Gravina detection.

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

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

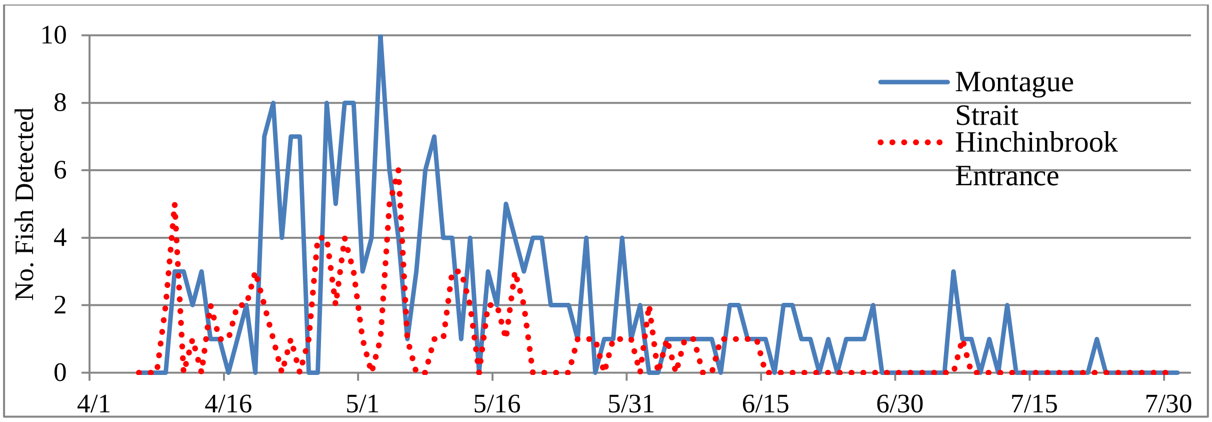

Figure 4. Number of acoustic tagged Pacific herring detected by date at Hinchinbrook Entrance and Montague Strait arrays. April 1 – July 30, 2013.

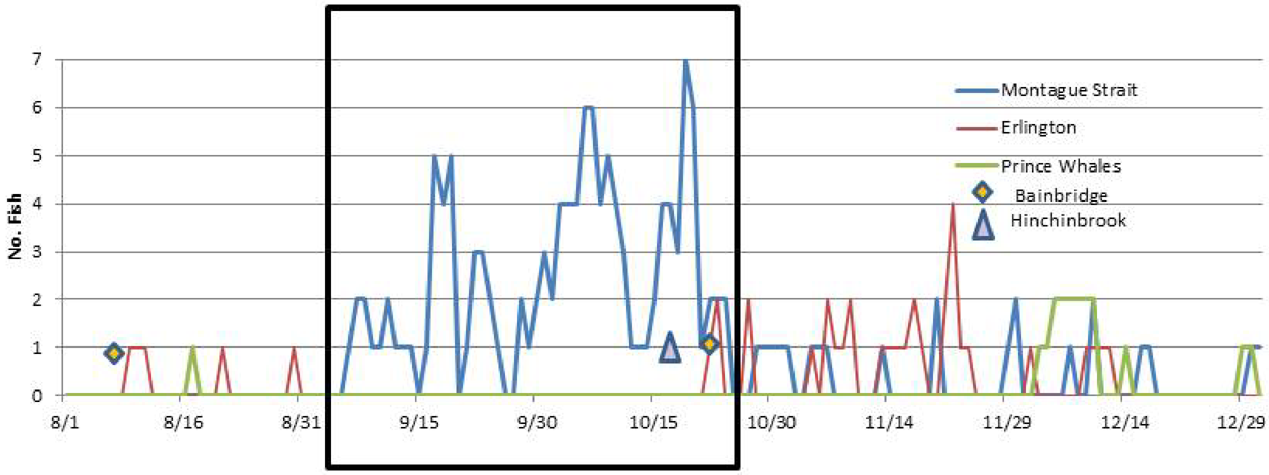

Figure 5. Number of acoustic tagged Pacific herring detected by date and array, August 1, 2013 -January 2, 2014. No detections occurred at LaTouche Passage. Box added to emphasize the predominance of fish at the Montague Strait array throughout September and October 2013.

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

No herring were detected at the Southwest Passages in April, but similar to Hinchinbrook Entrance and Montague Strait, detections peaked in May, then declined in June. However, in contrast to detection patterns from both Hinchinbrook Entrance and Montague Strait, tagged fish at the Southwest Passages were detected through August, although in small numbers (Fig. 5).

September 2013 through early January 2014. A total of 16 of the 43 herring initially detected between April and August at the OTN arrays were detected between September 2013 and early January 2014, when tags expired. First fall detections for 14 of the 16 herring occurred at Montague Strait, with fish pulsing through between 7 September and 21 October (Fig. 5). Most herring detected during fall at Montague Strait and the southwest passages were detected multiple days, and during at least 2 of the 4 months. Three of the 16 herring recorded during fall were detected on one day only at OTN arrays including one at Hinchinbrook Entrance (16 October). This same fish recorded at Hinchinbrook Entrance was also the only tagged herring detected in Port Gravina from October through December 2013 by receivers maintained by Stanford University.

DISCUSSION

This project is the first to document Pacific herring movements in spring from the spawning grounds to the major entrances into PWS from the Gulf of Alaska. Of the 69 fish that we tagged, almost 66% were detected at one or more of the six OTN arrays. We suggest that the high use of the entrances by herring during April and May followed by a sudden drop is related to the *Neocalanus* bloom and its subsequent decline as well as oceanographic conditions at the Gulf of Alaska entrances. Willette et al. (1999) examined diets of herring collected between late April and July over a three-year period and found that large calanoid copepods (primarily *Neocalanus plumchrus* and *Neocalanus flemingeri)* composed a significantly greater proportion of herring diets during May, with a June shift in diet to alternative prey (e.g. euphausiids, amphipods, pteropods and fish) coinciding with the decline of the bloom (Fig. 6). Similarly, during this study *Neocalanus* numbers in 2013 peaked during May at both Hinchinbrook Entrance and Montague Strait, and disappeared at Hinchinbrook by June and decreased by 80% at Montague Strait that same month (R. Campbell, PWS Science Center, unpubl. data).

Oceanographic conditions in PWS during April, may also be conducive to retention of *Neocalanus* around the entrances. By early spring, freshwater runoff is low in PWS, the through flow from the Alaska Coastal Current (inflow via Hinchinbrook Entrance and outflow via Montague Strait) is weak, and seasonal northeast winds are also weak (Wang et al. 2001). The reduced through-flow conditions may be entraining *Neocalanus* that originate from both the shelf and PWS, resulting in predictable, high density patches during their spring bloom at Hinchinbrook Entrance and Montague Strait.

The lack of herring at both Hinchinbrook Entrance and Montague Strait from mid to late July through early September while fish were still being detected in the southwest Passages is more difficult to interpret. Historically, July through late September was peak fishing for herring in PWS with most effort occurring in western PWS from Main Bay south to Montague Strait, including the southwest passages (Rousefell and Dahlgren 1932). More recently, EVOSTC Gulf Watch Alaska acoustic surveys and validation seines have detected adult herring in July at LaTouche and Port Etches (project 16120114-O, M. Armitsu, USGS, pers. comm.), sites close to the Montague and Hinchinbrook arrays, respectively. In addition, ADFG seine surveys and EVOSTC HRM juvenile herring aerial surveys have documented adult herring in northern PWS at Point Freemantle, Glacier Island, as well as close to the spawning grounds at Knowles Head (project 16120111-R, W. Pegau, PWSSC, pers. comm.; S. Moffitt, ADFG, unpubl. data). Future tagging efforts could elucidate the importance of PWS as summer habitat for adult herring.

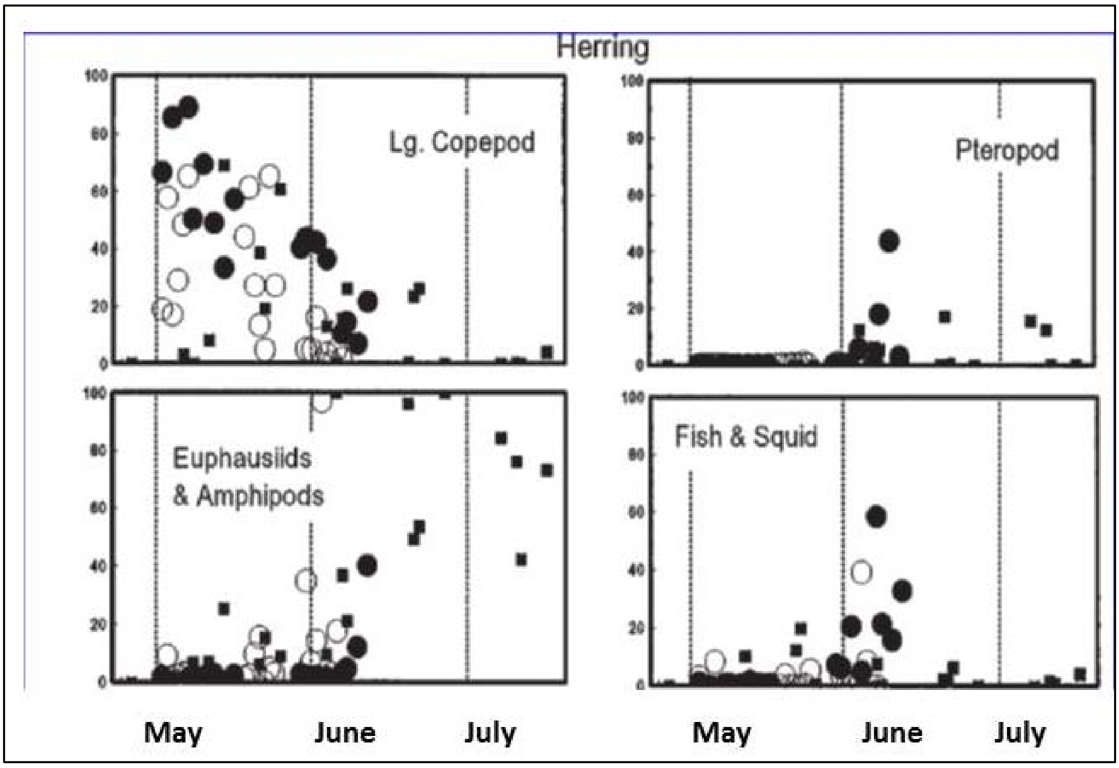

Figure 6. Mean percentage of the diet composed of large copepods, pteropods, euphausiids and amphipods, and nekton (fish and squid) for Pacific herring in western Prince William Sound during 1994 (solid squares), 1995 (solid circles), and 1996 (open circles). From Willette et al. (1999).

Based on final detection patterns of individual herring, it appears that post-spawn, schools of herring steadily move out into the Gulf of Alaska from April through the end of July. Some fish return in fall, as evidenced by the reappearance of 16 of the 43 herring initially detected at OTN arrays between April and August. While only one individual, the detection of one herring on 16 October at Hinchinbrook Entrance, and later that month at in Port Gravina is especially intriguing given that no other tagged fish were detected at the Stanford Port Gravina receivers.

The intermittent detections of individual fish at Montague Strait and the southwest passages over multiple months in fall suggest that residency in wintering areas is not stable but rather that fish schools are highly mobile. At the same time, the use of Montague Strait and the Southwest Passages during November and December suggest that some schools may be wintering in this area and/or outside of PWS and in the Gulf of Alaska. Brown et al. (2002) interviewed crab fisherman that fished in the northern Gulf of Alaska during winter. One of those fishers believed that herring spent winter between Wessels Reef, Cape Cleare and Middleton Island, and enter the Sound in spring via Hinchinbrook Entrance. If this is the case, overwintering in the Gulf of Alaska may explain why 27 of the 43 herring detected at the entrance arrays during spring and early summer, were never detected again.

