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

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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

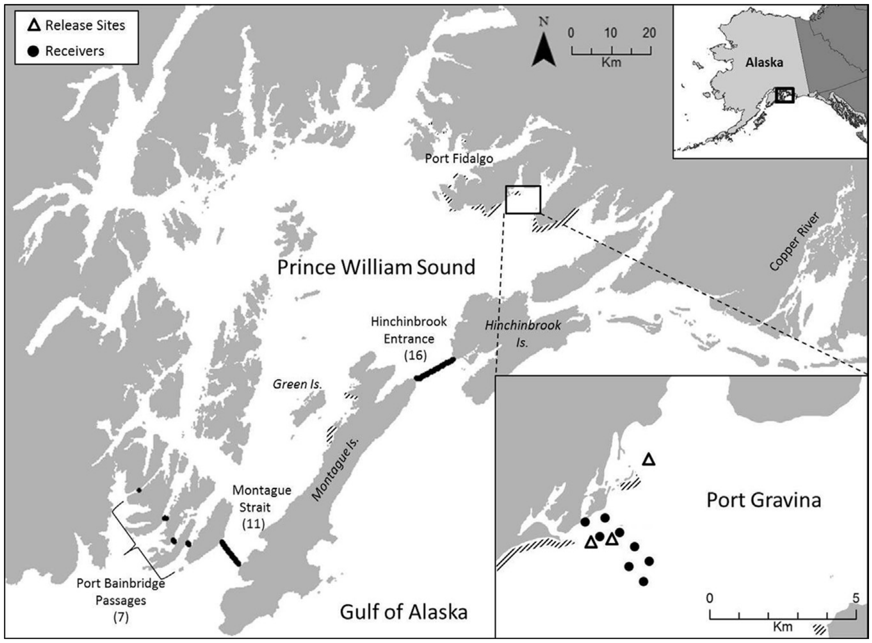

Fig. 1. Map of Prince William Sound, Alaska, showing the sites where acoustic-tagged Pacific herring were released in Port Gravina during April 2013 (see inset), and the location of the submerged acoustic receivers. Total numbers of acoustic receivers in the arrays at the principal entrances to Prince 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

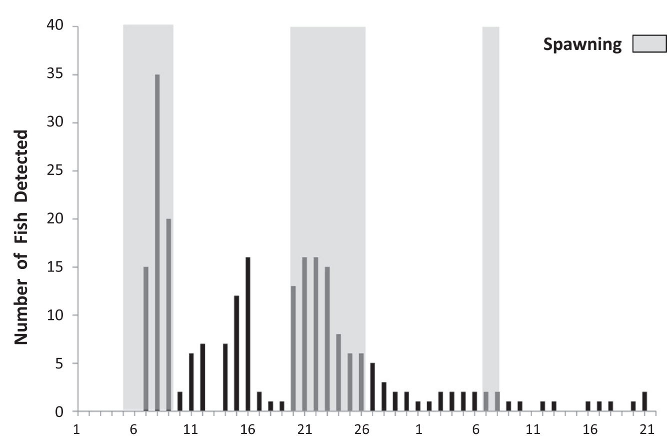

Fig. 2. Number of individual fish detected by date at the Port Gravina acoustic array, excluding detections on the day of release (6 and 7 April 2013). Occurrence of spawning activity in vicinity of Port Gravina is noted (gray shading). The 7–8 May spawning event occurred primarily in Port Fidalgo, a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

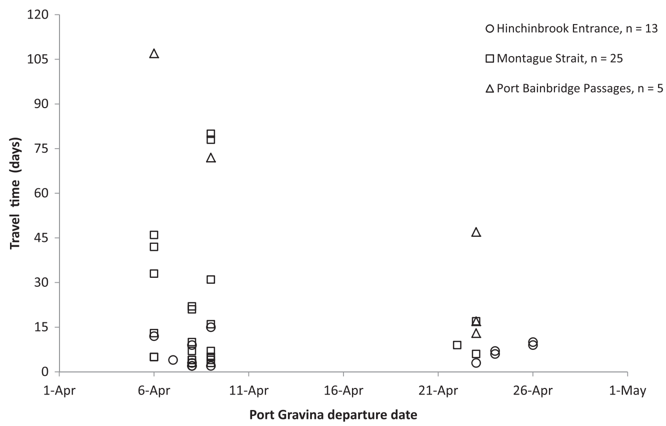

Fig. 3. Travel time (d) by acoustic-tagged herring to marine entrances of Prince William Sound during 2013 calculated as a function of their departure date from Port Gravina and their initial detection at the entrance arrays. Departure date was defined as the date of last detection at Port Gravina (n = 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

