Bryan *et al. Anim Biotelemetry (2021) 9:24*
https://doi.org/10.1186/s40317-021-00250-2

Animal Biotelemetry

RESEARCH

Open Access

Seasonal migratory patterns of Pacific cod (*Gadus macrocephalus*) in the Aleutian Islands

David R. Bryan[1,2*], Susanne F. McDermott[1], Julie K. Nielsen[3], Dave Fraser[4] and Kimberly M. Rand[5]

Abstract

Background: Pacific cod (*Gadus macrocephalus*) is an ecologically important species that supports a valuable commercial fishery throughout Alaska waters. Although its life history includes seasonal movement for spawning and feeding, little is known about its movement ecology. Here, we present results from the first study to use pop-up satellite archival tags (PSATs) to track the within-year movements of Pacific cod to understand their potential seasonal movement patterns within the Aleutian Islands. This study was part of a cooperative research project; tagging was conducted onboard commercial vessels during the winter fishing season while Pacific cod were aggregated to spawn in the central Aleutian Islands.

Results: Of the 36 PSATs deployed, we were able to obtain movement data from 13 Pacific cod that were at liberty between 60 and 360 days. We determined that three tagged Pacific cod were predated on by marine mammals and three were recaptured by the commercial fishery. Geolocation models were produced for four migrating individuals. Eight Pacific cod moved to a productive foraging ground near Seguam Island located 64 to 344 km from their release site and presumed spawning ground within a few weeks of their release. These movements indicate that some Pacific cod in the Aleutian Islands undergo seasonal migration. Three Pacific cod remained near their release locations (within 50 km) for more than 75 days suggesting the existence of partial migration in the population. Two Pacific cod undertook larger movements (378 and 394 km) during which they swam over deep passes and crossed several management boundaries highlighting the potential connectedness of Pacific cod throughout the Aleutian Islands.

Conclusions: This study provided important initial insights into the seasonal movement patterns of Pacific cod in the Aleutian Islands. Most tracked Pacific cod (77%) undertook migrations in the middle of March (64–394 km) from their winter spawning areas to summer foraging areas, but a few individuals remained in their capture location suggesting a partial migration strategy. Their ability to cross deep passes that were previously seen as potential barriers to movement has expanded our understanding of population connectivity.

Keywords: Movement ecology, Pop-up satellite archival tags, Gadidae, Alaska, Spawning aggregation, Geolocation, Partial migration

Background

The Aleutian Islands are an 1800-km-long archipelago west of the Alaska Peninsula consisting of hundreds of small, steep submarine volcanoes surrounded by a narrow shelf with steep drop-offs. Numerous straits and passes along the island chain connect the North Pacific Ocean to the Bering Sea and Gulf of Alaska [1]. The area is largely uninhabited and provides habitat for a tremendous diversity of fishes, seabirds, and marine mammals

*Correspondence: david.bryan@noaa.gov
[1] National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Alaska Fisheries Science Center, 7600 Sand Point Way Northeast, Seattle, WA 98115, USA
Full list of author information is available at the end of the article

[2]. It is also a highly productive area and supports a large abundance of several economically important fish species such as Pacific ocean perch (*Sebastes alutus*), Atka mackerel (*Pleurogrammus monopterygius*), and Pacific cod (*Gadus macrocephalus*) [3, 4].

Pacific cod is a wide-ranging species that can be found from the southern tip of the Korean Peninsula (Yellow Sea) in the western North Pacific Ocean across the Aleutian Islands and as far north as the Chukchi Sea and south to the California coast in the eastern North Pacific Ocean. Genetic research has shown that there is limited connectivity among spawning groups of Pacific cod, as well as a strong isolation by distance signal across its North American range [5–9]. Genetic work has shown strong support for significant differences between Bering Sea and Aleutian Islands cod, as well as the possibility for additional differentiation within spawning stocks found along the Aleutian Archipelago [5, 6]. In the United States, Pacific cod is the fifth most valuable finfish species with almost all of the commercial catch coming from Alaskan waters [10]. In Alaska, Pacific cod is currently managed as three separate stocks: Gulf of Alaska, Aleutian Islands, and Bering Sea.

In the eastern Bering Sea, Pacific cod undertake large seasonal migrations from annual summer feeding grounds to winter spawning sites [11, 12]. Persistent winter spawning locations have been observed, and genetics and tagging research suggest that individuals display homing tendencies and site fidelity during their spawning season [11, 13]. In the Gulf of Alaska (Prince William Sound), Pacific cod have high site fidelity to small fjords with limited partial migration (i.e., some tagged fish migrated after spawning season) [14]. The findings from these limited studies on Pacific cod appear to be similar to the larger body of research into the movement ecology of its congener, Atlantic cod, *Gadus morhua*, which has been shown to display both partial and long-distance migratory patterns including high site fidelity [15, 16]. There are regional differences in the migratory behaviors of Atlantic cod, thus it is likely that Pacific cod may also exhibit varying regional migration strategies [17, 18].

In this study, we used pop-up satellite archival tags (PSATs) to examine the seasonal movement of Pacific cod in the Aleutian Islands from a winter spawning ground to its feeding distribution in the summer and fall. This was the first study to use PSATs to track Pacific cod in the Aleutian Islands and two goals of the study were to test the feasibility of using commercial vessels as tagging platforms and determine the methodology of tagging these medium-bodied fish and evaluate success rates. Seasonal movement patterns of Pacific cod are especially important to management since the fishery independent survey that is used in its stock assessment is conducted in the summer, yet a large portion (~ 80%) of the commercial fishery takes place during the winter (January–April) when they aggregate to spawn [19]. Potential distribution changes of the Pacific cod population between the winter and summer, especially the crossing of management boundaries during migrations, has significant implications in our understanding of their population dynamics and stock structure and thus their stock assessment.

Methods

Fish capture and release

A total of 36 Pacific cod were captured and released during a cooperative venture on both bottom trawl and pot fishing vessels during commercial fishing operations targeting Pacific cod in the Aleutian Islands near Adak Island, Alaska (Fig. 1). Due to differences in the vessels and the gear deployed, the methods used to capture and release Pacific cod differed. However, the procedures for attaching the satellite tags to the Pacific cod were the same.

