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Evaluating Pacific cod migratory behavior and site fidelity in a fjord environment using acoustic telemetry

Sean A. Lewandoski, Mary Anne Bishop, Megan K. McKinzie

S.A. Lewandoski¹, M.A. Bishop, M.K. McKinzie². Prince William Sound Science Center, P.O. Box 705, Cordova, AK 99574, USA

Corresponding author: Sean A. Lewandoski (e-mail: sean_lewandoski@fws.gov)

¹Present address: Marquette Biological Station, US Fish and Wildlife Service, 3090 Wright St Marquette, MI 49855-9800, USA

²Present address: School of Fisheries, Aquaculture, and Aquatic Sciences, Auburn University, 8300 State Hwy 104 Fairhope, AL 36532-3322, USA

Abstract

Pacific cod inhabiting Prince William Sound (PWS) may constitute a localized population separate from Gulf of Alaska (GOA) populations; however, connectivity between these regions has not been previously explored. To address this knowledge gap Pacific cod migratory behavior and site fidelity was investigated using passive acoustic telemetry techniques. Acoustic-tagged Pacific cod were monitored by Ocean Tracking Network acoustic arrays located at the straits and passages connecting PWS with the GOA and arrays deployed in two PWS fjords. Few Pacific cod tagged in PWS moved to the PWS-GOA boundary (1.8%, $n=111$), indicating that demographic connectivity with the GOA was low. Furthermore, 77% of tagged cod spent at least 90% of the time they were known to be alive within small (less than 30 km²) fjords. Cod were present at monitored fjords every month of the study, though some cod migrated away from the fjords during the summer and returned the following winter (11% in 2015 and 5% in 2016). Using continuous-time multistate Markov models it was determined that movement behavior was related to fish length. Larger fish tended to emigrate from monitored fjords more often and undergo longer duration migrations.

Introduction

Pacific cod (*Gadus macrocephalus*) support commercial and recreational fisheries throughout its range and ranks as the second largest fishery in the United States. The greatest regional abundance and catch occurs within the Bering Sea (Thompson et al. 2010) with the Aleutian Islands and the Gulf of Alaska (GOA) including Kodiak, Cook Inlet, and Prince William Sound (PWS) also supporting large populations (Shimada and Kimura 1994). Understanding Pacific cod behavior is relevant to fishery management because when scaled up to the population level, individual behavior influences stock structure and response to exploitation (Metcalf 2006).

Pacific cod are known to exhibit a variety of complex seasonal migration patterns shifting between summer feeding and winter spawning grounds. Within the Eastern Bering Sea, mature individuals migrate to deeper, warmer water in the fall to avoid cooling inshore waters, followed by movement to winter spawning grounds. Subsequent shoreward feeding migrations during spring and summer coincided with warming of the coastal shelf environment (Bakkala 1984; Shimada and Kimura 1994). In northern British Columbia, Pacific cod also migrate to deeper waters to spawn during the winter and return to shallower warmer waters to feed during other times of the year (Ketchen 1961; Palsson 1990). However, in lower latitudes and along the southern edge of its range (e.g., Korea, Japan, Vancouver Island and Puget Sound, Washington) Pacific cod exhibit reverse patterns of seasonal migration, moving from deep to cool, shallow water to spawn in winter and then returning to deeper offshore waters to feed when shallow coastal waters warm (Bargmann 1980; Karp 1982; Mishima 1984; Westheim 1984; Zhang 1984).

Though seasonal large-scale migratory behavior has been documented, Pacific cod can exhibit fine-scale site fidelity. Furthermore, based on spatial patterns of tag recoveries, Rand et al. (2014) discovered that Pacific cod from the same stock can exhibit both migrant and resident life histories. A synthesis of four tagging studies from the Bering Sea, Aleutian Islands, and western GOA found that 70% of tagged fish were recovered < 80 km from their release location (Shi et al. 2007). In British Columbia, there was little evidence of mingling across tagging regions based on tag recovery data (Westrheim 1996). In Puget Sound, several acoustically-tagged Pacific cod were detected within a few hundred meters of their release location more than a year later (B. Berejikian, Northwest Fisheries Science Center, Seattle, WA, personal communication, 2012). Within Atlantic cod (*G. morhua*) populations, spawning site fidelity has been documented (e.g., Svedang et al. 2007; Bergstad et al. 2008), even at spatial scales < 1 km (Skjæraasen et al. 2011). Such localized spawning site fidelity has led to genetic differentiation among populations of Atlantic cod separated by as little as 30 km (Jorde et al. 2007), reinforcing the importance of spatial structure to gadoid fisheries management.