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

In conclusion, the results of this pilot study demonstrate the exceptional opportunity to document migration patterns by PWS herring, and specifically the connectivity between the Gulf of Alaska and PWS. The OTN is expected to last at least through spring of 2019. As currently configured, however, the OTN arrays do not permit determination of movement direction by tagged fish. With a relatively small investment, this could be remedied. We found that most detections occurred at the outermost receivers, therefore placement of receivers just above and below the outermost receivers would allow for determination of the movement direction for a large proportion of the detections. In addition, by using acoustic tag programmed at low power only, battery life on acoustic tags would be increased to of ~400 d days. This would allow us to monitor acoustic-tagged herring from one spawning season to the next.

ACKNOWLEDGEMENTS

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ARTICLE

Tagging Response and Postspawning Movements of Pacific Herring, a Small Pelagic Forage Fish Sensitive to Handling

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Abstract
Pacific Herring *Clupea pallasii* are an important forage fish in the northern Pacific Ocean and support commercial fisheries throughout the region, although numerous populations have experienced pronounced declines in abundance. Acoustic telemetry can enhance our understanding of the spatial and temporal distribution of depressed herring populations. However, herring are extremely sensitive to handling. During 2012–2013, we tagged 94 adult herring with acoustic transmitters on their spawning grounds in Prince William Sound, Alaska. The handling and tagging methods were specifically designed to minimize physical injuries and stress. Receiver arrays located near the spawning area (2012–2013) and at the principal entrances into the sound from the Gulf of Alaska (2013) were used to track the postspawning movements of the fish. The herring responded well to the tagging procedures. Most were subsequently detected by the arrays, ranging from 88.0% in 2012 to 92.8% in 2013, when the entire tracking system was operational. Forty-three (67.2%) of the 64 fish detected during 2013 were recorded near entrances to the sound, representing minimum travel distances of 50–180 km. Initial movements during the spring and summer were generally to the southwest and mirrored the prevailing currents, but a number of fish were subsequently observed moving east, including one individual detected near the spawning area during the late fall and winter. Larger herring were more frequently detected near the entrances to the sound. Although it is possible that smaller fish exhibit different migratory patterns, the lower detection rate may also suggest that these individuals were adversely affected by the tagging. Our findings suggest that large-scale telemetry studies on pelagic forage fish such as herring are feasible. These data provide new insights into the migratory patterns of herring and present an opportunity to address ongoing questions related to the factors affecting the status and recovery of depressed populations.

Pacific Herring *Clupea pallasii* are an important forage fish in the northern Pacific Ocean, providing food for marine mammals, seabirds, and other fish species. Herring also support important commercial fisheries throughout the region (Pearse 1982; Zheng et al. 1993), although pronounced declines in abundance have periodically resulted in severe restrictions or fishing closures (Schweigert et al. 2010; Botz et al. 2013; NMFS 2014). Detailed information from tagging studies can provide a better understanding of the factors affecting herring movements and timing, and the migratory patterns of this species in relation to sex, age, and reproductive maturity. However, herring have long been considered sensitive to handling (Rounsefell and Dahlgren 1933; Hardin Jones 1968), which complicates efforts to collect quantitative information on their spatial and temporal distribution.

Handling can impact fish in a variety of ways, ranging from minimal effect to impaired behavior, exhaustion, and death. For herring, in addition to both immediate and latent mortality

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from physical injuries and descaling (Jensen 1955; Blaxter and Holliday 1961), increased susceptibility to disease has also been reported (Hershberger et al. 1999; Kocan et al. 2001). The stress experienced from handling can also be a major factor on fish, affecting swimming performance (Schreck 1981, 2000, 2010), behavior (Schreck et al. 1997), and reproductive success (Schreck et al. 2001; Schreck 2010). Sublethal effects may also increase the vulnerability of the fish to other limiting factors, such as predation, adverse environmental conditions, increased performance demands, and the associated allostatic load (Schreck 1981, 2010). The severity of the effect may be influenced by a number of variables, including the handling methods used, ambient environmental conditions, and the maturity, physical condition, and size of the fish (Bridger and Booth 2003).

Nonetheless, numerous studies have reported varying degrees of success capturing and marking herring with external or passive tags, although substantial differences in return rate have been observed, depending on the type of tag used and the degree of injury experienced by the fish (Ancellin 1963; Parrish and McPherson 1963; Krieger 1982; Hay et al. 2001; Flostrand et al. 2009). The possibility of latent effects from handling and tagging, as well as the variable environmental factors experienced by the fish, further confounds efforts to determine tagging success and interpret recovery data. During laboratory studies, heavily descaled herring were initially (i.e., within the first 12 h) considered as viable and active as uninjured fish, but suffered higher mortality rates over longer periods (Parrish and McPherson 1963).

Acoustic telemetry, defined here as the detection of fish and other aquatic animals tagged with acoustic transmitters and located using submerged hydrophones, can provide detailed information on the distribution, movements, and habitat use of marine species. Recent advances in equipment (e.g., miniaturization of transmitter components, encoded transmitter signals) and tracking capabilities have substantially enhanced the utility of this approach (Welch et al. 2011; Adams et al. 2012; Pincock and Johnston 2012; Eiler et al. 2013). Acoustic telemetry has numerous advantages over more conventional tagging and recovery methods, which provide information based solely on where the tagged individuals were recaptured and can be biased by disproportional recovery efforts, vulnerability to capture, and variable reporting rates (Seber 1973; Buckland 1980). Individuals tagged with acoustic transmitters can be repeatedly located without having to be recaptured. This factor can be a major advantage particularly when working in isolated areas or studying species that are sensitive to handling, difficult to catch, or associated with substantial bycatch or large schools of conspecifics. The ability to repeatedly locate specific individuals also provides a way to evaluate the tagging response of the fish. However, the larger size of acoustic transmitters and the surgical procedures commonly used to tag the fish are more invasive than conventional tagging methods and may adversely affect the fish.

Recent evidence suggests that acoustic telemetry studies on herring are feasible. Herring acclimated to captivity, tagged with dummy tags (similar in size to acoustic transmitters suitable for this species), and monitored under laboratory conditions for an extended period (135 d), exhibited comparable survival and growth as the control (i.e., untagged) fish (Seitz et al. 2010). Similarly, free-ranging herring captured with cast nets, tagged with dummy tags, and held under laboratory conditions exhibited swimming behavior that was indistinguishable from that of untagged individuals within 10 min of release, and survived for over a year before the experiment was terminated (J. H. Eiler, unpublished data). Acoustic telemetry has also been used in situ to track Atlantic Herring *C. harengus* in a river estuary (Lacoste et al. 2001) and in a small, sheltered marine basin (Langard et al. 2015), further suggesting that telemetry studies under less controlled conditions are feasible. However, the limited scope, short duration, and small sample sizes associated with these studies leave a number of questions unanswered related to the utility of this approach under a wider range of conditions and on a larger scale.

Herring are an important component of the marine ecosystem in Prince William Sound, Alaska, and have historically supported important commercial fisheries, with annual harvests up to 20,000 metric tons (Botz et al. 2013). However, herring in the sound have declined dramatically since the late 1980s. Herring fisheries within the area have been closed nearly every year since 1993, and the lack of recovery exhibited by the population has been an ongoing concern (Hulson et al. 2008; Pearson et al. 2012). This decline has been attributed to a variety of factors, including impacts from the 1989 Exxon Valdez oil spill, which contaminated substantial portions of known staging areas and spawning habitat (Peterson et al. 2003); hatchery releases of juvenile Pink Salmon *Oncorhynchus gorbuscha*; changes in ocean conditions; and poor nutritional condition of the fish (Pearson et al. 2012). A significant increase in the abundance of humpback whales *Megaptera novaeangliae*—an important marine predator of herring—has been reported during this period within the sound (Teerlink et al. 2015) and may also be a contributing factor.

During 2012–2013, we used acoustic telemetry to determine the postspawning movements of Pacific Herring in Prince William Sound to provide a better understanding of the migratory patterns of the fish and the potential factors affecting herring movements, abundance, and population structure. Spawning generally occurs from late March to early May in intertidal and shallow subtidal zones in localized areas of the sound (Bishop and Green 2001; Norcross et al. 2001). Annual surveys are routinely conducted to determine the timing and extent of spawning within the area (Botz et al. 2013), but little information is available on the seasonal distribution of the fish. In this paper, we describe the tagging response and postspawning movements of herring tagged with acoustic transmitters in the sound; in a subsequent paper we will examine the migratory patterns and timing exhibited by the fish in relation to environmental conditions.

METHODS

Study area.—Prince William Sound is located along the coast of southcentral Alaska, and is separated from the Gulf of Alaska by a series of large, mountainous islands. A number of marine passageways provide access to the sound, including Hinchinbrook Entrance and Montague Strait (Figure 1). The sound is relatively large (approximately 5,040 km^2 per U.S. Forest Service, Cordova Ranger District) and geomorphically complex. The surrounding coastline is rugged and irregular, with numerous islands, bays, and fjords. Water depths in peripheral areas range from 50 to 400 m, with depths up to 700 m in the central portion. Surface water from the Gulf of Alaska flows into the sound pushed by the Alaska Coastal Current. This flow, combined with abundant rain, snow, and glacial runoff, results in a strong cyclonic circulation that generally travels from east to west (Niebauer et al. 1994). Marine waters in the sound are highly stratified during the summer. Severe storms are common from October through March (Wilson and Overland 1986), and result in extensive mixing within the water column (Niebauer et al. 1994). The northern half of the sound is strongly influenced by glacial runoff and tends to be colder and fresher than the southern and central section, which is more influenced by the Alaska Coastal Current and tends to be warmer and more saline (Wang et al. 2001). Sea surface temperatures can be as low as 1°C in late winter, and some bays and fjords can be blocked by ice (Gay and Vaughan 2001). Fish assemblages are diverse but biomass is typically dominated by Pacific Herring, Walleye Pollock *Gadus chalcogrammus*, and various salmonids of the genus *Oncorhynchus* (Willette et al. 1997). The area also supports a variety of marine mammals and piscivorous marine birds (Howse 1975; Bishop et al. 2015).

Fish capture and handling.—We captured adult herring from an 18-m fishing vessel using barbed fishing jigs from an 18-m fishing vessel near spawning areas in Port Gravina (Figure 1) during 10–11 April 2012 and 6–7 April 2013. The fish were placed in a holding tank (770-L capacity) on the vessel filled with fresh, circulating seawater. Individual fish were randomly selected for tagging, removed from the tank with a small plastic container to minimize descaling, and transferred

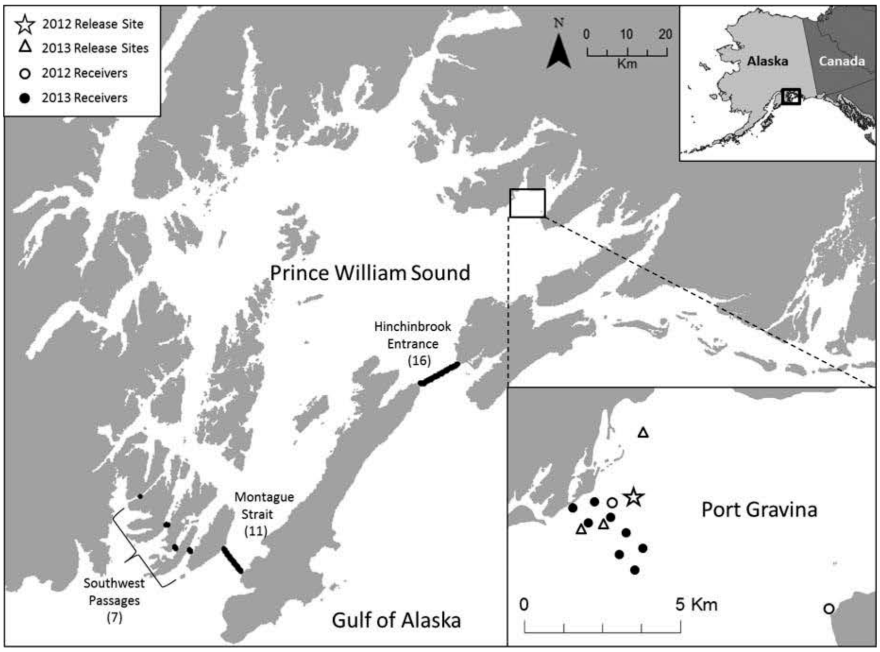

FIGURE 1. Map of Prince William Sound, Alaska, showing the sites where acoustic-tagged Pacific Herring were released in Port Gravina during 2012–2013 (see inset), and the location of the submerged acoustic receivers used to track the movements of the fish. The numbers of acoustic receivers in the arrays at the principal entrances to Prince William Sound are in parentheses.