Trawl vessel operations

We captured, tagged, and released 21 Pacific cod from the FV *Ocean Explorer* on 18–20 February 2019, in Nazan Bay near Atka Island (Fig. 1). Nazan Bay is a known spawning site for Pacific cod and tagging efforts coincided with time of peak spawning time. The FV *Ocean Explorer* is a 185-foot (56.4 m) bottom trawl vessel that conducted two, 6-h tows during daylight hours targeting Pacific cod. We retained and tagged Pacific cod opportunistically from each tow. After the net was brought on deck, the crew hand selected the most vigorous Pacific cod from the top of the trawl net (most recently captured) and immediately placed them into one of two large holding tanks, 1000 L each, that had a constant supply of untreated seawater. Once in the tanks, we further examined the Pacific cod for external signs of barotrauma and removed individuals that showed signs of injury. Pacific cod that were caught during the first haul were tagged within 2 h of capture and retained in the tank until fishing operations were completed for the day. The time between capture and release ranged from 6 to 8 h. Pacific cod that were captured during the second haul were tagged and released within 1.5 h. Water temperatures in the tank were within 1 °C of bottom temperatures as recorded by net mounted instruments. We carefully lowered tagged Pacific cod to the sea surface with a sling and then returned them to 50 m depth with a SeaQualizer™ descending device attached to a weighted line. The device included of a spring-loaded clamp that on the surface gripped the lower lip of the Pacific cod. This clamp was triggered by a change in water pressure to open up and release the fish. Most Pacific cod were

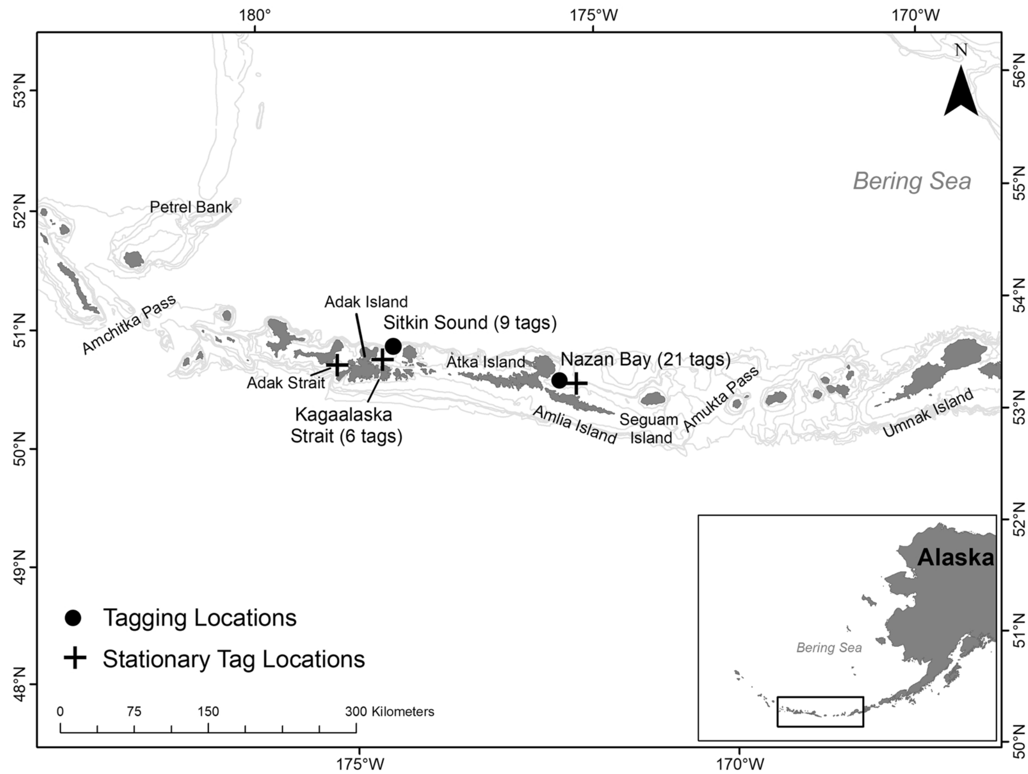

Fig. 1 Map of the study area in the central Aleutian Islands, three stationary tag locations, and three Pacific cod satellite tagging locations

released close to the recapture site in a location with a similar bottom depth from which they were captured. The average release depth from the trawl vessel was 115 m (min = 109, max = 118). Due to the high intensity of fishing within some capture areas, we released some Pacific cod up to 12 km away into areas that were not heavily fished in order to avoid immediate recapture by the fishery.

Pot vessel operations

We captured, tagged, and released 15 Pacific cod from the FV *Deliverance*, a 60-foot (18.29 m) pot vessel, during two fishing trips at two locations near Adak Island (Fig. 1). On February 22, 2019, we tagged nine Pacific cod in Sitkin Sound, and on February 28, we tagged six Pacific cod south of Adak near Kagalaska Strait (Fig. 1). In both locations, we tagged three Pacific cod per pot and all of the tagged Pacific cod were released at the same depth and within 1 km from where they were caught. The average release depth from the pot vessel was 100 m (min = 88, max = 117). The pots in Sitkin Sound had been in the water 48-h before we retrieved them, while those near Kagalaska Strait had been in the water for 24-h. Pacific cod were retrieved from pots and immediately placed into a 500 L seawater tank with flowing seawater. Individuals were selected for tags by looking for any outward signs of barotrauma and only Pacific cod in the best condition were selected for tagging. The time between capture and release ranged from 19 to 53 min. The Pacific cod were lowered off the boat to the sea surface with a sling and returned to 50 m depth with a SeaQualizer™ descending device.

Tag attachment

Tags were attached to Pacific cod using a “tag backpack” system that was and successfully used for tagging salmon [20–22]. The backpack system consisted of two components; the tag bridle (a harness that was implanted into the fish) and the tag that was attached to the bridle (Fig. 2). The tag bridle consisted of 1.2 mm braided spectra twine attached to two plastic oval backplates (50 mm × 11 mm × 1 mm) that each had a 1.5 mm thick silicon pad glued to the inside to reduce abrasion. The backplates and bridle were wired through the dorsal musculature of the Pacific cod, just forward of the first dorsal fin with 0.5 mm stainless steel wire that was covered in poly shrink tubing. The wire was guided through the Pacific cod using a pair of hypodermic needles that were held in parallel with a custom jig. The jig was designed to keep the needles separated at the same distance as the

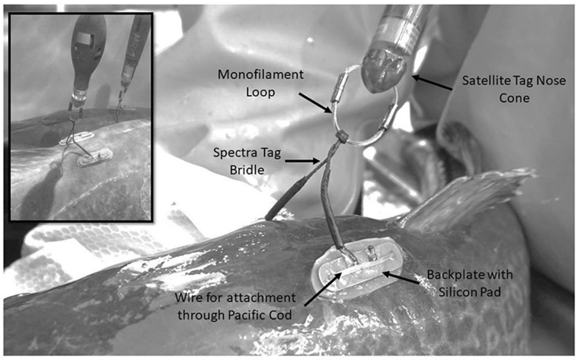

Fig. 2 Image of tag backpack for a pop-up satellite archival tag attachment to a Pacific cod. Insert shows a tag floating while on Pacific cod in a tank

holes in the backplates. The wire was pulled tight and crimped to secure and reduce movement of the bridle system. A small loop was attached to the nose cone of each satellite tag using 150-lb test monofilament line and two brass crimps. This loop (and the tag) were attached to the middle of the bridle system with a cow hitch prior to the bridle being attached to the Pacific cod.