The United States Pacific cod fisheries operating within the North Pacific Ocean are managed as three stocks, the Eastern Bering Sea, the Aleutian Island Region (Thompson 2015), and the GOA (A'mar and Palsson 2014). Within the GOA management area, the PWS Pacific cod fishery is managed by the Alaska Department of Fish and Game, but Pacific cod inhabiting PWS and the GOA are considered part of the same stock. The rationale for this management approach is that connectivity between PWS cod stocks and nearby GOA stocks may be high (Wessel et al. 2014). However, no genetic or tagging studies have been conducted to confirm connectivity between the GOA and PWS cod populations. Furthermore, Pacific cod in PWS may constitute a distinct population that do not migrate to the GOA because the bathymetry of

PWS and the presence of numerous fjords may provide the foraging habitat, spawning habitat, and thermal refugia needed to support the annual migration cycle of Pacific cod. Elsewhere Pacific cod populations residing in fjord environments have been found to be genetically isolated from nearby coastal stocks (Cunningham et al. 2009). Thus, the approach for generating total allowable catch recommendations for PWS may require reexamination if connectivity between PWS and GOA is low.

Here we investigated Pacific cod movements and site fidelity using passive acoustic telemetry techniques. Acoustic-tagged Pacific cod were continuously monitored within two telemetered PWS fjords and at the straits and passages connecting PWS with the GOA. Our objectives were to investigate movements of fjord-residing Pacific cod in PWS and determine if Pacific cod exhibit site fidelity to PWS and, at a finer spatial scale, to specific fjords within PWS. Based on localized population structure of other Pacific cod populations inhabiting fjord environments (Cunningham et al. 2009), we hypothesized that site fidelity would be high. However, seasonal emigration from fjords could be common because Pacific cod are known to undergo migrations between winter spawning and summer feeding grounds (Rand et al. 2014). As such, we hypothesized that Pacific cod would either exhibit seasonal, temporary emigrations after spawning or remain resident in fjords. Migratory behavior is often associated with size among fishes because the metabolic constraints of migration tend to diminish as body size increases (Nottestad et al. 1999). Thus, we hypothesized that migratory behavior would be positively associated with fish length.

Materials and methods

Study area and acoustic arrays

Prince William Sound (PWS) is a semi-enclosed sea located in the northern Gulf of Alaska (GOA), primarily between latitudes 60° and 61° N (Fig. 1). PWS is separated from the GOA by a series of large, mountainous islands. A number of marine passageways connect the GOA to PWS, including Hinchinbrook Entrance and Montague Strait (Fig. 1). The coastline and topography are complex and characterized by numerous fjords, bays, and islands. Water depths in fjords and bays range from <50 m to 400 m; further offshore are many marine basins and passages with depths up to 700 m.

Our two study sites were located in western PWS: Lower Herring Bay (max depth 175 m, area 29.3 km²) and West Twin Bay (max depth 155 m, area 22.6 km²; Fig. 1). Both water bodies are classified as fjords (Gay and Vaughan 1998) and support commercial and sport fishing for groundfish. At each fjord, two lines of acoustic receivers (model VR2W-69 kHz, Vemco Ltd, Halifax, Nova Scotia, Canada) were arranged as gates near fjord entrances at approximately 0.3 km intervals (Fig. 1). In West Twin Bay average receiver deployment depth was 58 m ($n=6$, $sd=36$, $min=13$, $max=111$) and in Lower Herring Bay average receiver deployment depth was 60 m, ($n=4$, $sd=64$, $min=6$, $max=144$). Drift tests conducted within Lower Herring Bay prior to array deployment concluded that average detection radius was 0.3 km for shallow water receivers (≤ 30 m water depth) and 0.6 km for deeper water receivers (≥ 100 m). Therefore, a 0.3 km receiver spacing was chosen to ensure we had complete array coverage at all depth ranges.

The two line receiver configuration allowed researchers to determine movement direction (Pacific cod last detected at the outer line were moving away from the fjord and those last detected at the inner line were moving into the fjord) and thereby assess fjord site fidelity and movement behavior. At West Twin Bay, the receiver line integrity was maintained from

December 2013 through May 2016. In Lower Herring Bay, data from multiple receivers (required to establish directionality of movement) were only available from February 2015 through May 2016 because only one receiver was recovered during the first year of the study.

To identify individuals that migrated to the PWS-GOA boundary, we used detections from six, single-line acoustic receiver arrays that had been previously deployed approximately 0.7 km apart ($sd=0.1$, $min=0.4$, $max=0.8$) across the principal entrances to PWS (Fig. 1) as part of the Ocean Tracking Network (OTN; Dalhousie University; <http://oceantrackingnetwork.org/>). These included Vemco VR4 series receivers at Hinchinbrook Entrance with average deployment depth of 239 m ($n=16$, $sd=106$, $min=26$, $max=364$) and Montague Strait with average deployment depth of 186 m ($n=11$, $sd=50$, $min=90$, $max=239$). In addition, VR2W receivers deployed at an average depth of 61 m ($n=7$, $sd=21$, $min=36$, $max=95$) provided coverage in the four southwestern passages to PWS.