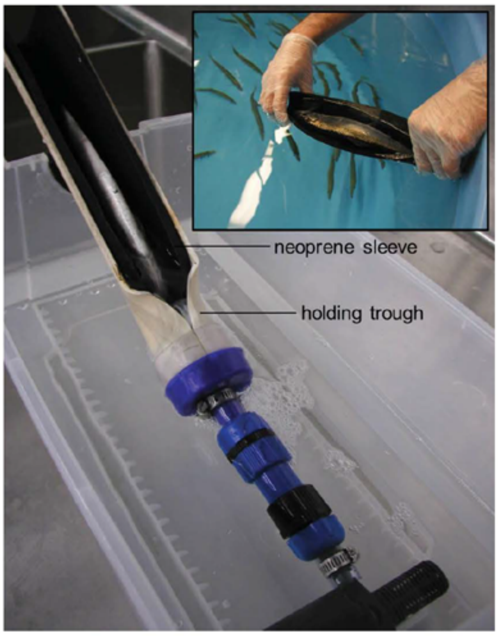

FIGURE 2. Tagging cradle used to surgically tag Pacific Herring with acoustic transmitters in Prince William Sound. The removable neoprene sleeve was used to minimize handling when placing the fish in the recovery tank prior to release (see inset).

to a circular tub filled with an anesthetizing solution of tricaine methanesulfonate (MS-222) at a concentration of 2–3 g/10 L of seawater. We removed the fish from the solution after they were fully immobilized and unresponsive.

The fish were weighed, measured (standard length), and transferred to a tagging cradle specifically designed for small pelagic fish (Figure 2). The outer container of the cradle was partially filled with seawater, and a small pump circulated water up into a narrow, V-shaped holding trough oriented at a 30° angle. The fish were placed in the trough ventral side up with the head positioned near the base so that water continually flowed over the gills. The lower end of the trough was flared to allow the water to spill out and to keep the abdomen of the fish dry. The speed of the pump could be adjusted to increase or reduce the water level in the trough. Loose, soft gauze at the base of the trough prevented the fish from slipping down without restricting the upward flow of water. A removable, neoprene sleeve was used to cushion the fish and restrict movement during surgery.

The fish were tagged with acoustic transmitters (Model V9-2L/2H, 69 kHz) manufactured by Vemco (Bedford, Nova Scotia, Canada). The transmitters were cylindrical (9-mm diameter, 29-mm length), weighed 4.7 g (2.9 g in water), and were programmed to transmit on low power (146 dB) for the first 120 d and high power (151 dB) for the remainder of their operational life (range, 143–158 d). The transmitters emitted a unique, encoded signal every 90–150 s while on low power and every 40–60 s while on high power. The encoded signals made it possible to identify individual fish. The transmitters were placed in separate pouches, sterilized with low temperature anprolene gas (http://www.andersenuerope.com/english/images/library/safety/Anprolene-Key-Operator-Study-Guide.pdf), and sealed prior to use in the field.

We made a small incision (11–12 mm) along the ventral midline of the fish, and gently inserted the transmitter into the abdominal cavity. The incision was closed with simple interrupted sutures (Lober 1996) using suture material suitable for small pelagic fish (PDS II, violet monofilament, 4-0, 19 mm × 3/8 C with cutting needle sutures and Chromic Gut 30″ GS-22 taper, #CG883, 2-0 i30 with cutting needle sutures; Ethicon, Cincinnati, Ohio). The surgical instruments were soaked in a sterilizing solution and rinsed with sterile water after each use. After surgery, the fish were transferred to a recovery tank (650-L capacity) filled with fresh, circulating seawater using the removable neoprene sleeve to minimize handling and injury. The sleeve was held in the water until the fish swam out of its own volition (Figure 2). Water temperature in both the holding and recovery tanks ranged from 5°C to 6°C. We placed a number of untagged individuals in the recovery tank for comparative purposes. Tagged fish were considered to have recovered when their swimming behavior was indistinguishable from that of the untagged fish.

After tagging was completed, all of the fish (including the untagged individuals) were released as a group. A net was used during 2012 to lower the fish into the sea. A plastic, water-filled container was used in 2013 to reduce injury (particularly descaling) and stress. When possible, the fish were released near a school of free-ranging herring.

Tracking procedures.—Stationary acoustic receivers (Models VR2W and VR4, Vemco) were used to monitor the movements of the tagged fish. When a fish was detected, the date, time, and identity of the fish were recorded. Fish were considered to be present at the receiver site on a given day if they were recorded multiple times within a 1-h period. The day of release was excluded from this assessment. Two receivers, located near the entrance to Port Gravina on both the eastern and western side (Figure 1), were used during 2012 to monitor the posttagging movements of the fish. Coverage was expanded in 2013, with an array of nine receivers (oriented in an inner and outer line) located near the western shore. One of the receivers deployed as part of the outer line was never recovered. As part of the Ocean Tracking Network (http://members.oceantrack.org/data/discovery/GLOBAL.htm), receiver arrays were also deployed across the principal entrances into the sound from the Gulf of Alaska during 2013, including Hinchinbrook Entrance, Montague Strait, and a series of smaller passageways in the southwestern section (Figure 1). The receivers were placed approximately 0.7 km apart (SD = 0.1, range = 0.4–0.8 km) to provide adequate coverage based on anticipated reception range. Receivers were periodically accessed over the course of the study to download the data. Transmitter range tests were conducted to evaluate the effectiveness of the arrays (Appendix 1).

Statistical analysis.—Annual differences in fish length and weight by sex were determined using two-way ANOVA. Logistic regression was used to determine if the biological characteristics of the fish influenced the probability of being detected by the receiver arrays near the entrances to the sound. The explanatory variables included the weight, length, sex, condition (based on Fulton's condition factor k = weight/length^3; Kvamme et al. 2003), and release group. Pairwise comparisons were made of all continuous variables using Pearson's product-moment correlation coefficient (r). Variables with values less than −0.7 or greater than 0.7 were considered highly correlated (Moore and McCabe 1993). Due to multicollinearity between weight and length ($r^2 = 0.843$), we constructed a series of univariate models and compared each model to a reduced single mean model, using likelihood ratio tests as described by Wilks (1937). A goodness-of-fit test was performed to check for binomial variation. We used the weight-only model for making inferences from the data.

RESULTS

Capture and Tagging

We captured 219 herring during the 2 years of the study. A total of 94 fish were tagged, including 25 fish in 2012 and 69 fish in 2013 (Table 1). Most (95%) of the fish were in spawning or prespawning condition, and the number of males (45) and females (46) in the sample was comparable. Fish length averaged 229 mm, ranging from 194 to 255 mm. Differences in length were not significant between years ($F_{1,\,87} = 1.51$, $P = 0.222$) or sex ($F_{1,\,87} = 1.69$, $P = 0.196$), although there was compelling evidence that the interaction between year and sex was significant ($F_{1,\,87} = 6.37$, $P = 0.013$) due to differences in 2012 (Figure 3). Fish weights averaged 181 g, ranging from 100 to 250 g. Differences in weight were not significant between years ($F_{1,\,87} = 0.98$, $P = 0.326$), but there was suggestive evidence that female herring weighed significantly more than their male counterparts ($F_{1,\,87} = 3.69$, $P = 0.058$) and compelling evidence that the interaction between year and sex was significant ($F_{1,\,87} = 5.92$, $P = 0.017$) due again to differences in 2012 (Figure 3). The proportion of the transmitter's weight to the weight of the fish averaged 2.8% (2.0–4.7%) in 2012 and 2.5% (2.0–3.2%) in 2013. Most (89%) of the fish were age-7 or older based on age–length–weight relationships for herring in the sound (S. Moffitt, Alaska Department of Fish and Game, unpublished data).

We tagged and released four groups of fish, including one group in 2012 and three groups in 2013 (Table 1). The time needed to tag the fish (from sedation to recovery) was minimal, averaging about 10 min/fish. Sedation took <5 min and surgery <7 min (Table 2). Information from 2013 suggests that the fish responded well to the handling and tagging procedures, with recovery time averaging <5 min. With the exception of the three fish held overnight for observation (and released with group 1), the entire process (from capture to release) took from 2.5 to 7.5 h depending on when the fish were captured (i.e., longer holding periods for the first fish caught).

The fish in group 4 were released about 3 km to the northeast from the receivers in Port Gravina (Figure 1) and provided the best measure of movements past the Gravina array. Due to logistical constraints, groups 2 and 3 were released in the general vicinity of the array the day before the receivers were deployed and provided less definitive information. Fish in group 1 were released about 1 km northeast from the western receiver in Port Gravina during 2012, when receiver coverage was minimal (i.e., limited to the two receivers near the tagging area).

Posttagging Movements

Most (86 or 91.5%) of the 94 fish tagged were subsequently detected within Prince William Sound, including 22 fish (88.0%) in 2012 and 64 fish (92.8%) in 2013

TABLE 1. Tagging dates and numbers of Pacific Herring tagged with acoustic transmitters, held without being tagged, and released in Prince William Sound during 2012–2013.

Year	Release date	Group	Tagged	Untagged	Released
2012	Apr 11	1[a]	25	12	37
2013	Apr 06	2	24	40	64
	Apr 06	3	20	28	48
	Apr 07	4	25	45	70
	Apr 06–07	2–4	69	113	182
Total		1–4	94	125	219

[a]Includes three fish captured and tagged on Apr 10 and held overnight for observation.

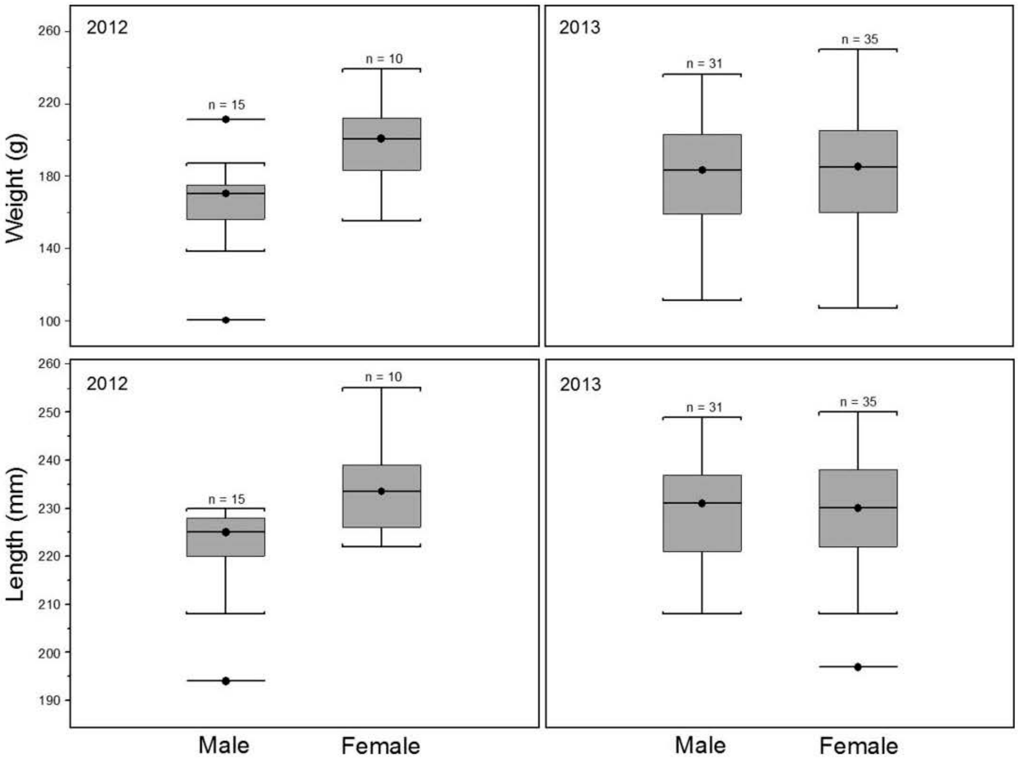

FIGURE 3. Box plots showing the weights and standard lengths of male and female Pacific Herring tagged with acoustic transmitters in Prince William Sound during 2012 and 2013.