The latitude, longitude, and time of capture and release, and fork length were recorded for each individual tagged Pacific cod.

Satellite tag programming

Three different types of PSATs built by Wildlife Computers (Redmond, WA) were used: mark–recapture tags (mrPAT), survival tags (sPAT), and archival tags (MiniPAT). Tag attachments were the same for all tags. The mrPAT is slightly longer and narrower than the sPAT and MiniPATs and is 8% more buoyant in seawater. All tag types provided pop-up locations generated by the Argos satellite network (http://www.argos-system.org/), but differed in the amount and type of data provided. The mrPATs did not record any data, so the pop-up location was the only information provided by these tags. The sPATs generated daily minimum and maximum depth and temperature values during the entire deployment and 10-min times-series depth data for the last 5 days prior to their scheduled pop-up. The MiniPATs recorded depth, temperature, acceleration (for deployments < 90 days), and light intensity data at resolutions ranging from 1 to 5 s depending on programmed deployment duration. This high-resolution data could be retrieved if a tag was recaptured and returned for data download. The following archived data were summarized for transmission to the satellite network: (1) light levels at dusk and dawn; (2) daily minimum and maximum temperature and depth; (3) time-series of depth and temperature, and (4) temperature–depth profiles. MiniPATs deployed for 90 days also provided accelerometer-derived activity metrics [23].

Programmed pop-up dates were staggered throughout the year in order to provide pop-up locations in each season and tag deployments ranged from 60 to 360 days. The sPATs ($n = 3$) were deployed for 60 days (the maximum deployment duration). Pop-up dates for the mrPATs were programmed for 90 days ($n = 2$), 180 days ($n = 4$), 270 days ($n = 2$), and 360 days ($n = 4$). Pop-up dates for the MiniPATs were programmed for 90 days ($n = 3$), 180 days ($n = 8$), 270 days ($n = 2$), and 360 days ($n = 8$). MiniPAT time-series depth and temperature information was generated for 90-day tags at 150-s intervals and for 180-day tags at 450-s intervals. Time-series depth for 270-day tags was generated at 600-s intervals for all days and temperature for alternate days. Time-series depth and temperature was generated for alternate days at 600-s intervals for all 360-day tags.

Stationary tags

Three stationary MiniPATs were deployed 1 m off the seafloor (at a bottom depth of 114, 118, and 114 m) in areas close to the Pacific cod capture and release locations to record environmental data at the capture site as baseline data for the geolocation model (Fig. 1). The MiniPATs were attached to 30 kg of steel weight with a 1-m-long section of 12 mm copolymer braided rope with stainless steel thimbles splices onto each end and a 20-cm T-float in between. The rope was attached to the weight with a galvanized swivel jaw and eye with a shackle. A 180-kg mono-loop was secured to the nose of the MiniPATs with a copper crimp. This mono-loop was then attached to the thimble on the rope through a stainless steel corkscrew with a barrel swivel connected to a stainless steel wire loop. Stationary tags assisted the process of geolocation by providing empirical variance estimates of light-based latitude and longitude utilized in the geolocation model and by recording temperature and depth at known locations that could be compared to tagged fish temperature–depth profiles. These tags were programmed to pop-up after 360 days and transmit daily light levels, minimum and maximum temperature, and depth. They were also programmed to transmit time-series temperature data at 600-s intervals for every day and time-series depth data for alternative days.

Fish plant data collection

Length and maturity data of Pacific cod landed at the Adak processing plant were collected to determine whether the length distributions of the tagged fish were representative of the population targeted by the commercial fishery and if tagged Pacific cod could be expected to be mature based on their lengths. Samples were randomly selected from opportunistically chosen deliveries of Pacific cod to the plant. Each random length collection represented one vessel delivery. Fish fork length was measured to the nearest centimeter and fish weight was recorded to the nearest gram. Maturity state was determine through visual examination of gonad tissues using established maturity keys with methods similar to previous studies [13].

Tagging, natural, and fishing mortality analysis

A generalized linear regression model with a logit link function was used to test for factors that may have had an influence on tagging mortality in the statistical program R (R Core Team, 2019). Factors included in the model were total length, the gear type fish were captured with (e.g., trawl or pot), and the amount of time spent on the vessel before release. Only tags for which the fate of the Pacific cod was known (tagging mortality vs. survived) based on transmitted data were used. Tag mortality was determined through the visual inspection of the entire time-series depth profiles of tags that popped-up early. Any tag with a constant depth from more than 48 h that occurred within 10 days of release was classified as a tagging mortality event.

Movement and geolocation model

Total horizontal movements were calculated as the great circle (shortest) distance between the location at which the Pacific cod was released and the location of the first accurate transmitted position following tag pop-up. Directed movement was defined as any horizontal movement greater than 50 km. Movement pathways for fish tagged with MiniPATs were reconstructed using a hidden Markov geolocation model (HMM) adapted for demersal fishes in the North Pacific Ocean [24–26]. The HMM consists of a coupled movement model (diffusion) and a data likelihood model that links tag data to known distributions of geolocation variables within a gridded study area. The model consists of a forward filter followed by backward smoothing. The forward filter begins with all location probability in the release location grid cell. For each day, location probabilities in study area grid cells are updated first by the movement model and then the data likelihood model. The HMM handles missing data easily by updating probabilities with the movement model only on days when PSAT data are not available. Once the end of the PSAT data set is reached, the daily location probabilities are backward-smoothed from the end location to the release location to provide the probability that the tagged fish occupied each grid cell on each day of the trajectory.

The data likelihood model for Pacific cod in the Aleutian Islands is based on maximum daily depth and light-based longitude. In the Aleutian Islands, depth gradients are parallel to latitude (except for passes), so light-based longitude and depth provide orthogonal geolocation information. The maximum daily depth likelihood for demersal fishes assumes that once a day the fish is near to the seafloor [26]. Pacific cod in our study area were likely to have some degree of off-bottom behavior during recovery from tagging, where Pacific cod seek shallower depths as they recuperate from barotrauma [27], crossing of deep passes during migration, and foraging in areas where sharp gradients in depth exist. Therefore, we modified the maximum depth likelihood to allow the maximum daily depth recorded by the fish to occur at some distance above the seafloor by using a split-normal distribution that accounts for grid cell bathymetry heterogeneity as well as off-bottom behavior. We used a 100-m resolution bathymetry grid [28] aggregated to a model grid size of 2 km to calculate the daily maximum depth likelihood.