The performance of OTN acoustic arrays was monitored by deploying sentinel tags (Vemco V16T-4H, $dB=158$) near shoreward sections of the Hinchinbrook Entrance and Montague Strait arrays and one of the southwest passages (Prince of Wales Passage). Average detection probability (*i.e.*, proportion of expected sentinel tag transmissions detected by a receiver) during 2015 was negatively related to distance at Montague Strait receivers (range=464-652 m), but not at Hinchinbrook Entrance (range=465-592 m) or Prince of Wales Passage (range=469-615 m) receivers. Mean detection probability at these distances (464-652 m) was 0.66 ($n=8$, $sd=0.18$, $min=0.38$, $max=0.86$). Range tests had previously been conducted at an open-water section of the Hinchinbrook Entrance array using sentinel tags that were lower powered than the ones used in this study (Vemco V9-2L/2H, $dB=146$ and 151) and detection probability was 0.89 at 500 m (Eiler and Bishop 2016).

Tagging procedures

During December 2013, February 2014, and December 2014 Pacific cod were captured in Lower Herring and West Twin bays using longlines and groundfish pots and placed in a holding tank (770 l) containing aerated, fresh seawater. Healthy Pacific cod > 49 cm that were not showing physical signs of barotrauma or swimbladder rupture were measured (total length, TL) to the nearest mm, weighed (g), and moved to an aerated tagging cradle. A Vemco series coded V16-4H (16 mm diameter, 24 g in air, dB = 158) acoustic transmitter programmed to transmit an individually-coded signal at 125-175 second random intervals was surgically implanted within the peritoneal cavity through a small incision made approximately 1 cm from the ventral midline between the pelvic fins and vent. Relative tag burden (in air tag weight/fish weight) ranged from 0.3% to 2.6% (mean=1.2%, sd=0.5%). The incision was closed with 2-3 discontinuous, dissolvable sutures (Ethicon Inc.; Chromic Gut). To reduce the risk of an immune-rejection response, transmitters were covered with a paraffin and beeswax mixture (2.3:1). Additionally, a broad spectrum antibiotic ointment was spread over the wound to further reduce the risk of infection (*e.g.*, Lowe et al. 2003). Finally, cod were externally tagged in the dorsal musculature with a t-bar tag (46mm x 2mm; Floy Tag & Manufacturing, Inc.) containing a unique identification number and contact information for the PWS Science Center. Signs describing the study and requesting fish harvesters to return tagged cod to the PWS Science Center were posted at port facilities throughout the PWS region.

Upon completion of surgical procedures, Pacific cod were transferred to a post-surgery holding tank (770 l capacity) containing aerated, fresh seawater and monitored (min=0.8 hours, max=6.0 hours) for signs of tagging and handling related stress. Once cod were fully recovered from the tagging procedure (*e.g.*, regular opercular pumping, control of body orientation, normal

swimming behavior) they were released at the site of capture using a top-weighted jig with a barbless hook to return them to depth and mitigate the effects of barotrauma (Jarvis and Lowe 2008, Rogers et al. 2011). Length of time from initial capture to release ranged from 0.8 to 6.0 hours. Pacific cod are physoclistic fish that inhabit deep water and, therefore, some swimbladders could have been ruptured as captured cod were brought to the surface. However, this event is not catastrophic and swimbladders are expected to repair within 24 hours (Nichol and Chilton 2006).

Large-scale movements and residency

Large-scale directed movements of PWS Pacific cod towards the GOA and residency to specific fjords were evaluated using data from the acoustic receivers. Large scale movement analyses required only presence and absence data and used the entire dataset for each fjord. For Lower Herring Bay a restricted dataset (February 2015 through May 2016) was used for analyses of fjord residency and movement behavior because these analyses required movement directionality and only one receiver was recovered prior to this period.

The possibility of false detections influencing our results was minimized by removing from the dataset all single detections with no additional detections within one hour before or after (Stehfest et al. 2014). False detections can occur due to tag collisions or interference in difficult acoustic environments (Pincock 2012). In total, 38 456 detections (0.4%) of the 10.65 million detections in the unscreened dataset were flagged and removed from the dataset prior to analysis. Tagged cod that were not detected at an acoustic array ($n=3$) or that ceased movement within 10 days of release ($n=9$) were considered tagging and handling related mortalities. Movement was defined as detection at different receivers over time or intermittent gaps between

203 detections at the same set of receivers. Tagging and handling related mortalities were removed
204 from the dataset and not included in subsequent analyses.

205 Large scale movement was investigated by calculating the proportion of acoustically-
206 tagged Pacific cod that were detected at the Ocean Tracking Network arrays located at the PWS-
207 GOA boundary (Fig. 1). Each movement was classified as a potential outmigration to the GOA
208 (last detected at the PWS-GOA boundary) or temporary emigration (detected within PWS after
209 detection at the PWS-GOA boundary).