TABLE 2. Mean and range in elapsed time to tag Pacific Herring with acoustic transmitters in Prince William Sound during 2012–2013. The time taken for the entire process (from capture to release) is also shown.

			Tagging procedure			
Year	Group	Number tagged	Sedation (min)	Surgery (min)	Recovery (min)	Entire process from capture to release (h)
2012	1	25	2.3 (2.0–4.0)	3.8 (2.9–4.7)	[a]	5.5–7.5[b]
2013	2	24	2.9 (2.0–4.6)	4.5 (3.2–6.2)	3.3 (1.0–10.1)	4.4–5.1
	3	20	2.5 (2.3–2.7)	4.2 (3.3–5.4)	2.5 (1.0–5.4)	2.5–3.4
	4	25	2.4 (2.2–3.8)	3.7 (2.9–5.0)	4.1 (1.6–8.8)	3.3–4.0
	2–4	69	2.6 (2.0–4.6)	4.1 (2.9–6.2)	3.3 (1.0–10.1)	2.5–5.1

[a]Recovery time was not recorded in 2012.
[b]Does not include three fish captured, tagged, and held overnight for observation.

APPENDIX 1

TABLE 3. Number of tagged Pacific Herring by release group detected by receiver arrays in Prince William Sound during 2012–2013. Percentages (in parentheses) of the total number of fish detected are based on the number of fish tagged. Percentages of fish recorded at specific locations are based on the total number of fish detected.

				Detected in tagging area		Detected at entrances to the sound		
Year	Group	Total tagged	Total detected	Gravina	Gravina[a]	Hinchinbrook	Montague	Southwest
2012	1	25	22(88.0)	22(88.0)	b	b	b	b
2013	2	24	20(83.3)	18(90.0)	6(30.0)	4(20.0)	12(60.0)	8(40.0)
	3	20	20(100.0)	14(70.0)	9(45.0)	2(10.0)	10(50.0)	7(35.0)
	4	25	24(96.0)	24(100.0)	6(25.0)	8(33.3)	13(54.2)	7(29.2)
	2–4	69	64(92.8)	56(87.5)	21(32.8)	14(21.9)	35(54.7)	22(34.4)
Total	1–4	94	86(91.5)	78(83.0)	b	b	b	b

[a]Fish only detected in Port Gravina, i.e., not detected near marine entrances to the sound.

[b]Receivers were only operated in Port Gravina in 2012, so there is no information for detections near the entrances to the sound during this year and no combined totals for the two years of the study.

(Table 3). Seventy-eight (83.0%) of the 86 fish detected were recorded by the Gravina array, ranging from 70.0% (group 3) to 100% (groups 1 and 4). The fish were typically detected multiple times over several days following their release. The pattern of detections for fish in group 1 is shown in Figure 4; fish in the other release groups exhibited similar patterns. All of the fish detected during 2012 were recorded on the western receiver. One of these fish appeared to have died near the receiver 2 d after release, based on the continuous signals recorded. Eight individuals were never detected, including three fish in 2012 and five fish in 2013.

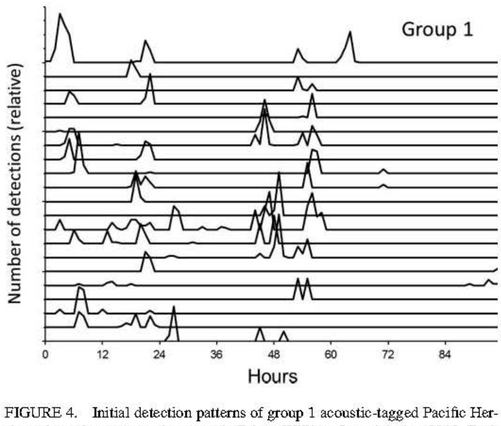

FIGURE 4. Initial detection patterns of group 1 acoustic-tagged Pacific Herring released near spawning areas in Prince William Sound during 2012. Each line represents an individual fish and the number of detections by hour starting the day after release (0 hour).

Forty-three (67.2%) of the 64 fish detected during 2013 were recorded near entrances to the sound, including eight individuals (from groups 2 and 3) not recorded by the Gravina array. The distances to reach the Hinchinbrook (50 km), Montague (118 km), and southwestern (130–180 km) arrays were the minimums (shortest possible route). The fish were recorded from mid-April 2013 to early January 2014 when the battery life of the transmitters expired. Twenty-four of these fish were recorded at multiple entrances over the course of the study (Appendix 2). In fact, most (20 or 90.9%) of the 22 fish detected near the southwestern entrances to the sound were also recorded near Hinchinbrook Entrance or Montague Strait. A number of individuals were recorded several times over the course of the study near the entrance to Montague Strait, and one fish was detected on numerous occasions from late October to early January by acoustic receivers operated by Stanford University (A. Carlisle, Stanford University, personal communication) in the headwaters of Port Gravina.

There was compelling evidence that the probability of being detected by the receiver arrays at the entrances to the sound was related to fish weight (χ^2 = 7.39, df = 1, P = 0.007) and length (χ^2 = 6.50, df = 1, P = 0.011). Conversely, there was little evidence that sex (χ^2 = 0.16, df = 1, P = 0.691), condition (χ^2 = 0.72, df = 1, P = 0.395), or release group (χ^2 = 1.65, df = 2, P = 0.439) were associated with the probability of detection. An increase in weight of 10 g was associated with a 28% increase in the probability of the fish being detected at the entrance arrays (95% CI from 7 to 58%). On the probabilistic scale, a 110-g herring would have a 0.22 probability of being detected (95% CI = 0.06–0.54) compared with a 0.90 probability of detection for a 250-g herring (95% CI = 0.68–0.98) (Figure 5).

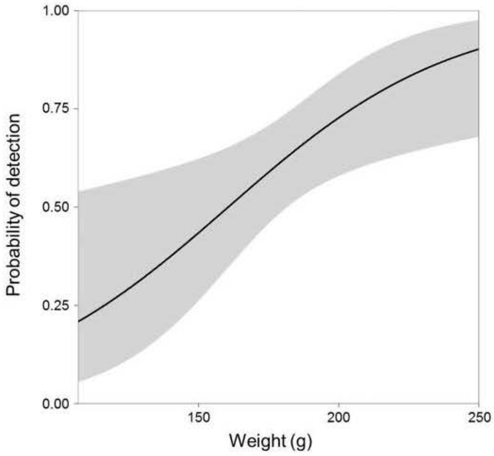

FIGURE 5. Logistic regression model for acoustic-tagged Pacific Herring in Prince William Sound, showing a strong association between fish weight and the probability of the fish being detected by acoustic receivers near the entrances to the sound. The solid line represents the median estimate and the shaded area represents the 0.025–0.975 percentiles.

DISCUSSION

To our knowledge, this study represents the first case where acoustic telemetry was used to determine the in situ movements of large numbers of herring over a prolonged period (9 months) and extended distances in the marine environment. In spite of their sensitivity to handling, the fish responded well to the tagging procedures. The time needed to complete the process was minimal, and the fish were actively swimming a short time after surgery. Although side by side comparisons were not made with other tagging methods, the equipment and procedures used were specifically designed to minimize handling and stress, and likely improved tagging success. The tagging cradle we used restricted the movements of the fish, continuously aerated the gills, and provided a suitable platform for surgery even under remote field conditions. The neoprene sleeve and smooth plastic containers used to hold and transfer the fish minimized handling and reduced descaling and other handling-related injuries.

Individual fish are often released immediately after tagging to reduce handling time and the associated stress. However, releasing the fish as a group (including both tagged and untagged individuals) had a number of potential advantages. Herring typically school, and this approach ostensibly lessened posttagging stress and the associated allostatic load. Numerous marine predators were present in the tagging area including Steller sea lions *Eumetopias jubatus*, humpback whales, harbor porpoise *Phocoena phocoena*, as well as a variety of piscivorous birds. Releasing the herring as a group probably reduced the susceptibility of the tagged fish to initial predation, as evidenced by the high proportion of the sample subsequently detected after the day of release. Confining large numbers of herring in close proximity (thousands of fish at densities of 17–61 kg/m^3) over extended periods (days) has been linked to an increased prevalence of disease particularly in younger individuals (Hershberger et al. 1999, 2006). However, the fish we held for several hours during the tagging process did not appear to have an adverse effect and provided an opportunity to evaluate their condition and behavior prior to release. Repeated detections by the Gravina array during both years of the study also suggest that the fish were actively moving throughout the spawning period. Most of the fish were not detected by the array after spawning activity had ceased, suggesting that they had left the area.

The postspawning movements observed during 2013 indicate that the fish traveled extensively throughout the sound and probably into the Gulf of Alaska, further suggesting that any adverse effects associated with tagging were minimal. Although the initial movements during the spring and summer were generally to the southwest and mirrored the prevailing currents, a number of fish were subsequently observed moving east, including the one individual that returned to Port Gravina in late fall and remained in the area into winter. These movements were consistent with the general migratory pattern described by Hay (1992), where herring in the northeastern Pacific Ocean typically inhabit shallow, nearshore waters during winter and spring but travel to summer foraging areas along the continental shelf. Commercial fishers have reported the presence of herring in the entrances to the sound during spring and fall (Brown et al. 2002), leading to speculation that the fish travel to foraging areas in the Gulf of Alaska after spawning. A detailed description of the migratory patterns and timing of the fish tagged in 2013 will be presented in a companion paper (authors' unpublished data).

About a third of our fish were not detected by the acoustic arrays located near the entrances to the sound. These individuals may represent natural (predation) or tagging-induced mortality, continued residency within the sound (i.e., fish not moving into the Gulf of Alaska), transmitter loss or malfunctions, or limitations with the acoustic tracking system. Herring are a primary forage fish within the sound, and some degree of predation would be expected. Similarly, laboratory-based studies suggest that some tagging-induced mortality and tag loss is likely. Limited mortality (4%) was reported for herring tagged with dummy transmitters and monitored under laboratory conditions, although the rate observed was not significantly different than the control (untagged) sample (Seitz et al. 2010).

During our study, larger herring (in weight and length) were more frequently detected near the entrances to Prince William Sound. Although it is possible that smaller fish exhibit different migratory patterns, the disparate detection rates suggest that these individuals may have been adversely affected by the tagging. Numerous studies have reported tagging effects related to transmitter size, particularly for smaller fish species or juvenile life stages (Adams et al. 1998; Paukert et al. 2001; Bridger and Booth 2003). As a general guideline, Winter (1983) proposed that transmitters should not exceed 2% of the fish's weight. This guideline has been generally accepted by the scientific community (Cooke et al. 2011), although some studies have reported adverse effects at lower levels (Zale et al. 2005). Conversely, Brown et al. (1999) reported that swimming performance was not adversely affected at substantially higher proportions (6–12%). Most (91.3%) of the fish we tagged during 2013 exceeded the 2% guideline, but the postspawning movements exhibited by the fish suggests that this was not a major factor. Similarly, Seitz et al. (2010) reported that post-tagging mortalities in the laboratory were not observed for the smaller herring implanted with dummy transmitters even though the tags weighed up to 3.8% of their body weight.