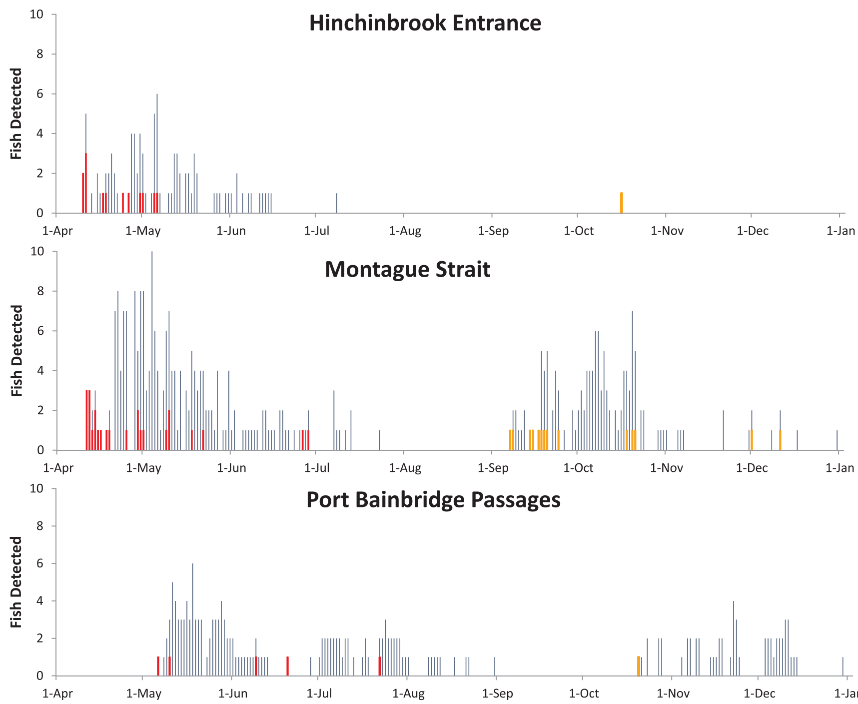

Fig. 4. Number of tagged herring detected by date at acoustic arrays located at the entrances to Prince William Sound from 10 April 2013 to 2 January 2014. Initial detection of individual fish during spring/summer (in red) and fall/winter (in orange) are shown.

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.

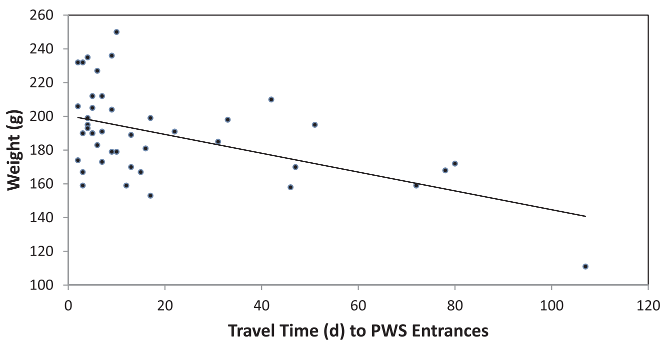

Fig. 5. Linear regression for acoustic-tagged Pacific Herring in Prince William Sound (PWS), showing a negative relationship between fish weight (g) and travel time (d) to acoustic arrays at the entrances to the Sound. Adjusted $r^2 = 0.25$, $p < 0.001$, $df = 1,41$. Travel time = date of first detection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

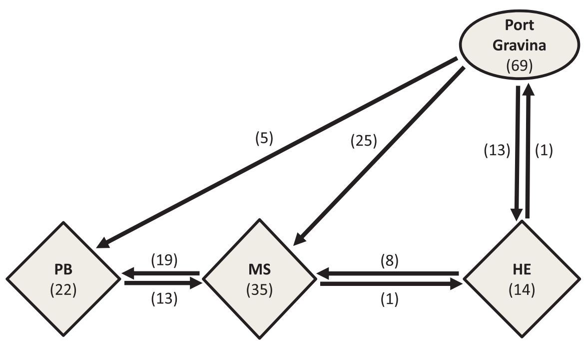

Fig. 6. Direction of movements of acoustic-tagged Pacific herring between the receiver arrays at the tag and release site (Port Gravina) and at the entrances to Prince William Sound (diamond shapes), including Hinchinbrook Entrance (HE), Montague Strait (MS) and Port Bainbridge passages (PB), 6 April 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).

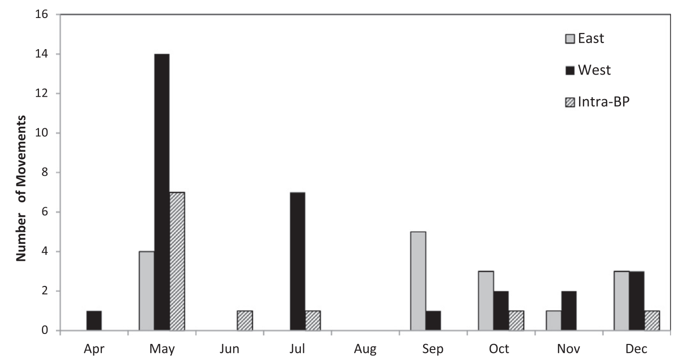

Fig. 7. Number of movements between arrays by direction and month for acoustic tagged Pacific herring (n = 23 fish). East = movements from Port Bainbridge passages to Montague Strait (n = 14 movements), or from Montague Strait to Hinchinbrook Entrance (n = 2). West = movements from Hinchinbrook Entrance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