210 A residency index (RI) was calculated based on the proportion of time at liberty that an
211 individual was present at a fjord. Time at liberty is the minimum length of time a tagged cod
212 was known to be alive, defined as the duration of time between release and the last detection
213 (Reubens et al. 2013). Individuals were considered migratory and not present at a fjord if they
214 were not detected for at least 24 hours and were last detected on an outer receiver line. We
215 assumed that fish last detected on the inner line of receivers moved towards the head of the fjord
216 and remained in the fjord habitat. Using this approach, RI values were calculated and tagged
217 individuals were classified as highly resident ($RI > 0.9$), partial resident ($RI = 0.9 - 0.3$), or
218 migratory ($RI < 0.3$). Additionally, a Kolmogorov-Smirnov test was used to evaluate if the RI of
219 large cod (≥ 60 cm TL) and small cod (49 to 59 cm TL) were substantially different. Finally,
220 seasonal movements away from the monitored fjords were investigated by calculating the
221 proportion of cod present at the fjords during the prespawning and spawning season (December-
222 April) that were not present during the previous foraging season (May-November). The
223 prespawning and spawning season was delineated based on maturity indices of GOA Pacific cod
224 (Stark 2007).

We assigned tagged cod that moved away from the fjord acoustic arrays to resident or migrant states based on the last line (inner or outer) they were detected on. The reliability of this approach and the integrity of the fjord acoustic arrays were investigated by calculating the proportion of returning migrants that were first detected on outer line receivers. A first detection on the inner line by a migrant cod would indicate a failure of either the inner line (resident fish wrongly assigned to migrant state) or outer line (undetected on the outer line upon return). Of the 292 recorded transitions from migrant to resident states, all first detections occurred on outer line receivers. This suggests that migratory state assignments were reliable and detection probability of tagged cod moving into and out of monitored fjords was high.

Movement models

Pacific cod movements into and out of monitored fjords were modeled using continuous-time multistate Markov models. Using this approach, instantaneous transition rates q_{ij} from state i to state j are estimated using maximum likelihood (Jackson 2011). We developed a model with three states: resident, migrant, and permanent emigration. Individuals could transition from the resident to the migrant state ($q_{1,2}$; emigration), from the migrant state to the resident state ($q_{2,1}$; immigration), and from the resident state to the permanent emigration state ($q_{1,3}$; permanent emigration). Data input for continuous-time multistate Markov models requires a vector of transition times and associated transition type for each individual. Telemetry data were converted to a series of transitions and associated transition times with the same methodology used to calculate residency. Tagged Pacific cod undetected for at least 24 hours and last detected at the outer line of fjord receivers were considered migratory at the time of last detection and those last detected at the inner line remained in the resident state. Finally, tagged fish transitioned into the permanent emigration state immediately after their final detection.

Data from Lower Herring Bay and West Twin Bay were modeled separately.

Associations between fish length and movement were investigated by including fish length and time-varying covariates in the model for season (December-April = prespawning and spawning; May-November = foraging). For each location, the most general model had covariates for fish length and season. All possible reduced models were considered and model selection was conducted using AIC_c (Burnham and Anderson 2002). The model with the lowest AIC_c was considered the most parsimonious model. All models with $\Delta AIC_c < 2$ were considered well supported by the data while models with $\Delta AIC_c > 4$ were considered poorly supported. All models were developed and analyzed using the *msm* (Jackson 2011) package for R (version 3.2.3; R Core Team 2015).

We used pattern-oriented modeling (Grimm et al. 2005; Stehfest et al. 2014) to determine if observed ecological metrics associated with Pacific cod could be generated using parameter estimates from our continuous-time multistate Markov models. Tagging experiments with the same duration, sample size and tagged-fish length distribution as our study were simulated ($n=1000$) by probabilistically projecting individuals forward in time using transition rate and covariate parameter estimates from the most supported multistate model for each fjord. Simulations were conducted using the *sim.msm* function from the *msm* package. Metrics quantified for each simulation included RI, average resident length of stay, and average migrant sojourn (*i.e.*, length of time in the migrant state). Because we hypothesized that size would be an important predictor of Pacific cod behavior, these metrics were quantified by two size classes: small cod (49 to 59 cm TL) and large cod (≥ 60 cm TL). Means and standard deviations of observed and predicted values were calculated for each size group. Simulated distributions were compared to observed values using 2-sample Kolmogorov-Smirnov tests. Similarity between

observed and simulated distributions was assessed with bootstrapped p-values using the *ks.boot* function from the *Matching* package because the data were not continuous and in some instances samples sizes of observed values were low (Sekhon 2011).

Results

Of the 123 cod tagged in western Prince William Sound, 90% ($n=111$) survived at least 10 days post-tagging. Average number of detections per tagged cod was 61 007, but the spread was large ($sd=139\ 221$, $min=2$, $max=770\ 744$). Pacific cod tagged in West Twin Bay had lower mean TL (cm; $n=45$, $mean=58.5$, $sd=10.1$) than cod captured in Lower Herring Bay ($n=66$, $mean=66.5$, $sd=12.4$) and a high proportion of fish between 50 and 55 cm (Fig. 2). Pacific cod tagged in Lower Herring Bay last detected prior to February 2015 ($n=35$) were not included in residency index (RI) or multistate movement analyses because data were only available from a single receiver during this period, but all surviving tagged fish were included for large scale movement analyses (Fig. 2). No tagged cod were reported by fish harvesters.