Stobo and Fowler (1992) reported that fish length was an important factor when tagging Atlantic Herring with external tags and suggested a minimum size limit of 170 mm to reduce tagging mortality. Although the fish we tagged surgically exceeded this standard, the detection rates observed in Port Gravina and near the entrances to the sound and the survival rates reported by Seitz et al. (2010) suggest that this was not an issue. Factors other than size are often a consideration, including the condition of the fish. Gravid females were not tagged during a telemetry study on Capelin *Mallotus villosus* due to concerns over tagging-induced mortality (Davoren 2013). Detection rates for male Capelin (146–179 mm) ranged from 40% to 53% annually during their 2-year study. In contrast, most of the female herring we tagged were gravid.

In conclusion, our findings suggest that large-scale telemetry studies on pelagic forage fish such as herring are feasible. Despite their sensitivity to handling, the fish responded well to the tagging procedures, traveled extensively throughout the sound after tagging, and probably moved into the Gulf of Alaska. The extent of these movements, both spatially and temporally, suggests that any adverse effects associated with tagging were minimal. These data, in conjunction with the physical and biological characteristics of the area, provide new insights into the migratory patterns of Pacific Herring in Prince William Sound and present an opportunity to address ongoing questions related to the factors affecting the status and recovery of depressed populations.

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Appendix 1: Reception Range of the Receiver Arrays

Being able to effectively relocate fish that have been tagged is essential to the success of any telemetry study, and ultimately depends on the equipment and tracking methods used, the physical characteristics of the area, and the behavior of the fish. Three reference transmitters were deployed near Hinchinbrook Entrance to estimate the reception range of acoustic-tagged fish swimming past the receivers. The transmitters were positioned in the vicinity of three receivers and oriented so that the test distances ranged from 15 to 1,050 m. The transmitters alternately emitted low-power and high-power signals at intervals of 3,600 and 3,300 s, respectively. Test data were collected for 236 d from September 2013 to May 2014, and the number of transmitter signals detected by the receivers was compared with the total number of signals transmitted.

The high-power signals were regularly detected (>90% of the time) at distances between 200 and 400 m, and similar results (89.1%) were recorded at 500 m (Figure A.1.1). Detection rates were substantially less at greater distances. A similar pattern was observed for the transmitters emitting low-power signals, with slightly lower detection rates (88.2–98.3%) between 200 and 400 m. Differences between the two power signals were more pronounced at greater distances (Figure A.1.1). Substantially fewer detections were made for transmitters located close to the receivers (e.g., 15 m), probably due to excessive signal from the transmitters or signal obstructions associated with the geomorphology of the area and the position of the tag in relation to the receiver (Dale Webber, Vemco, personal communication).

Prince William Sound provided an ideal setting for determining the seasonal movements of herring. The geomorphology of the area (i.e., a large, enclosed body of water with a series of constricted passageways to the open ocean) made it possible to cordon off and monitor the potential migratory routes using the receiver arrays. Based on our test results, the coverage provided by the arrays was deemed to be sufficient to detect fish traveling between receivers, which were separated by distances ranging from 0.4 to 0.8 km. Due to the configuration of the arrays (a single line of receivers at each entrance), detections by the receivers simply indicated that the fish were present within the general vicinity, complicating efforts to document directed movements into the Gulf of Alaska. More geometrically complex arrays (e.g., dual lines of receivers) would be needed to provide more definitive information on whether the fish had passed through the area.

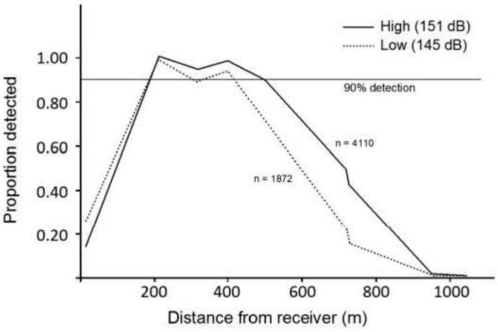

FIGURE A.1.1. Proportion of reference transmitter signals (at both low and high power) detected by acoustic receivers near Hinchinbrook Entrance in Prince William Sound. The potential number of detections for both power levels and the 90% detection level are indicated.

Appendix 2: Herring Tagging Locations

TABLE A.2.1. Locations of Pacific Herring tagged with acoustic transmitters in Port Gravina and recorded by receiver arrays in Prince William Sound during 2013. Principal and secondary (southwestern) entrances to the sound are shown. Sequential observations by entrance are indicated (e.g., 1 = first observation, 2 = second observation).

			Principal entrances		Southwestern entrances			
Fish number[a]	Release group	Gravina	Hinchinbrook	Montague	Latouche	Elrington	Prince of Wales	Bainbridge
9383	2							
9384	2	1		2				
9385	2	1	1					
9386	2							
9387	2	1						
9388	2	1						
9389	2			1				
9390	2			1,3		2	4	
9391	2	1	2					
9392	2							
9393	2	1		2,4		5	3	
9394	2	1						
9395	2	1	2	3		4		
9396	2	1		2				
9397	2	1		2,5		4	3	
9398	2	1		2			3	
9399	2	1						
9400	2							
9401	2	1						
9402	2	1		2		4	5	3
9403	2	1	2	3,5			4	
9405	2	1		2				
9406	2	1		4		2	3,5	
9407	2	1						
9408	3			1				
9409	3			1,3			2	
9410	3	1		7		2,4,6	3,5	
9411	3	1	2	3		4		
9412	3	1		2		3	4	
9413	3	1						
9414	3			2,4		3,5	1	
9415	3	1						
9416	3	1		2		3	4	
9417	3	1		2				
9418	3	1						
9419	3	1						
9420	3		1					
9421	3	1						
9422	3			1,3				2
9423	3	1						
9424	3	1						
9425	3			1				
9426	3	1						

TABLE A.2.1. Continued.

			Principal entrances		Southwestern entrances			
Fish number[a]	Release group	Gravina	Hinchinbrook	Montague	Latouche	Elrington	Prince of Wales	Bainbridge
9427	3	1						
9428	4	1						
9429	4	1	2					
9430	4	1		2				
9431	4	1		2,4		3		
9432	4	1	2	3				
9433	4	1						
9434	4	1		2,6	3	4	5	
9435	4	1	2	3			4	
9436	4	1	2	3				
9437	4	1	2	3,5		4		
9438	4							
9439	4	1	2					
9440	4	1						
9441	4	1						
9442	4	1			2			
9443	4	1		2				
9444	4	1						
9445	4	1		2				
9446	4	1		2,4		3		
9447	4	1		2				
9448	4	1			2	3		
9449	4	1		2				
9450	4	1,6	3,5	2,4				
9451	4	1						
9452	4	1	2					

[a]Unique identification number assigned to the fish.

APPENDIX 2
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Migration patterns of post-spawning Pacific herring in a subarctic sound

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Forage fish
Post-spawning movements
Feeding migration
Overwinter
Acoustic telemetry
Transmitters
Subarctic
Gulf of Alaska
Prince William Sound
Ocean Tracking Network

ABSTRACT

Understanding the distribution of Pacific herring (*Clupea pallasii*) can be challenging because spawning, feeding and overwintering may take place in different areas separated by 1000s of kilometers. Along the northern Gulf of Alaska, Pacific herring movements after spring spawning are largely unknown. During the fall and spring, herring have been seen moving from the Gulf of Alaska into Prince William Sound, a large embayment, suggesting that fish spawning in the Sound migrate out into the Gulf of Alaska. We acoustic-tagged 69 adult herring on spawning grounds in Prince William Sound during April 2013 to determine seasonal migratory patterns. We monitored departures from the spawning grounds as well as herring arrivals and movements between the major entrances connecting Prince William Sound and the Gulf of Alaska. Departures of herring from the spawning grounds coincided with cessation of major spawning events in the immediate area. After spawning, 43 of 69 tagged herring (62%) moved to the entrances of Prince William Sound over a span of 104 d, although most fish arrived within 10 d of their departure from the spawning grounds. A large proportion remained in these areas until mid-June, most likely foraging on the seasonal bloom of large, *Neocalanus* copepods. Pulses of tagged herring detected during September and October at Montague Strait suggest that some herring returned from the Gulf of Alaska. Intermittent detections at Montague Strait and the Port Bainbridge passages from September through early January (when the transmitters expired) indicate that herring schools are highly mobile and are overwintering in this area. The pattern of detections at the entrances to Prince William Sound suggest that some herring remain in the Gulf of Alaska until late winter. The results of this study confirm the connectivity between local herring stocks in Prince William Sound and the Gulf of Alaska.

1. Introduction

Pacific herring (*Clupea pallasii*) are an abundant schooling fish in the northern Pacific Ocean, and serve as important prey for other fish, marine mammals, and birds (Bishop and Green, 2001; Gende et al., 2001; Bishop et al., 2015; Moran et al., in this issue). Pacific herring are also an important commercial species (Hay et al., 2001). Historically, up to 20,000 metric tonnes were harvested annually in Alaska's Prince William Sound (PWS) (Botz et al., 2013). Subsequent to the March 1989 *Exxon Valdez* oil spill, the PWS herring population collapsed. While there is still uncertainty as to whether the cause of the collapse was natural variability, disease, the oil spill, or a combination of various factors, the PWS herring population has yet to recover (Hulson et al., 2008; *Exxon Valdez* Oil Spill Trustee Council, 2014).

One important knowledge gap for the PWS herring population is where post-spawning adults migrate to feed and overwinter. Elsewhere in both Pacific and Atlantic herring (*C. harengus*) populations, spawning, feeding and overwintering may take place in different areas separated by as much as 1000s of kilometers (*c.f.* Holst et al., 2002; Tojo et al., 2007; Beacham et al., 2008). It is common for Pacific herring that spawn along coastal British Columbia to migrate from nearshore spawning areas to summer feeding areas along the continental shelf. During winter these herring often return to coastal areas and remain in nearshore channels close to spawning areas (Hay and McCarter, 1997; Hay et al., 2008). At the same time, some herring in British Columbia do not migrate after spawning, but instead remain as residents in the Strait of Georgia throughout the summer (Hay, 1985; Beacham et al., 2008).

Herring migration patterns can vary by local populations within a spawning aggregation. Pacific herring spawning in northern Bristol Bay have geographically distinct northern and southern feeding and overwintering grounds in the eastern Bering Sea (Tojo et al., 2007). In British Columbia, resident and migratory adult herring often occur within the same stock. Fish spawning in exposed coastal areas are thought to migrate offshore while fish spawning in mainland inlets remain as residents (Beacham et al., 2008).

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Conservation concerns about the lack of recovery of the PWS herring population make it increasingly important to document migration patterns to improve our understanding of adult herring survival. Aerial forage fish surveys conducted during June and July throughout PWS have noted the persistence of adult herring schools (Arimitsu et al., in this issue), suggesting that areas within PWS may serve as summer feeding grounds. Furthermore, the major biomass of adult herring currently overwinters close to the spring spawning grounds (Thorne, 2010). However, commercial fishers have reported large schools of herring moving from the Gulf of Alaska into PWS during both fall and spring while others have observed herring during winter in nearby Gulf of Alaska waters (Brown et al., 2002). These observations suggest that the PWS herring population includes both resident as well as migratory fish that regularly move out of PWS and onto the continental shelf to feed and overwinter in the Gulf of Alaska.

Determining how herring migrate between spawning, feeding, and wintering areas can be challenging because of technological, logistical, and financial constraints. Previous studies of Pacific herring movements in the eastern Pacific have utilized traditional mark-recapture techniques (*e.g.* Hay and McKinnell, 2002) or catch-per-unit effort (cpue; Tojo et al., 2007). Unfortunately, these methods are limited because they are fishery-dependent. Specifically, fishing effort may not be consistent in all locations or across seasons, and recapture rates are typically low (e.g. < 1%, Hay and McKinnell, 2002). Furthermore, mark-recapture and cpue data typically provide poor temporal and spatial resolution on the degree of movement or actual timing of large-scale migrations.