Light measurements from PSATs can be used to determine latitude and longitude estimates for fish that occupy photic zone depths [29], however longitude estimates are more reliable than latitude for demersal fish [30]. PSAT light measurements were converted to longitude using Wildlife Computers GPE2 software and manually filtered to remove spurious longitude values. A variance of 1.5 degrees was assigned to the longitude likelihood following analysis of longitude estimates from three stationary tags deployed in release locations. Depth and longitude likelihood surfaces for each day were combined by cell-wise multiplication [31, 32].

Movement states may be specified for the HMM by assigning different values of diffusion to days when movement rates are likely to be faster or slower based on auxiliary data. In this study, two movement states were assigned to tagged cod for the HMM: a recovery/spawning state, during which fish were assumed to have limited movement, and a non-spawning state during which fish were likely to have larger movement rates during migration and summer foraging. Limited initial movement rates in the release area were likely due to recovery from barotrauma associated with capture [27] as well as by nature of their capture at known spawning grounds during the spawning period [13], for which site fidelity and homing have been observed for Pacific cod [11, 14]. Therefore, the recovery/spawning state was defined by (1) time periods where fish exhibited characteristic barotrauma recovery patterns [27], and (2) time periods where temperature at depth measured by tagged cod matched temperature at depth measured by stationary tags and other tagged cod with pop-up locations at the release location [33]. The value of diffusion used for the recovery/spawning state for all geolocated fish was determined based on optimal diffusion values from two fish that were recaptured in the commercial fishery (#178701) or predated upon (#178696) in the release areas after 21 and 32 days, respectively. Larger values of diffusion were assigned to the non-spawning state and were calculated separately for individual geolocated fish by minimizing the RMSE difference error between the depth measured by the fish and the depth at model-estimated locations.

The primary model output consists of the probability that the tagged animal occupied each grid cell in the study area for each day of the data record. The most probable track was determined by simulating 20 random walk movement paths using the same values of diffusion as the HMM. At each time step, proposed locations were accepted only if they had probability greater than a specified value (e.g., the 99.99 percentile probability) for that day. The simulated path with the highest total sum of probability was selected as the most probable track. Horizontal displacement from the release location over time was calculated based on most probable track daily position estimates. Migration end dates were defined as the date when horizontal displacement from the release locations no longer increased. Migratory rates (km/day) were calculated as the mean daily differences in displacement distances when an individual was in the migratory state. Polygons that encompassed the smallest number of grid cells containing 50% and 99% of the probability were generated for each day. To visualize geolocation results, 50% daily location error polygons were classified as (1) recovery/spawning, (2) migration, or (3) summer foraging (all days after the migration end date), while the 99% daily polygons denote the overall uncertainty associated with the geolocation.

Results

Biological data

The average fork length of Pacific cod tagged in this study was 81.1 cm with a range from 65 to 104 cm ($n = 36$). This average fork length was the same as a random sample of Pacific cod that were landed at the fish plant in Adak, Alaska, during the study period ($\bar{x} = 81.2$; range = 49 to 114 cm; $n = 429$), indicating that the Pacific cod that were tagged and released likely came from the same part of the population that was being caught by the fishery. Out of the 100 maturity samples taken at the plant, only 6 Pacific cod were immature and they were all less than 66 cm (fork length). There was no significant difference in the length of tagged Pacific cod between vessel types (t test, p-value = 0.12).

Data summary

A total of 26 out of 36 PSATs popped-up before their scheduled release date (early pop-up) (Tables 1 and 2, Additional file 1). We were able to determine, with data transmitted from the MiniPATs, that 11 of these early pop-ups were the result of post-tagging mortality. The general post-release behavior of both Pacific and Atlantic cod that have suffered barotrauma is a gradual descent to depth that can take several days [27, 34] (Fig. 3a). The 11 Pacific cod with MiniPATs that popped-up early did not display this behavior. Instead, they had only minimal vertical movements after their release and within a few days, the time-series depth profile showed only tidal changes indicating that the fish had died (Fig. 3). It took between 11 and 42 days (average = 19.5 days) for fish to decompose and for the MiniPATs tags to float to the sea surface and begin transmitting data. Fork length was the best indicator of post-tagging mortality (p-value = 0.015), with larger Pacific cod more likely to have died (Fig. 4). No tagged Pacific cod over 90 cm survived. There was also an apparent, yet not statistically significant, difference in mortality rate based on the type of gear (p-value = 0.55). On the trawl vessel, 43% of the Pacific cod died compared to 30% that were caught with a pot. The amount of time that each fish spent out of the water before their release was not a significant factor (p-value = 0.47).

The cause of the early pop-up for 9 PSATs (2 MiniPATs with limited data transmission and 7 mrPATs) could not be determined. Five of the mrPATs came to the surface within 11 days of release and the 2 MiniPATs popped-up within 40 days of their release. These tags were not used for further analysis. The two other mrPATs with early releases were on Pacific cod for a longer period of time, 78 and 164 days, and the horizontal movement was calculated for these tags.

Three other early pop-ups were Pacific cod that were caught and their PSATs returned to us by commercial fishers (Table 2). One of these recaptures occurred 21 days after the Pacific cod was released and 25 km from its release location. A few pictures and qualitative reports on the condition of these fish were received. In the pictures, all individuals had some minor wounds in the area where the wires for the backplates were attached, but the overall conditions of the fish were reported as normal.

Three Pacific cod with early pop-ups had transmitted temperature and depth information that suggested that they were predated on by marine mammals (Fig. 5). In general, each of these tags (#178696, #178699, and #178704) recorded a rapid ascent followed by increase in temperature to between 36 and 37 °C that took between 2 and 3 h (Table 1). Two of the tags recorded subsequent dives while temperatures were elevate with a maximum recorded depth of

Table 1 Information on the length, tag type, release date, and release location of 16 Pacific cod, as well as the pop-up date, reason for early pop-up (FIS = caught by commercial fisher, MML = marine mammal predation, UNK = unknown), location, days at liberty, distance between release and pop-up, number of transmissions from MiniPATs and geographic pop-up location