Connectivity to the Gulf of Alaska

Two (1.8%) of the Pacific cod tagged in western PWS fjords were detected at the PWS–GOA boundary, indicating that movements from fjords in western PWS to the GOA are uncommon. Both cod were tagged in Lower Herring Bay during February 2014. One of these cod moved to West Twin Bay during March, was not detected for almost a year, and was subsequently detected during March 2015 at Hinchinbrook Entrance. The other cod was detected at Montague Strait and several other passages connecting PWS and GOA shortly after tagging during March and April 2014. Both cod migrated to the PWS-GOA boundary during late spring, suggesting that these were migrations towards summer feeding areas. Finally, both

cod were classified as potential emigrants to the GOA because they were not detected within PWS after detection at the PWS-GOA boundary.

Pacific cod site fidelity

Pacific cod were detected in both West Twin and Lower Herring bays during every month of the research period. The number of individuals detected declined sharply the month after cohorts were released then continued to decline gradually (Fig. 3, 4). Final detections for 30% of tagged cod occurred within one month after tagging. Other than this initial post-tagging decline, the number of unique individuals detected at each fjord did not exhibit remarkable seasonality. However, some cod migrated out of the fjords from May through November and returned during subsequent prespawning and spawning seasons (site-faithful migrants). Of the tagged cod detected at the fjords during the prespawning and spawning season, 11% ($n=4$) were site-faithful migrants in 2015 and 5% ($n=2$) were site-faithful migrants in 2016.

Tagged cod detected at fjords were at liberty for on average 393 days ($n=71$, $sd=290$, $min=1$, $max=894$). Pacific cod length had a strong effect on RI for cod tagged in West Twin Bay, but not for cod tagged in Lower Herring Bay. Residency index for small cod ($mean=0.94$, $sd=0.20$, $n=27$) and large cod ($mean=0.77$, $sd=0.35$, $n=13$) tagged in West Twin Bay was substantially different ($D=0.43$, $p=0.02$), whereas RI for small cod ($mean=0.89$, $sd=0.25$, $n=10$) and large cod ($mean=0.86$, $sd=0.27$, $n=21$) tagged in Lower Herring Bay was similar ($D=0.14$, $p=0.79$). Additionally, 77% ($n=55$) were considered highly resident ($RI>0.90$), 15% ($n=11$) were partial residents ($RI=0.90-0.30$), and 7% ($n=5$) were migratory ($RI<0.30$).

Modeling movement patterns

Continuous-time multistate Markov movement models including Pacific cod TL and season were strongly supported by the data for both the West Twin and Lower Herring datasets

(Table 1). Using models most supported by the data for inference, our hypothesis that larger fish would tend to move out of fjords more often and for longer durations of time was supported. There was strong support for a positive association between cod TL and emigration from fjords. A 1 cm increase in TL was associated with an 11% (95% CI: 8–15%) increase in emigration rate for West Twin cod and a 4% (95% CI: 3–5%) increase for Lower Herring cod (Fig. 5). Furthermore, larger fish tended to undertake longer duration migrations (*i.e.*, had lower immigration rate). A 1 cm increase in TL was associated with a 2% decrease (95% CI: 1–3%) in immigration rate for Lower Herring cod and a 6% decrease (95% CI: 1–11%) for West Twin cod (Fig. 5).

Pacific cod exhibited seasonal changes in movement behavior. Cod tagged in West Twin Bay were more likely to permanently emigrate during prespawning and spawning seasons, but the precision of this estimate was low. Pacific cod permanent emigration rate increased by 98% (95% CI: 8-265%) during prespawning and spawning seasons. This association was reversed in Lower Herring Bay, where permanent emigration rate decreased by 74% (95% CI: 27-91%). Season also influenced emigration rate in Lower Herring Bay. During prespawning and spawning seasons, the emigration rate increased by 72% (95% CI: 31-125%).

Based on simulation results, we determined that estimated movement parameters from the continuous-time multistate Markov models could be used to generate mean migratory sojourn similar to observed values, but not mean residency length of stay nor RI (Table 2). The null hypothesis (that simulated and observed values had the same probability distribution) was not rejected for all comparisons of simulated and observed mean migrant sojourn distributions except for large cod at West Twin Bay. The null hypothesis for mean residency length of stay and RI was rejected for all comparisons except for large cod at West Twin Bay (Table 2).

Finally, while discrepancies between observed and simulated distribution were evident, patterns of relative differences or similarities between large and small Pacific cod observed in the data (*e.g.*, higher RI for small compared to large West Twin cod) were reliably generated by the multistate movement models (Table 2).