We examine the spatial and temporal post-spawning migratory patterns of Pacific herring. Of particular interest was whether herring remained in PWS after spawning or moved out into the Gulf of Alaska and the environmental factors associated with these movements. Our study utilized acoustic telemetry, a fishery-independent approach, and represents the first case in which it has been used to determine the *in situ* movements of large numbers of herring over a prolonged (nine month) period and extensive distances in the marine environment. In a previous paper, we described our handling and tagging methods, and the biological characteristics, tagging response and general movements exhibited by herring (Eiler and Bishop, 2016). Here we expand on those results by providing detailed information on the migratory patterns of herring, including the timing of departure from the spawning grounds, temporal and spatial movements within the Sound based on observations at marine passageways to the Gulf of Alaska, and the marine conditions associated with these movements.

2. Materials and methods

2.1. Study area

Prince William Sound is located on the coast of southcentral Alaska, primarily between latitude 60° and 61° N. The Sound is separated from the Gulf of Alaska by a series of large, mountainous islands. A number of marine passageways provide access to the Sound, including Hinchinbrook Entrance (HE) and Montague Strait (MS) (Fig. 1). The coastline is rugged and varied, with many islands, fjords and bays. Water depths in fjords and bays range from < 50 m to 400 m; outside of these areas are many marine basins and passages with depths ranging up to 700 m. There are several large icefields bordering the Sound and more than 20 tidewater glaciers (Molnia, 2001).

Oceanic conditions in PWS vary seasonally. During summer, the waters are highly stratified (Niebauer et al., 1994). The northern half of PWS is strongly influenced by glacial runoff and tends to be colder and fresher, whereas the southern portion (which is heavily influenced by the Alaska Coastal Current) is warmer and more saline (Wang et al., 2001). During winter, wind plays a prominent role and waters are more mixed (Niebauer et al., 1994; Okkonen et al., 2005).

Circulation in PWS is largely driven by wind, tides, and the freshwater flux (Okkonen and Belanger, 2008). Surface water from the Gulf of Alaska generally flows into the Sound through HE pushed by the Alaska Coastal Current. Abundant rain, snow, and glacial melt combined with this flow result in a strong cyclonic circulation (Niebauer et al., 1994). While the current at MS flows predominantly into the Gulf of Alaska, the normally counter-clockwise circulation in PWS can occasionally reverse direction during the summer months, resulting in surface waters from the Gulf of Alaska entering the Sound through MS (Vaughan et al., 2001; Halverson et al., 2013a, 2013b). At HE, the late-spring intrusion of freshwater from the nearby Copper River creates a temperature/salinity gradient (front) near HE that remains through October (Okkonen et al., 2005), with both outflow from the Sound and inflow from the Gulf of Alaska occurring simultaneously (Halverson, 2013a; Musgrave et al., 2013).

2.2. Fish capture and handling

Adult Pacific herring were captured along the southwestern shore of Port Gravina (60° 40' N; 146° 20' W), a large bay in northeastern PWS (Fig. 1) that is historically an important overwintering and spring spawning area (Brown et al., 2002). Details regarding the methods used to capture, handle, and tag the fish have been previously described (Eiler and Bishop, 2016). Briefly, we captured herring during three, separate fishing events between 6 and 7 April 2013. The fish were captured while in prespawning aggregations using barbed fishing jigs and placed in a holding tank (770 L capacity). Individual fish were randomly selected from the holding tank, transferred to a circular tub and anesthetized with tricaine methanesulfonate (MS-222), weighed to the nearest 0.1 g, measured (standard length), and placed in a tagging cradle. We made a small incision along the ventral midline of the fish to determine sex and surgically implant an acoustic transmitter (Model V9-2L/2H, 69 kHz; Vemco, Halifax, Nova Scotia, Canada). The tags were programmed to transmit on low power (146 db) for the first 120 d and high power (151 db) for the remainder of their operational life (~143–158 d). The post-surgery holding tank also contained untagged herring from the capture event that served as a control (i.e. not sedated, measured, or tagged). We released each of the three groups, consisting of both tagged and untagged fish near a herring school. Groups 1 and 2 were each released in the middle of the receiver array on 6 April, while group 3 was released ~3 km north of the array on 7 April (Fig. 1).

2.3. Tracking procedures

We used stationary acoustic receivers (Models VR2W and VR4, Vemco, Halifax, Nova Scotia, Canada) to monitor the movements of the tagged fish. Fish within reception range were detected and the date, time, and identity of the fish recorded. Range tests showed that at 500 m, high-power and low-power transmitter signals were detected 89% and 70% of the time, respectively (Eiler and Bishop, 2016).

At Port Gravina, nine acoustic receivers (VR2W series) arranged in two parallel lines were deployed from 7–8 April through 21 May 2013 (Fig. 1). The receivers were tethered to stationary moorings on the ocean floor at depths ranging from 3 to 66 m and at distances from the shoreline ranging from 278 to 2807 m. Distances between adjacent receivers ranged from 550 to 790 m. One of the receivers deployed as part of the more southerly line was never recovered.

Six single-line receiver arrays were previously deployed across the principal entrances to the Sound (Fig. 1) as part of the Ocean Tracking Network (OTN) (http://oceantrackingnetwork.org/). Acoustic receivers (VR4 series) at HE ranged in depth from 21 to 359 m; distances between adjacent receivers ranged from 529–835 m. Acoustic receivers (VR4 series) at MS ranged in depth from 85 to 232 m; distances between adjacent receivers ranged from 641 to 813 m. Seven VR2W receivers were deployed to provide coverage for the four southwestern passages to the Sound, hereafter referred to as Port Bainbridge (PB). These receivers ranged in depth from 20 to 92 m; distances between adjacent receivers ranged from 378 to 528 m. Data were downloaded from the

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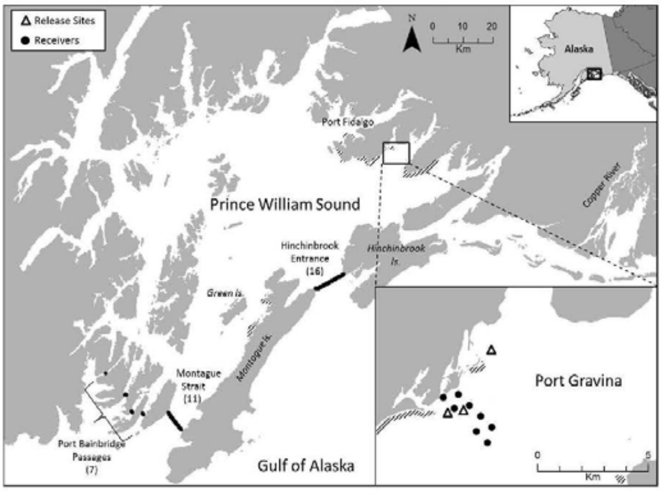

Fig. 1. Map of Prince William Sound, Alaska, showing the sites where acoustic-tagged Pacific herring were released in Port Gravina during April 2013 (see inset), and the location of the submerged acoustic receivers. Total numbers of acoustic receivers in the arrays at the principal entrances to Prince William Sound are shown in parentheses. Hatched areas show where spawn was recorded during aerial surveys conducted by Alaska Department of Fish and Game.

OTN receivers periodically with final downloads occurring in February (MS and PB) and May 2014 (HE), after transmitters had expired.

2.4. Statistical analyses

Fish were considered to be present at the array on a given day if they were recorded more than once within a 1-h period. The day of release was excluded from this assessment. The day individual fish were last detected by the Port Gravina array was designated as their departure date from the spawning grounds. We used the day of release as the departure date for fish not subsequently detected at the Port Gravina array. Travel time (days) from Port Gravina to the entrances was calculated by subtracting the departure date from Port Gravina from the date of first detection at the initial entrance array encountered. For purposes of this paper, we regarded the receivers at the four PB passages as one array. We considered a fish to have moved when it arrived at a different array or when it was detected at the same array after being absent for ≥8 d.

Significant differences in group means were determined using *t*-tests. Differences in fish weight by release group and by initial OTN detection location were determined using two-way ANOVA. The relationship between weight and the timing of first detection was examined using linear regression. Logistic regression was used to determine if the biological characteristics of the fish influenced the probability of detection during the fall/winter season (1 September–2 January). Explanatory variables included the weight, length, sex, and condition of the fish (based on Fulton's condition factor k = weight x length^{-3} as described by Kvamme et al. (2003)). Model selection was conducted using AIC_c (Burnham and Anderson, 2003). The model with the lowest AIC_c value was considered most parsimonious, but all models with $\Delta AIC_c < 2$ were considered to support the data (Burnham and Anderson, 2003).

3. Results

3.1. Spawning grounds release site detections and departures

We captured 182 adult herring and acoustically tagged 69 fish between 6 and 7 April 2013. Most (96%) of the tagged fish were in spawning or prespawning condition (35 females, 31 males); sex was not determined for three spawned-out herring. We released fish in three groups (Fig. 1), with each group consisting of a mix of tagged (24, 20, 25) and untagged (40, 28, 45) herring, respectively. Fish length averaged 230.1 mm (sd = 11.3 mm, range 197–250 mm) and weight averaged 182.9 g (sd = 29.5 g, range 107–250 g). Differences in fish length and weight were not significant between release groups (ANOVA; both $p > 0.36$). Most (88%) of the fish were ≥7 years of age based on age-length-weight relationships for herring in the Sound (S. Moffitt, Alaska Department of Fish and Game, unpublished data).

Sixty-four of the 69 fish (93%) were detected at one or more array; five fish (7%) were not detected after release. At Port Gravina, 56 (81%) fish were detected between 7 April and 21 May, when the array was removed (Fig. 2). Length of stay in Port Gravina (based on first and last detection) averaged 9.0 d (sd = 10.7 d, range 1–45 d, n = 56). Herring were detected most often (90%, n = 16,207 total detections) by the four middle receivers in the array, located 758–2135 m from shore. The two

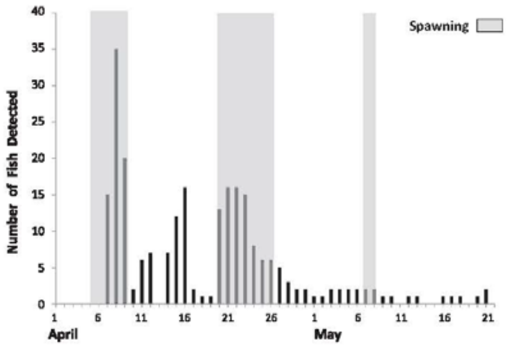

Fig. 2. Number of individual fish detected by date at the Port Gravina acoustic array, excluding detections on the day of release (6 and 7 April 2013). Occurrence of spawning activity in vicinity of Port Gravina is noted (gray shading). The 7–8 May spawning event occurred primarily in Port Fidalgo, a bay adjacent and northwest of Port Gravina. The acoustic array was removed on 21 May 2013.

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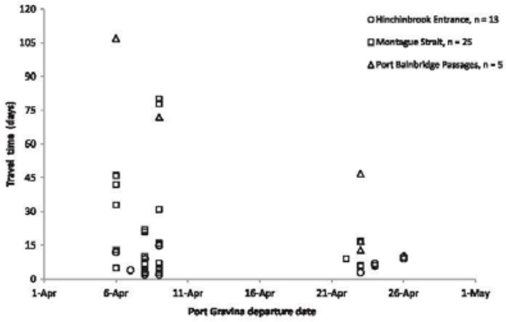

Fig. 3. Travel time (d) by acoustic-tagged herring to marine entrances of Prince William Sound during 2013 calculated as a function of their departure date from Port Gravina and their initial detection at the entrance arrays. Departure date was defined as the date of last detection at Port Gravina (n = 35) or the date of release (6 or 7 April) for fish not detected at the Port Gravina array (n = 8).

receivers closest to (278 and 292 m) and farthest from the shore (2395 and 2806 m) recorded 7% and 3% of the detections, respectively. Although group 3 was released ~3 km north of the array, 90% (4988 of 5927) of its detections were also recorded by the four middle receivers.