Ptt #	Length (cm)	Tag type	Release location	Release date	Release latitude	Release longitude	Early pop-up	Pop-up date	Pop-up latitude	Pop-up longitude	Days at liberty	Distance between release and pop-up (km)	Transmissions	Pop-up location
177,954	70	sPAT	Nazan Bay	18-02-2019	52.2535	− 173.62083	No	19-04-2019	52.1525	− 172.702	60	64	NA	Seguam Pass
177,953	82	sPAT	Nazan Bay	20-02-2019	52.35467	− 173.85883	No	22-04-2019	52.1511	− 172.7285	61	80	NA	Seguam Pass
177,955	81	sPAT	Sitkin Sound	22-02-2019	51.90583	− 176.43467	No	24-04-2019	52.0766	− 175.0203	61	99	NA	Atka Island
177,958	77	mrPAT	Nazan Bay	18-02-2019	52.253	− 173.5405	Yes (FIS)	17-08-2019	52.03333	− 171.90333	180	114	NA	South of Seguam
177,962	71	mrPAT	Nazan Bay	19-02-2019	52.25933	− 173.55433	No	16-11-2019	53.5276	− 168.3339	270	378	NA	North of Unmak
177,967	74	mrPAT	Sitkin Sound	22-02-2019	51.92333	− 176.43183	Yes (UNK)	10-05-2019	51.9094	− 176.4933	77	4	NA	Sitkin Sound
177,966	65	mrPAT	Sitkin Sound	22-02-2019	51.90767	− 176.43183	Yes (UNK)	05-08-2019	52.576	− 171.7923	164	325	NA	Amukta Pass North
177,961	86	mrPAT	Sitkin Sound	22-02-2019	51.922	− 176.4325	No	21-08-2019	51.8978	− 176.4108	180	3	NA	Sitkin Sound
178,701	70	miniPAT	Nazan Bay	19-02-2019	52.2565	− 173.572	Yes (FIS)	12-03-2019	52.405	− 173.8317	21	24	NA	Nazan Bay
178,690	74	miniPAT	Nazan Bay	20-02-2019	52.35483	− 173.85817	No	2-05-2019	52.5514	− 179.6625	91	394	2783	Petrel Bank
178,704	73	miniPAT	Nazan Bay	19-02-2019	52.276667	− 173.5295	Yes (MMP)	23-11-2019	52.525	− 172.5873	277	70	1207	North of Seguam
178,696	77	miniPAT	Sitkin Sound	22-02-2019	51.92383	− 176.43017	Yes (MMP)	28-03-2019	52.0579	− 176.5112	33	16	2282	Sitkin Sound
178,709	88	miniPAT	Sitkin Sound	22-02-2019	51.9235	− 176.42733	Yes (FIS)	08-06-2019	52.09	− 172.1233	106	295	NA	South of Seguam
178,697	74	miniPAT	Sitkin Sound	22-02-2019	51.9225	− 176.43017	No	22-08-2019	52.077	− 171.4197	181	344	2386	Amukta Pass South
178,708	79	miniPAT	Sitkin Sound	22-02-2019	51.92333	− 176.43183	No	19-02-2020	51.7147	− 176.9818	360	44	119	Adak Strait
178,699	83	miniPAT	South Adak	01-03-2019	51.71082	− 176.35295	Yes (MMP)	26-03-2019	51.9445	− 176.8127	25	41	82	North Adak

Pacific cod that had tag mortality ($n = 11$), that had early releases that were less than 60 days with an unknown cause ($n = 7$), or did not transmit a pop-up location ($n = 2$) were excluded from this table. Information on all tags can be found in Additional file 1

Table 2 Fate of satellite tags by type

Pop-up reason	sPAT	MiniPAT	mrPAT	Total	Percentage (%)
Scheduled	3	3	4	10	27.8
Early—unknown		2	7	9	25.0
Early—suspected predation		3		3	8.3
Caught by commercial fishing fleet		2	1	3	8.3
Post-tagging mortality		11		11	30.5

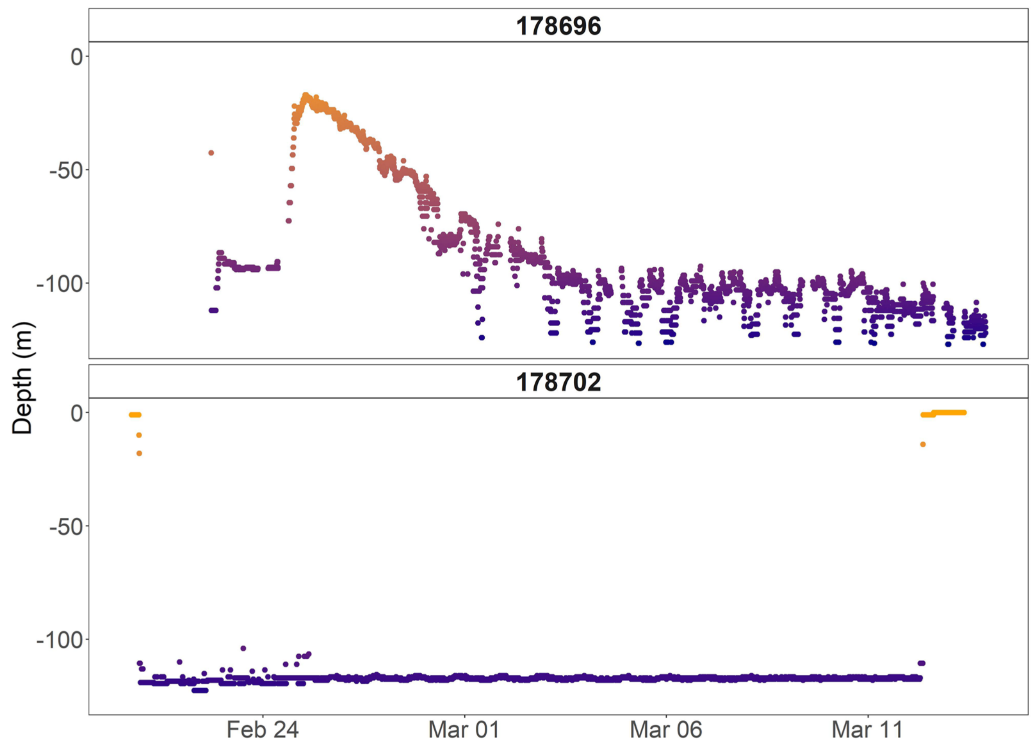

Fig. 3 Time-series depth profile of two satellite-tagged Pacific cod directly after their release. The top panel is for a Pacific cod with a typical recuperation period were it returns to shallower water shortly after release and then gradually returns to its original depth after several days. The bottom panel illustrates a Pacific cod that died shortly after its release and the subsequent period during which body decomposed and then the tag came to the surface

160 m. Temperature and depth data indicated that the tags remained within the marine mammal between 21 and 41 h prior to be expelled.

All three of the stationary tags popped-up early; 172, 199, and 259 days after they were deployed. Depth records from the stationary tags indicated no change in depth greater than tidal fluctuations; therefore, the moorings are unlikely to have dragged. However, since the tags were not recovered, we could not determine where the failure occurred.