Discussion

Pacific cod large scale movements and site fidelity

Based on 30 months of telemetry data, we determined that Pacific cod tagged in western PWS fjords rarely migrated outside of PWS. Furthermore, at a finer spatial scale, most tagged cod exhibited high site fidelity to small fjords ($<30 \text{ km}^2$) within PWS. The relatively consistent number of cod detected at the fjords throughout the duration of the study suggests that coastal fjords in western PWS are well suited to Pacific cod throughout the year. However, a small proportion of the population migrated out of the fjords after the prespawning and spawning season indicating that partial migration, which has been documented in Atlantic cod populations (Chapman et al. 2012) and in Pacific cod populations inhabiting the shelf environment (Rand et al. 2014), also occurs in Pacific cod populations inhabiting fjord environments. Migratory behavior is related to tradeoffs in growth and survival in fishes, which dictate reproductive output (Jonsson and Jonsson 1993). As such, in western PWS fjords it appears the costs of migration (*e.g.*, energetic, increased predation risk) tend to outweigh the benefits (*e.g.*, more foraging opportunities). Further research into how predation risks and foraging opportunities influence migratory behavior among Pacific cod populations could provide insight into why Pacific cod populations throughout the North Pacific Ocean adopt variable migration strategies.

Based on the threshold model of migration, the decision to migrate is both heritable and influenced by environmental conditions (Pulido et al. 1996). In fishes, environmental conditions

leading to slower growth rate during early life is linked with migratory behavior (Kerr and Secor 2010; Jonsson and Jonsson 1993). It is unclear if the prevalence of migratory individuals in Pacific cod populations is driven by genetic differences, ecological factors influencing growth, or both. Examining otolith microchemistry and back-casting growth patterns could elucidate potential linkages between early life growth rate and migratory behavior in Pacific cod (e.g., Kerr and Secor 2010).

Based on our research, Pacific cod in PWS commonly inhabit fjord habitat throughout the year. Fjords are also important habitat for forage fishes in PWS; juvenile Pacific herring (*Clupea pallasii*) and walleye pollock (*G. chalcogrammus*) aggregate in fjords and bays that serve as nursery habitat (Stokesbury et al. 2000; Lewandoski and Bishop 2018). We hypothesize that Pacific cod predation could be an important driver of early life survival of forage fishes in PWS due to this spatial and temporal overlap. Furthermore, diets of Pacific cod captured in fjords throughout PWS commonly contained Pacific herring and walleye pollock (Gray et al. in review). Top-down control by Pacific cod on forage fish populations has been documented in other regions in the North Pacific Ocean (Walters et al. 1986; Van Kirk et al. 2010). Similar top-down control by Pacific cod on Pacific herring and walleye pollock may be occurring in PWS. Multispecies stock assessment models could be developed (e.g., Van Kirk et al. 2010) to test this hypothesis and improve understanding of forage fish recruitment dynamics in PWS.

Prince William Sound-Gulf of Alaska Connectivity

Our research corroborates genetic evidence of localized Pacific cod population structure in fjord environments (Cunningham et al. 2009). Site fidelity is a likely mechanism contributing to localized population structure; tagged Pacific cod were highly resident to small PWS fjords. Observed site fidelity of Pacific cod in PWS could indicate that Pacific cod exhibit fine-scale

385 spawning site fidelity and that genetic separation may occur at spatial scales similar to Atlantic
386 cod (Jorde et al. 2007). However, inferences regarding spawning site fidelity from this research
387 are limited because reproductive status was unknown for most tagged fish. Further genetic work
388 and tagging studies with known-reproductive-status Pacific cod would provide insight into the
389 spatial scale of genetic differentiation among Pacific cod populations.

390 The PWS cod fishery is currently managed under the GOA stock assessment model due
391 to data deficiencies within the PWS region (A'mar and Palsson, 2014). The PWS fishery has a
392 state component with total allowable catch based on the GOA Pacific cod stock assessment
393 (Wessel et al. 2014) and a federal component managed concurrently with the GOA Pacific cod
394 stock. However, PWS is typically not sampled during the National Marine Fisheries Service
395 GOA bottom trawl survey, the fishery independent Pacific cod biomass dataset used in the GOA
396 Pacific cod stock assessment (A'mar and Palsson 2014). As such, the current management
397 approach for the PWS Pacific cod fishery relies on regional GOA spawning stock biomass
398 estimates to inform management. Our research suggests that Pacific cod biomass trends in
399 western PWS may be independent of those in the GOA due to limited demographic connectivity.
400 Furthermore, growth rate, natural survival rate, and maturation schedule of PWS Pacific cod
401 could be different than Pacific cod in the GOA if the populations are isolated genetically (*e.g.*,
402 Ormseth and Norcross 2008). Investigations into the potential stock-specific differences in vital
403 rates among Pacific cod stocks in the northern GOA region could provide useful data for stock
404 assessment scientists.