Departures from Port Gravina for the 69-tagged herring were concentrated during two time periods: 6–9 April (68%) and 22–26 April (17%). For fish later detected at the PWS entrances (Fig. 3), departure date from Port Gravina was significantly earlier (*t*-test, $p = 0.05$; $\bar{x} = 11$ April, sd = 7.1 d, n = 43) than for herring not detected at the entrances ($\bar{x} = 16$ April, sd = 13.8 d, n = 26).

3.2. Movement from Port Gravina to PWS entrances

We recorded 43 fish at the entrances to PWS including 8 fish that were not detected at the Port Gravina array after being released. Montague Strait had the highest number of initial detections (25, 58%), followed by HE (13, 30%) and PB (5, 12%) (Fig. 3). We found significant differences in fish weights between first arrival location ($F_{2,40} = 4.93$, $p = 0.012$). Herring first detected at PB ($\bar{x} = 162$ g; sd = 32 g) weighed significantly less than herring initially detected at either MS or HE (ANOVA, $p < 0.033$ for both entrances; MS: $\bar{x} = 188$ g; sd = 17 g; HE: $\bar{x} = 202$ g; sd = 33 g).

Arrival dates at the PWS entrances were protracted across the spring/summer season, with first-time arrivals occurring over a 104 d period between April and July 2013 (Fig. 4). Initial detections at the two major entrances to the Sound were recorded as early as 10 April (HE) and 11 April (MS) while the first detection at PB did not occur until 6 May, more than 3.5 weeks later (Table 1). Overall, the majority of fish recorded at the PWS entrances arrived in April (26, 60%) with new arrivals decreasing steadily during May (12, 30%), June (4, 9%), and July (1, 2%).

Travel time from Port Gravina to the PWS entrances was rapid for some tagged fish with 26% of the tagged herring recorded within 4 d of their final Port Gravina detection at both HE (50 km from Port Gravina array, n = 6) and MS (115 km from Port Gravina array, n = 5) (Table 2, Fig. 3). Overall, fish initially moving to MS travelled slightly faster ($\bar{x} = 15.1$ km d^{-1}; sd = 11.7 km d^{-1}, n = 25), than fish migrating to HE ($\bar{x} = 12.3$ km d^{-1}; sd = 8.4 km d^{-1}, n = 13) although the difference was not significant (*t*-test, $p = 0.41$). Fish initially moving to PB, approximately 130–180 km from the Port Gravina array, had the slowest travel rates ($\bar{x} = 5.3$ km d^{-1}; sd = 4.6 km d^{-1}, n = 5) and were significantly different from both HE and MS (*t*-test, both *p*'s $\leq$ 0.04). Travel time from Port Gravina to the PWS entrances was related to fish weight (adjusted $r^2 = 0.25$, $p < 0.001$, $df = 1,41$) with heavier herring arriving sooner (Fig. 5). An increase in one ordinal date in travel time was associated with a 0.56 g decrease in fish weight (95% CI = 0.27– 0.85 g; Fig. 5). We also found evidence of tagged fish arriving in the same school with three instances of first detections within < 60 min of each other (ranging from 5–57 min). These observations included a group of two herring (on two instances) and a group of three herring.

At both HE and MS arrays (which consisted of 16 and 11 receivers, respectively), first detections occurred almost exclusively at receivers located closest to shore. Most (85%) of the 13 fish arriving at HE were initially recorded at the westernmost receiver while the remaining 15% of the fish were initially recorded at the two easternmost receivers. Similarly, 80% of the 25 fish arriving at MS were first detected at the westernmost receiver, while 16% of the fish were first detected at the easternmost receiver.

3.3. Phenology at entrance arrays

Total number of days an individual fish was detected at the PWS entrances ranged from 1 to 42 d ($\bar{x} = 14.8$; sd = 11.1 d, n = 42). Distinct seasonal patterns were apparent with more individuals recorded at the entrance arrays during the spring/summer season (April–August). At both HE and MS, the number of fish detected per day peaked in early May and remained relatively high throughout the month. Detections were much lower in June, and by 9 July and 24 July detections ceased until fall at HE and MS, respectively (Fig. 4). No herring were detected at PB during April, but similar to detections at HE and MS, detections at PB peaked in May, then declined in June. However, in contrast to detection patterns at both HE and MS, small numbers of tagged fish were detected at PB through August (Fig. 4). Three of the 43 herring recorded during spring/summer season were detected on one day only at the PWS entrances, suggesting they were en route to or from the Gulf of Alaska.

During the fall/winter season from September 2013 to early January 2014 (when the tags expired), 16 of the 43 herring returned to the PWS entrances. When we modeled the probability of herring returning in fall, the most supported model included only the intercept. Models including either sex ($\Delta AIC_c = 0.28$), condition ($\Delta AIC_c = 0.41$), or length ($\Delta AIC_c = 1.91$) were also supported, although none of these variables had *p* values $\leq$ 0.05. First fall detections for 14 of the 16 returning herring occurred at MS, with several pulses of fish detected between 7 September and 21 October (Fig. 4, Table 1). Most herring (10 of 16) detected during fall/winter season were recorded over multiple days and in more than one month (max = 4 months). Three of the 16 herring recorded during fall/winter season were detected on one day only at the PWS entrances suggesting they were displaying directed movements to or from the Gulf of Alaska.

3.4. Movements between entrances

Of the 43 fish recorded at entrances to the Sound, 53% were detected at more than one array (Fig. 6, Table 3). Seven of the 13 herring (54%) initially detected at HE moved to MS including 5 fish later detected at PB. Twenty herring were detected at both MS and PB. Similarly, 11 of 22 fish (50%) that traveled to PB were detected at multiple passages with the middle two passages (Elrington and Prince of Wales) both used by 10 of the 11 fish. Maximum number of movements between arrays recorded for an individual herring was five (n = 1) for a herring that moved from PB to MS to PB to MS and back to PB.

Successive observations at the same entrance (i.e. the fish detected by the array after an absence of ≥8 d) was the most common movement exhibited by the fish. More than 54% of all movements recorded (69 of 126 movements) reflected this pattern. The dominant direction of movement between arrays was westward (38 of 126 movements) with only 19 eastward movements recorded (Fig. 7). However, these movements exhibited a seasonal pattern. Based on the day of arrival, westward movements between arrays spiked in May and included 5 of 8

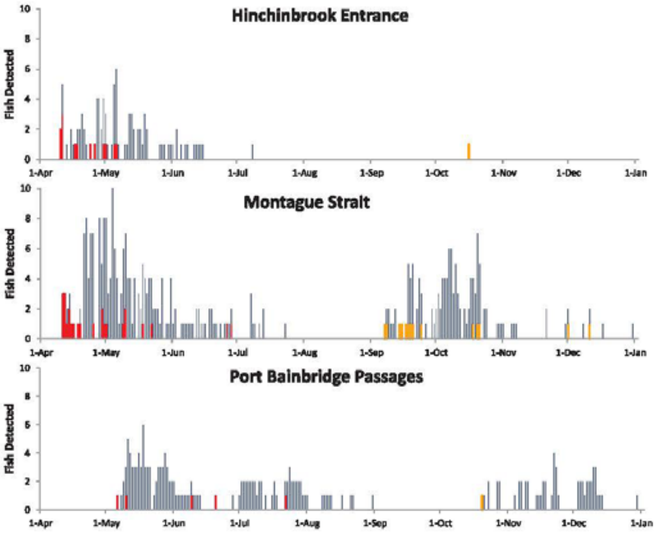

Fig. 4. Number of tagged herring detected by date at acoustic arrays located at the entrances to Prince William Sound from 10 April 2013 to 2 January 2014. Initial detection of individual fish during spring/summer (in red) and fall/winter (in orange) are shown.

fish moving from HE to MS and 9 of 20 fish moving from MS to PB. A second spike in movements was recorded in July with 6 of 20 fish moving from MS to PB. Eastward movements were more frequent during fall and winter, with 8 of 14 fish returning to MS that had most recently been recorded at PB (Fig. 7).

4. Discussion

4.1. Migratory patterns and regional connectivity

The migratory patterns of herring observed during this study suggest a high degree of connectivity between the northeastern PWS spawning grounds and the primary passageways to the Gulf of Alaska. About two-thirds of the 69 tagged fish were subsequently detected at one or more of the marine entrances to the Sound with most of the fish detected initially at HE and MS. Although these entrances are closer to Port Gravina than PB, the geomorphology of the Sound (i.e. the lack of any physical obstruction to movement across the central basin) and the oceanographic conditions encountered by the fish (the prevailing

Table 2
Travel time for herring with the shortest time intervals between their last detection at Port Gravina tagging array and first detection at Hinchinbrook Entrance and Montague Strait Ocean Tracking Network arrays during 2013. Distance is based on the shortest possible route.

Port Gravina to:	Distance (km)	Travel time (d)	$km\ d^{-1}$	m/s
Hinchinbrook Entrance west side	50.4	1.94	26.0	0.30
Montague Strait west side	115.1	3.18	36.2	0.41

Table 1
Number of first and final detections by season/month for acoustic tagged herring at Ocean Tracking Network receiver arrays. Spring/Summer = 10 April (date of first detection) – 31 August 2013; Fall/Winter = 1 September 2013– 2 January 2014. Acoustic transmitter operational life was 263 d, with battery expiration estimated at ~25 December 2013.

		Spring/Summer							Fall/Winter					
		No. Individuals/Month							No. Individuals/Month					
Array Location	*n*	A	M	J	J	A	Range of Dates	*n*	S	O	N	D	J	Range of Dates
Hinchinbrook Entrance														
First Detection	13	10	3	0	0	0	10 Apr–6 May	1	0	1	0	0	0	16 Oct
Final Detection	7	2	3	1	1	0	11 Apr–8 Jul	1	0	1	0	0	0	16 Oct
Montague Strait														
First Detection	25	16	7	2	0	0	11 Apr–28 Jun	14	9	3	0	2	0	7 Sep–11 Dec
Final Detection	19	2	6	6	5	0	12 Apr–23 Jul	10	0	5	1	3	1	10 Oct–2 Jan
Port Bainbridge Passages														
First Detection	5	0	2	2	1	0	6 May–22 Jul	1	0	1	0	0	0	20 Oct
Final Detection	16[a]	0	4	4	5	3	18 May–31 Aug	5	0	0	1	4	0	23 Nov–30 Dec
All OTN Arrays														
First Detection,	43	26	12	4	1	0	10 Apr–22 Jul	16	9	5	0	2	0	7 Sep–11 Dec
Last Detection	42[a]	4	13	11	11	3	11 Apr–31 Aug	17	0	6	2	7	1	10 Oct–2 Jan

[a] One transmitter detected continuously at one receiver from mid-July through December was excluded from final detections.

APPENDIX 2
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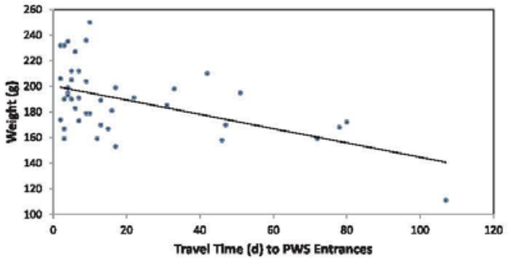

Fig. 5. Linear regression for acoustic-tagged Pacific Herring in Prince William Sound (PWS), showing a negative relationship between fish weight (g) and travel time (d) to acoustic arrays at the entrances to the Sound. Adjusted $r^2 = 0.25$, $p < 0.001$, $df = 1,41$. Travel time = date of first detection at PWS entrance array minus date of final detection at Port Gravina array.