Pacific cod movements (> 60 days)

PSAT pop-up locations were received from 13 Pacific cod at liberty for more than 60 days (Figs. 6, 7, and Table 1). Six of these Pacific cod were tagged in Nazan Bay and seven were tagged in Sitkin Sound. None of the Pacific cod tagged in Kagalaska Strait provided movement data after 60 days. Horizontal movement from release location to pop-up location ranged from 3 to 394 km (Fig. 7 and Table 1). Six PSATs popped-up in the spring (March 2019–June 2019), five PSATs

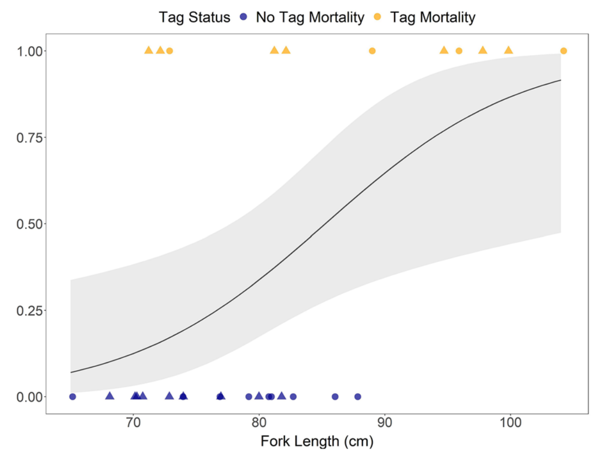

Fig. 4 Logistic regression of fork length and fate (no tag mortality = 0 or tag mortality = 1) of 29 Pacific cod equipped with pop-up satellite tags. Gray shading represents standard error. Circles indicate Pacific cod that were caught with pot gear and triangles indicate those caught with a trawl

popped-up in the summer (August 2019) between 164 and 181 days after their release of which four provided a location, two PSATs popped-up in the fall (November 2019), and one PSAT popped-up in the winter (February 2020).

One Pacific cod moved west 394 km from its release location to Petrel Bank within 90 days (Fig. 6A; #178690). While at liberty, this Pacific cod averaged a daily change in depth of 78 m and reached a maximum depth of 368 m (Fig. 8). Based on its modeled travel path, this Pacific cod swam mid-water across Amchitka Pass, which is characterized by 40 km of seafloor at depths exceeding 500 m at its narrowest point.

Nine Pacific cod moved east; eight to areas near Seguam Island and Amukta Pass with pop-ups in the spring, summer, and fall (Fig. 6) and one (#177962) to an area just north of Umnak Island that required the crossing of two deep island passes (horizontal movement = 378 km). The total distances moved for the other eight fish depended on their release location and ranged from 64 to 344 km.

Three Pacific cod that were tagged in Sitkin Sound had their PSATs pop-up close to their release location (horizontal movement = 4, 3, and 44 km) after 77, 180, and 360 days, respectively. This includes the only PSAT

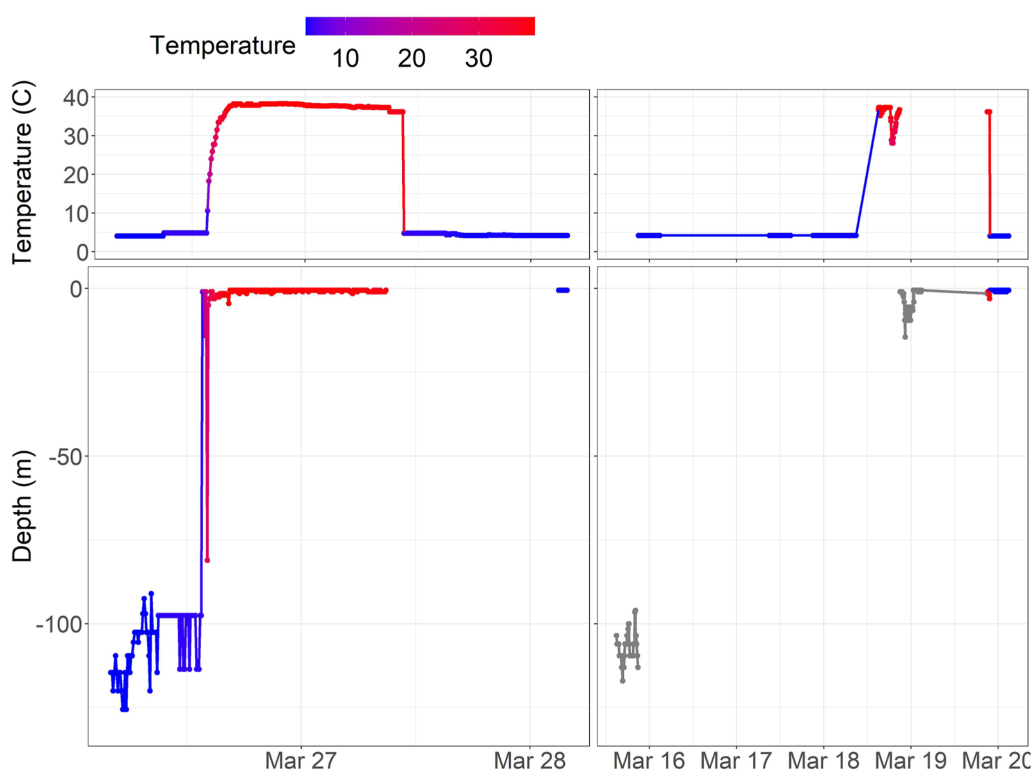

Fig. 5 Time-series temperature (°C) and depth (m) data from two Pacific cod (tag #178696 and #178699) that were suspected to have been predated on by marine mammals