405 Although demographic connectivity appears low, regional environmental conditions
406 could cause correlations between the recruitment dynamics of PWS and GOA Pacific cod
407 populations. Environmental factors such as wind and sea surface temperature are hypothesized

drivers of marine fish recruitment at spatial scales up to approximately 500 km (Myers et al. 1997). Further investigations into the environmental drivers of Pacific cod recruitment dynamics and correlation of PWS and GOA year class strength are necessary to address this hypothesis for Pacific cod stocks in the North Pacific Ocean. However, given the uncertainty in using GOA population dynamics as a surrogate for PWS, developing stock assessment methods that include estimates of current PWS biomass or depletion could reduce risk of overfishing or underutilization of the fishery (Carruthers et al. 2014)

Length-based movement behavior

Pacific cod movement behavior was related to body size. Larger cod tended to both leave fjords more often and stay away longer, suggesting that larger Pacific cod had larger home ranges. A physiological explanation for this observation is that the metabolic cost of movement for fish tends to decline as body size increases due to more efficient swimming and lower energy costs of movement relative to overall metabolic energy requirements (Nottestad et al. 1999). Additionally, the observed relationship between movement behavior and fish size could have been caused by length-based foraging tactics. Evidence from nitrogen isotopic signatures (Marsh et al. 2012) and diet studies (Clausen 1981) indicate that Pacific cod become increasing piscivorous as they grow in length. As a result of this ontogenetic change in diet, larger cod may increase home range size to target more mobile piscine prey.

While our analysis revealed an association between movement behavior and size, spatial usage was not empirically quantified because methods available to estimate utilization distributions are not well suited to acoustic telemetry studies with long temporal gaps between detections (Horne et al. 2007; Pages et al. 2013). Further telemetry research with a more

extensive acoustic array or archival tags is necessary to further clarify the relationship between Pacific cod home range size and individual biological characteristics.

As we used the same acoustic tag type for all tagged Pacific cod, we could not distinguish between length-related movement effects driven by Pacific cod behavioral traits and potential relative tag burden effects that were an artefact of our study design. However, we do not suspect that observed length-based movement behaviors were driven by variable tag burden effects because tagged cod in this study experienced tag burden amounts (0.3-2.6%) similar to the heuristic 2% rule adopted in many tagging studies (Cooke et al. 2011). Nonetheless, inferences regarding Pacific cod behaviors based on telemetry data could be improved by data-driven tag burden recommendations because, as Cooke et al. (2011) caution, the 2% rule is not a catchall rule and guidelines should be driven by the biology of the tagged fish and study intent. Investigating the influence of implanted acoustic tags on Pacific cod swimming performance and growth (*e.g.*, Zale et al. 2005) would provide improved guidelines for future Pacific cod tagging studies. Additionally, field based studies that cross Pacific cod size class with tag size would allow researcher to examine *in situ* effects of relative tag burden.

Markovian movement model

Modeling telemetry data as Markov processes addressed the stochastic nature of these data and provided a framework for developing a mechanistic understanding of movements using well established statistical methods and model selection techniques (Patterson et al. 2008). We used continuous-time models to analyze Pacific cod movement data, which eliminated the need to discretize our data. While continuous-time multistate Markov models have not been used to analyze passive acoustic telemetry data, they have been used in a fisheries context to model archival and conventional tagging data (Miller and Andersen 2008) and PIT tag data (Bravener

and McLaughlin 2013). Continuous-time models are advantageous because instantaneous movement rates are well suited to integration with traditional population dynamics models and ecosystem based assessments (Miller and Andersen 2008; Sippel et al. 2015).

Based on pattern-oriented modeling, estimated movement rates generated reliable mean migrant sojourn values but not mean resident length of stay nor RI. These limitations could have been due to unmodeled heterogeneity in movement behavior. Continuous-time multistate Markov models that allow for individual heterogeneity may be useful for modeling movement data collected with passive acoustic telemetry (Hooten et al. 2016), though these methods also introduce more complexity. Finally, our modeling approach could be improved by incorporating time-series environmental or biological data hypothesized to influence movement and modeling these factors as time-varying covariates (Jackson 2011). This approach would advance a mechanistic understanding of the ecological factors that drive movement rates.

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Table 1. Model selection results for multistate Markovian movement models for Pacific cod tagged in two fjords, Lower Herring Bay (LH) and West Twin Bay (WT).

Location	Model description	k	Log like- lihood	AIC_c	ΔAIC_c
LH	$q_{1,2} \sim \text{length} + \text{season}$, $q_{2,1} \sim \text{length}$, $q_{1,3} \sim \text{season}$	7	-1722.41	3463.68	0.00
	$q_{1,2} \sim \text{length} + \text{season}$, $q_{2,1} \sim \text{length} + \text{season}$, $q_{1,3} \sim \text{season}$	8	-1720.83	3464.20	0.51
	$q_{1,2} \sim \text{length} + \text{season}$, $q_{2,1} \sim \text{length}$, $q_{1,3} \sim \text{length} + \text{season}$	8	-1722.40	3467.36	3.68
WT	$q_{1,2} \sim \text{length}$, $q_{2,1} \sim \text{length}$, $q_{1,3} \sim \text{length} + \text{season}$	7	-784.53	1595.35	0.00
	$q_{1,2} \sim \text{length}$, $q_{2,1} \sim \text{length}$, $q_{1,3} \sim \text{length}$	6	-786.59	1596.19	1.55
	$q_{1,2} \sim \text{length} + \text{season}$, $q_{2,1} \sim \text{length}$, $q_{1,3} \sim \text{length} + \text{season}$	8	-789.05	1598.00	2.87
	$q_{1,2} \sim \text{length}$, $q_{2,1} \sim \text{length} + \text{season}$, $q_{1,3} \sim \text{length} + \text{season}$	8	-784.13	1598.02	2.87
	$q_{1,2} \sim \text{length}$, $q_{2,1} \sim 1$, $q_{1,3} \sim \text{length} + \text{season}$	6	-786.19	1598.67	3.41