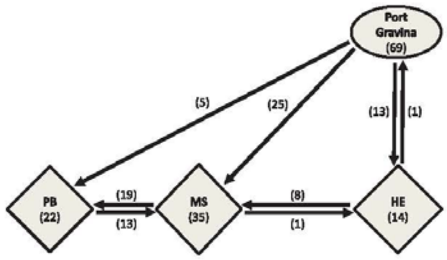

Fig. 6. Direction of movements of acoustic-tagged Pacific herring between the receiver arrays at the tag and release site (Port Gravina) and at the entrances to Prince William Sound (diamond shapes), including Hinchinbrook Entrance (HE), Montague Strait (MS) and Port Bainbridge passages (PB), 6 April 2013 to 2 January 2014. Numbers in parentheses represents the number of individual fish detected at the sites or moving between sites (see directional arrows).

Table 3
Patterns of movement by individual herring at entrances to Prince William Sound by season and the number of entrances a fish was detected.

Detected at:	Spring/Summer 10 Apr–31 Aug	Fall/Winter 1 Sep–2 Jan
One major entrance		
Hinchinbrook Entrance	6	1
Montague Strait	17	8
Port Bainbridge Passages	2	1
Two major entrances		
Hinchinbrook Entrance & Montague Strait	3	0
Montague Strait & Port Bainbridge passages	11	6
All three major entrances Hinchinbrook, Montague & Port Bainbridge	4	0
Total fish	43	16

current generally flowing cyclonically from east to west) likely contributed to this pattern. The number of herring initially observed at HE and MS and subsequently detected at PB, suggests a pronounced southwesterly progression during the spring and early summer (Fig. 4).

The status of the tagged herring that left Port Gravina but were not detected near the entrances to the Sound is unknown due to the lack of receiver coverage within the central basin. These fish may have exhibited different migratory patterns and remained in PWS throughout the spring and summer. Annual aerial surveys and historic seine surveys (in June and July) have documented the presence of herring schools near Port Gravina and in northern PWS (Arimitsu et al., in this issue; S. Moffitt, Alaska Department of Fish and Game, unpublished results).

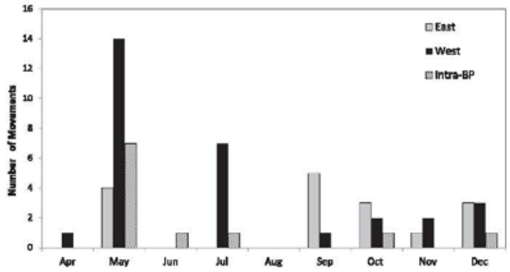

Fig. 7. Number of movements between arrays by direction and month for acoustic tagged Pacific herring (n = 23 fish). East = movements from Port Bainbridge passages to Montague Strait (n = 14 movements), or from Montague Strait to Hinchinbrook Entrance (n = 2). West = movements from Hinchinbrook Entrance to Montague Strait (n = 8) or from Montague Strait to the Port Bainbridge passages (n = 22). Intra-BP = movements among the four Port Bainbridge passages (n = 11).

Similarly, hydroacoustic surveys in July have found schools of adult herring in northern PWS (Arimitsu et al., in this issue). These schools may represent resident aggregations of herring. Nøttestad et al., (1999) and Slotte (2001) reported that smaller forage fish or individuals in poorer condition often display shorter migrations. During our study, larger herring (in weight and length) were more frequently detected at the entrances to the Sound (Eiler and Bishop, 2016). Telemetry studies that examine the movements of herring within PWS would provide a better understanding of the migratory patterns during this period.

Due to the configuration of the entrance arrays (single line of receivers), it was not possible to definitively determine the direction of travel exhibited by the tagged fish. Detections by an array simply indicated that fish were present within the immediate area. However, the pattern of detections suggests herring moved out into the Gulf of Alaska from April to late July. Individual fish were repeatedly observed moving back and forth between MS and PB. It is unlikely that these movements occurred within the inner waters of the Sound due to the proximity of the arrays to the open ocean and the prevailing currents within these areas. Similarly, individual herring were periodically recorded on consecutive days by the receiver arrays in the two middle passageways in PB (Fig. 1) and in one instance an individual fish was detected by both arrays on the same day. There is also ancillary evidence that herring left PWS after spawning. Herring periodically have been caught in the Gulf of Alaska southeast of HE during biennial groundfish surveys conducted during July along the continental shelf (NOAA, 2016), which supports this contention and provides some information on the location of summer foraging areas. Herring also have been caught to the northeast of HE during the surveys, although these catches may consist of herring that spawn by Kayak Island located ~135 km east of HE.

Over a third (37%) of the 43 herring detected at entrances to the Sound during the spring and summer were subsequently observed again during the fall. Most of these fish were detected intermittently over several months near both MS and PB, including several individuals observed during late December and early January (when the tags expired). These observations suggest that a sizable number of herring do not overwinter near spawning grounds in the northeastern section of the Sound, but return instead to areas near the southwestern entrances. Our findings also suggest that some schools of herring are highly mobile and may periodically move into the Gulf of Alaska during the winter months.

Only one tagged fish returned to PWS via HE in the fall, traveling past the entrance array during mid-October and moving into Port Gravina later in the month (based on records from two acoustic receivers maintained by Stanford University located in central and northern Port Gravina) where it remained through the duration of our

APPENDIX 2
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study. That only one fish exhibited this pattern was surprising considering that herring are typically observed in the vicinity of Port Gravina during the winter months (Thorne, 2010). About half of the 13 fish initially detected at HE after spawning were never detected at another entrance and presumably moved directly into the Gulf of Alaska. It is possible these individuals remained along the continental shelf during winter (or returned sometime after their transmitters had expired). Overwintering in the Gulf of Alaska or predation may explain why over 60% of the 43 herring detected at the entrance arrays during spring and summer were never detected again. This hypothesis is reinforced by information from local fishers, who have reported that herring are present during the winter in waters south and west of HE (specifically between the southeastern end of Montague Island and Middleton Island, located ~100 km south of HE), and that these fish enter PWS through HE, MS, and PB before March (Brown et al., 2002).

4.2. *Factors affecting herring movements*

4.2.1. *Ocean currents*

A number of factors likely affect the post-spawning movements of herring within PWS, including the ocean conditions encountered by the fish. The predominant migratory pattern exhibited by PWS herring is probably influenced by a geostrophic flow to the south that is generally observed within the Sound from April through December (Musgrave et al., 2013). However, seasonal shifts in marine conditions may alter these movements. In early spring when herring spawn, both circulation in PWS and seasonal northeast winds are weak (Wang et al., 2001), creating conditions that favor herring moving to either HE or MS. From June through October, circulation patterns shift such that freshwater inflow into HE, originating primarily from the nearby Copper River, is strong and creates a gradient (front) at HE (Okkonen et al., 2005). During these months both inflow and outflow can occur simultaneously at HE while at MS outflow remains weak (Musgrave et al., 2013; Halverson et al., 2013a). These patterns may explain the almost total lack of fish at HE by mid-June and the presence of fish in MS and PB during the fall and winter.

4.2.2. *Prey availability*

We anticipated that herring would move out of PWS immediately after spawning, travel to foraging areas in the Gulf of Alaska, and return to the Sound during the fall to overwinter. However, in contrast to this prediction, the fish moved among the principal entrances to the Sound and remained in these areas for extended periods of time from mid-April through late July. We suggest this pattern is related to the timing of the spring plankton bloom and the associated increase in herring prey. Satellite imagery and *in situ* measurements indicate that the plankton bloom occurs earlier in PWS than along the continental shelf (Coyle and Pinchuk, 2005; Weingartner, 2005) and has a longer duration, lasting from mid-April through mid-July (Henson, 2007). This protracted bloom is associated with elevated chl-*a* levels resulting from the infusion of freshwater into the Sound originating from riverine runoff (Henson, 2007).

Previous work in PWS has shown that, after spawning, herring initially feed on copepods. Willette et al. (1999) examined herring diets based on samples collected in PWS between late April and July, and found that large calanoid copepods (primarily *Neocalanus plumchrus* and *N. flemingeri*) composed a significantly greater proportion of herring diets during May. However, there was a pronounced shift in June to alternative prey (e.g. euphausiids, amphipods, pteropods, and fish) coinciding with the period when *Neocalanus* begin their ontogenetic migration out of the surface waters (Coyle and Pinchuk, 2005). Coyle and Pinchuk (2005) found the mean abundance of *Neocalanus plumchrus-flemingeri* in April was consistently higher in PWS than in the adjacent waters of the Gulf of Alaska, and attributed these differences to the earlier spring phytoplankton bloom in PWS. Surveys of zooplankton abundance across the Sound in May found that *Neocalanus* spp. was the seasonal dominant zooplankton (44% by number, 79% by weight) with the highest densities of adult *Neocalanus* found at HE and in northwest PWS (Kirsch et al., 2000). During the course of our study, *Neocalanus plumchrus-flemingeri* abundance peaked during May 2013 at open-water stations including both HE and MS, and declined in June (McKinstry and Campbell, in this issue). Likewise, detections of tagged herring peaked in May and declined the following month, suggesting that *Neocalanus plumchrus-flemingeri* abundance influences herring behavior.

4.2.3. *Depredation*

Historical shifts in herring distribution in PWS have been noted in relation to both commercial fishing and marine mammal predation. Our study detected few fish at the entrances to the Sound from July through mid-September. In contrast, commercial harvests of herring peaked during these months in the 1920s (when herring reduction plants and salteries were common in PWS), with most fishing effort occurring in western areas of the Sound including MS and PB (Rounsefell and Dahlgren, 1932). More recently, both overwintering and pre-spawning distributions of adult herring have shifted presumably in response to a growing population of humpback whales (*Megaptera novaeangliae*) and the associated increase in predation (Thorne, 2010; Moran et al., in this issue). Until the late 1990s, major concentrations of herring were present from November through February near Port Gravina, as well as in the vicinity of MS, primarily between Montague and Green islands (Fig. 1). Since 2003, the distribution of overwintering and pre-spawning aggregations of herring has been more restricted, with herring only located consistently in the northeastern section of PWS just outside of Port Gravina and Port Fidalgo (Thorne, 2010). This shift in distribution has coincided with the substantial increases in humpback whales during winter in PWS.

Interestingly, the distribution of humpback whales between 2006 and 2014 mirrors the herring movement patterns we observed during our study. The number of humpback whales was lowest during July coinciding with the steep decline of tagged herring detections at the entrances. As the fish began to return to the entrances in September and October, whale numbers more than doubled and were concentrated primarily in MS with some also found at Port Gravina. During December, humpback whales were scattered throughout PB and at the northern end of MS, as well as up by Port Gravina although in small numbers (Moran et al., 2015).

5. Conclusions

After spawning in early April, the tagged herring moved relatively quickly to the entrances between PWS and the Gulf of Alaska where they remained until the end of July. The protracted presence of the fish near these sites is most likely related to the seasonal bloom of *Neocalanus* copepods since most herring disappeared from these areas as copepod populations declined and did not reappear until September. Herring that returned in fall were intermittently detected over several months suggesting that they may be moving back and forth into the Gulf of Alaska even during winter months.

The detection of only one fish in Port Gravina during fall/winter as well as the absence of 26 fish previously detected near the entrances to PWS during spring/summer suggest that some herring overwinter in the Gulf of Alaska. Herring movements reflected a high degree of connectivity across the Sound with a substantial number of herring moving at least once during a season between the three major entrances. Southwestward movements were common from HE to MS during spring and from MS to PB throughout both spring/summer and fall/winter. Future telemetry studies and acoustic arrays that make it possible to determine the direction of movement through these marine passageways will serve to elucidate how long and how often herring are moving out into the Gulf of Alaska.

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