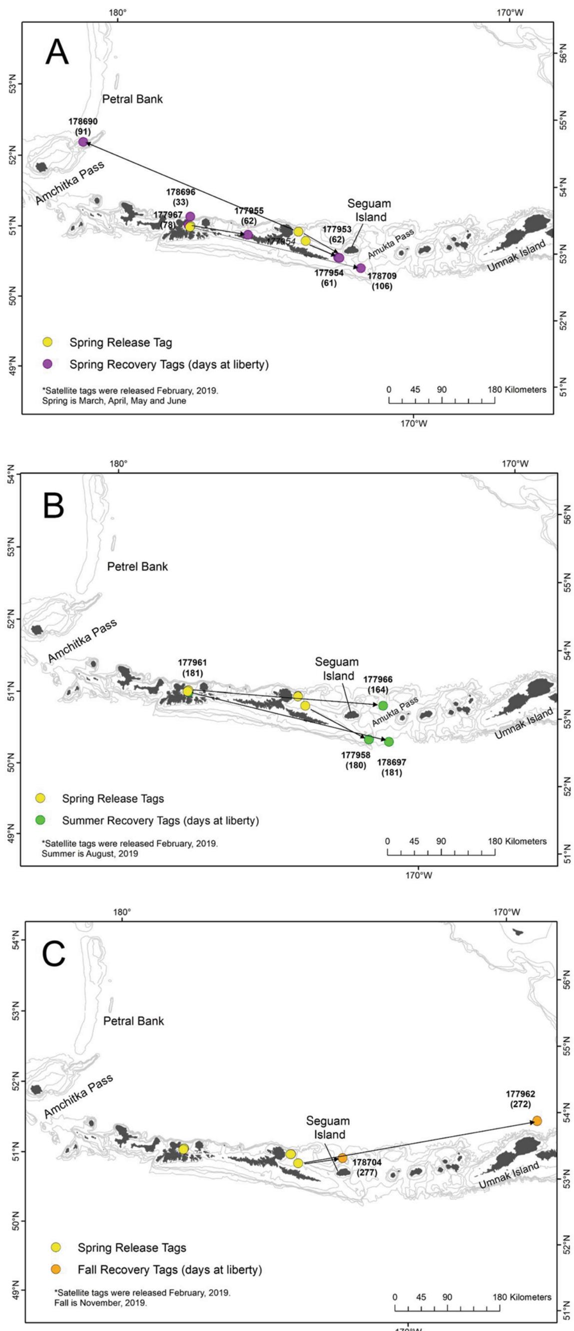

Fig. 6 Release and recovery locations for 7 tags that popped off in the Spring (March–June) (**A**). Release and recovery locations for 4 tags that popped off in the Summer (August) (**B**) and release and recovery locations for 2 tags that popped off in the Fall (November) (**C**). Black lines represent straight horizontal movement and do not indicate the pathway that each Pacific cod may have followed

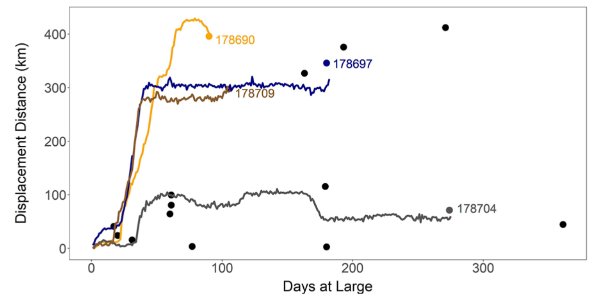

Fig. 7 Horizontal displacement distance (km) from release to pop-up location of PSAT tagged Pacific cod by days at large. Colored lines indicate the daily estimated position for four Pacific cod for which geolocation models were created. Tag #178704 was predated on by a marine mammal; the line indicates the last estimated location prior to predation whereas the circle indicates the pop-up location several days after when the tag was expelled

to remain on a Pacific cod for a full year and successfully transmitted its location (#178708). Only a few days of data were received, but the light information suggested that the tagged Pacific cod did not move more than 100 km over the course of the year.

Migration timing, potential pathways, and movement rates

PSAT longitude estimates provided valuable information about the timing of east–west movements and were thus key for determining migration timing (Fig. 9). The root mean square error (RMSE) of stationary tag PSAT longitude estimates compared to known longitudes from February through May was 0.6°, and during the summer months the RMSE increased to 1.3°. Two fish (#178701 and #178696) with end locations in release areas after 21 and 32 days had standard deviations of 0.7° and 0.6°, respectively. Therefore, precision of longitude estimates during the spawning and migratory periods was approximately 50 km increasing to 100 km during the summer foraging period. Geolocation data were available for a mean of 88% of days (range 59–100%) for geolocated fish.

Reconstruction of movement paths for the four Pacific cod that had geolocation data for more than 50% of days at liberty and were at liberty for more than 1 month provided some initial insights into the timing of movements. All four Pacific cod were likely to have left their respective tagging locations between March 12 and March 27, an average of 24.3 days after they had been released (Fig. 10). Tags #178709 and #178697, which were both tagged and released in Sitkin Sound, were estimated to take 24 and 18 days, respectively, to travel the roughly 270 km to Seguam Pass where they remained during the rest of the tracking duration. Their movement rates during the migration time period were 10.8 (±1.7 SE) and 13.1 (±1.8 SE) km/day, respectively [35]. Tag #178690 was estimated to move at an average rate of 8.2 (±1.4 SE) km/day for 44 days to reach to Petrel Bank where it remained for the duration of the tracking period. This