Note: Model descriptions include three types of individual movements by cod: resident state to migrant state ($q_{1,2}$); migrant state to resident state ($q_{2,1}$); and, resident state to permanent emigration state ($q_{1,3}$). Season is a time-varying categorical covariate with two levels, spawning (December-April) and summer foraging (May-November), and length is an individual covariate for total length of Pacific cod at release.

Table 2. Pattern oriented modeling results for small (TL = 49-59 cm) and large (TL ≥ 60 cm) Pacific cod tagged in West Twin Bay (WT) and Lower Herring Bay (LH).

		Small (TL 49 – 59 cm)				Large (TL ≥ 60 cm)			
	Location	<i>n</i>	Observed	Predicted	Kolmogorov-Smirnov	<i>n</i>	Observed	Predicted	Kolmogorov-Smirnov
Residency index									
	WT	32	0.94 (0.20)	0.96 (0.07)	0.28 (p=0.02)	14	0.77 (0.35)	0.78 (0.32)	0.10 (p=0.95)
	LH	10	0.89 (0.25)	0.98 (0.03)	0.52 (p<0.01)	21	0.86 (0.27)	0.92 (0.07)	0.56 (p<0.01)
Mean residency sojourn									
	WT	32	307.75 (341.62)	200.42 (173.97)	0.25 (p=0.03)	14	80.41 (221.96)	42.86 (55.64)	0.37 (p=0.04)
	LH	10	329.48 (212.10)	83.80 (56.83)	0.70 (p<0.01)	21	293.15 (213.78)	45.96 (32.21)	0.63 (p<0.01)
Mean migrant sojourn									
	WT	9	9.35 (10.82)	19.54 (16.95)	0.43 (p=0.06)	7	68.38 (121.70)	70.17 (83.1)	0.49 (p=0.04)
	LH	3	4.70 (4.26)	2.32 (1.64)	0.49 (p=0.36)	8	5.94 (6.21)	3.7 (2.21)	0.23 (p=0.72)

Note: For observed and predicted values standard deviations are in parentheses. Predicted distributions are simulated tagging studies ($n=1000$) using parameter estimates from multistate Markov movement models for each location. Kolmogorov-Smirnov tests in which the null hypothesis (simulated and observed values are similarly distributed) was not rejected at $\alpha=0.05$ are in bold.

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Fig. 1. Map of Prince William Sound, Alaska, showing the sites where acoustic-tagged Pacific cod were captured and released and the location of the submerged acoustic receivers at Lower Herring and West Twin Bays (see inset). Data were available from February 2015 through May 2016 at sites with lost receivers. Total numbers of acoustic receivers in the Ocean Tracking Network arrays located at the principal entrances to Prince William Sound are shown in parentheses. Alaska coastline GIS data (1:63 360) from the Alaska Department of Natural Resources was used to create this map.

247x174mm (150 x 150 DPI)

Fig. 2. Histogram of Pacific cod total length with 1 cm length bins (A=Lower Herring, B= West Twin). Dark grey bars correspond to acoustic-tagged cod with directional movement data available and light grey bars correspond to cod that were only used in site fidelity and large scale movement analyses.

203x270mm (300 x 300 DPI)

Fig. 3. Frequency and timing of releases, detections, and movements of Pacific cod tagged in West Twin Bay based on total length (TL) size class: (A) small (49-59 cm TL) and (B) large (> 60 cm). Top: The line depicts cumulative releases of tagged cod and the broken line depicts cumulative last detections. Middle: number of individual cod detected per month. Bottom: number of movements into (immigration) and away from (emigration) West Twin Bay for December 2013 through May 2016 (individual cod could move multiple times per month).

254x298mm (300 x 300 DPI)

Fig. 4. Frequency and timing of releases, detections, and movements of Pacific cod tagged in Lower Herring Bay based on total length (TL) size class: (A) small (49-59 cm TL) and (B) large (> 60 cm). Top: The line depicts cumulative releases of tagged cod and the broken line depicts cumulative last detections. Middle: number of individual cod detected per month. Bottom: number of movements into (immigration) and away from (emigration) Lower Herring Bay for February 2015 through May 2016 (individual cod could move multiple times per month). Information on directional movements was unavailable prior to February 2015 because only one acoustic receiver was recovered from this time period.

254x298mm (300 x 300 DPI)

Fig. 5. Emigration and immigration rate of Pacific cod from two fjords in Prince William Sound showing strong associations with total length. The line represents the mean estimate and the shaded area represents the 95% confidence interval.

177x248mm (600 x 600 DPI)