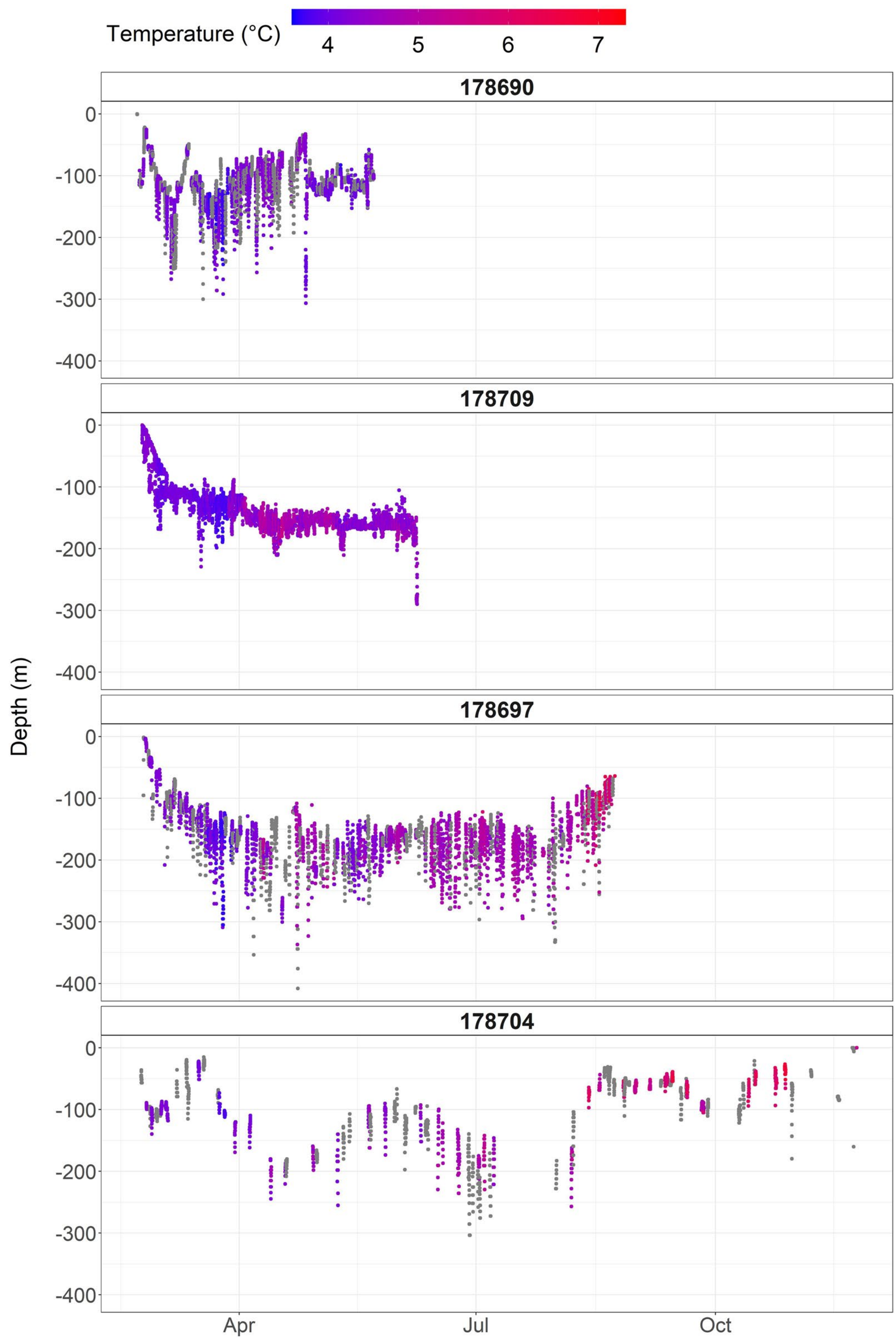

Fig. 8 Time-series plots of depth (m) and temperature (°C) for four geolocated Pacific cod (Tags #178690, 178709 178697, and 178704). Data points in gray had missing temperature data

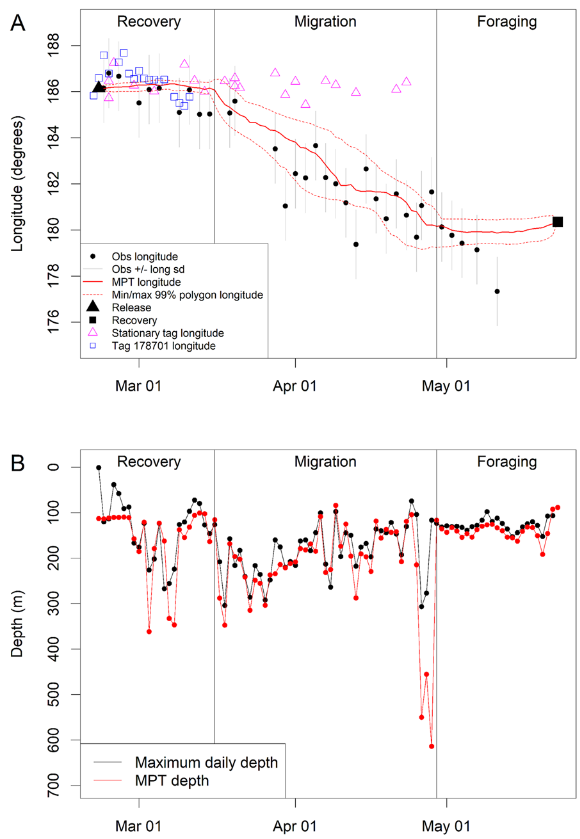

Fig. 9 Example of observed and modeled geolocation variables for tag #178690 during recovery/spawning, migration, and foraging periods. **A** Observed PSAT longitude values compared to known longitude values in the release area (Nazan Bay stationary tag #178710 and recaptured tag #178701) and model estimated (most probable track) longitudes. **B** Observed PSAT maximum daily depth values (black lines) compared to model estimated (most probable track) depths

individual also traveled south of the Aleutian Island chain, but since the Pacific cod headed west, it likely took advantage of the prevailing currents. Tag #178704 traveled the shortest distance for any individual with a geolocation model; its presumed foraging grounds were less than 100 km from where it was tagged and its migration period was estimated to last 7 days. Its movement rate during its time period was 6.6 (±2.0 SE) km/day. It was also one of our longest tracked Pacific cod and was still at its presumed foraging grounds on November 22, 276 days after it was released, when it may have been predated upon by a marine mammal.

Discussion

Pacific cod movement and migration

This study showed a range of seasonal movement patterns for Pacific cod in the Aleutian Islands. Horizontal movements of Pacific cod of up to 400 km were documented both east and west of their spawning grounds that included crossings of several deep island passes. An affinity for certain probable foraging locations was also documented, such as Seguam Pass, and it appears that once Pacific cod have reached these areas they display limited horizontal movement. These directed movements between winter spawning grounds and summer foraging areas suggest seasonal migration of some Pacific cod in the Aleutian Islands. While 77% ($n=10$) of the tracked Pacific cod migrated to separate foraging grounds directly after their spawning season, three Pacific cod that were released in Sitkin Sound remained there during the duration they were tracked.

Our results are comparable to other tagging studies in Alaska waters that have described both resident and migratory individuals found at the same site [11, 12, 14]. The occurrence of both resident and migratory individuals within a population (partial migration) is common among marine fishes including Atlantic cod [35–37]. The reasons for partial migration in fishes are not well known, but competition for scarce food resources is a likely driver for migration for a number of species [38]. Pacific cod have high consumption and growth rates and despite being general carnivores it would seem plausible that at least some of the population would be forced to leave its spawning grounds to forage for food elsewhere [39, 40]. The four Pacific cod for which geolocation models were created displayed an almost synchronous departure from their spawning grounds after 25 days. Atlantic cod appear to begin their migrations in groups, so it is not surprising that these Pacific cod left the spawning grounds at a similar time [41, 42]. The mean movement rates during migration these four individuals (3.6 to 12.7 km/day) was comparable to rates that have been calculated for Atlantic cod [43].

In the area near Seguam Island, where a majority of the tagged fish migrated after spawning in Nazan Bay, the nutrient rich waters from the Alaskan Stream are vertically mixed within the strong currents of Seguam Pass [44, 45]. Nutrient levels and overall productivity is high which in return attracts a number of species [46–48]. Pacific cod are generalist carnivores with spatially and temporally variable diet that includes a wide range of both benthic and pelagic species including decapods, cephalopods and a variety of fish [40, 49–51]. As such, it is not surprising that they would seek out highly productive areas such as Seguam Pass for their summer foraging grounds. Furthermore, they are the dominate predator of Atka mackerel which have a large spawning location near Seguam Island in the summer [52, 53].

The distance between the Pacific cod that went furthest west (Petrel Bank, 394 km) and east (Umnak Island,

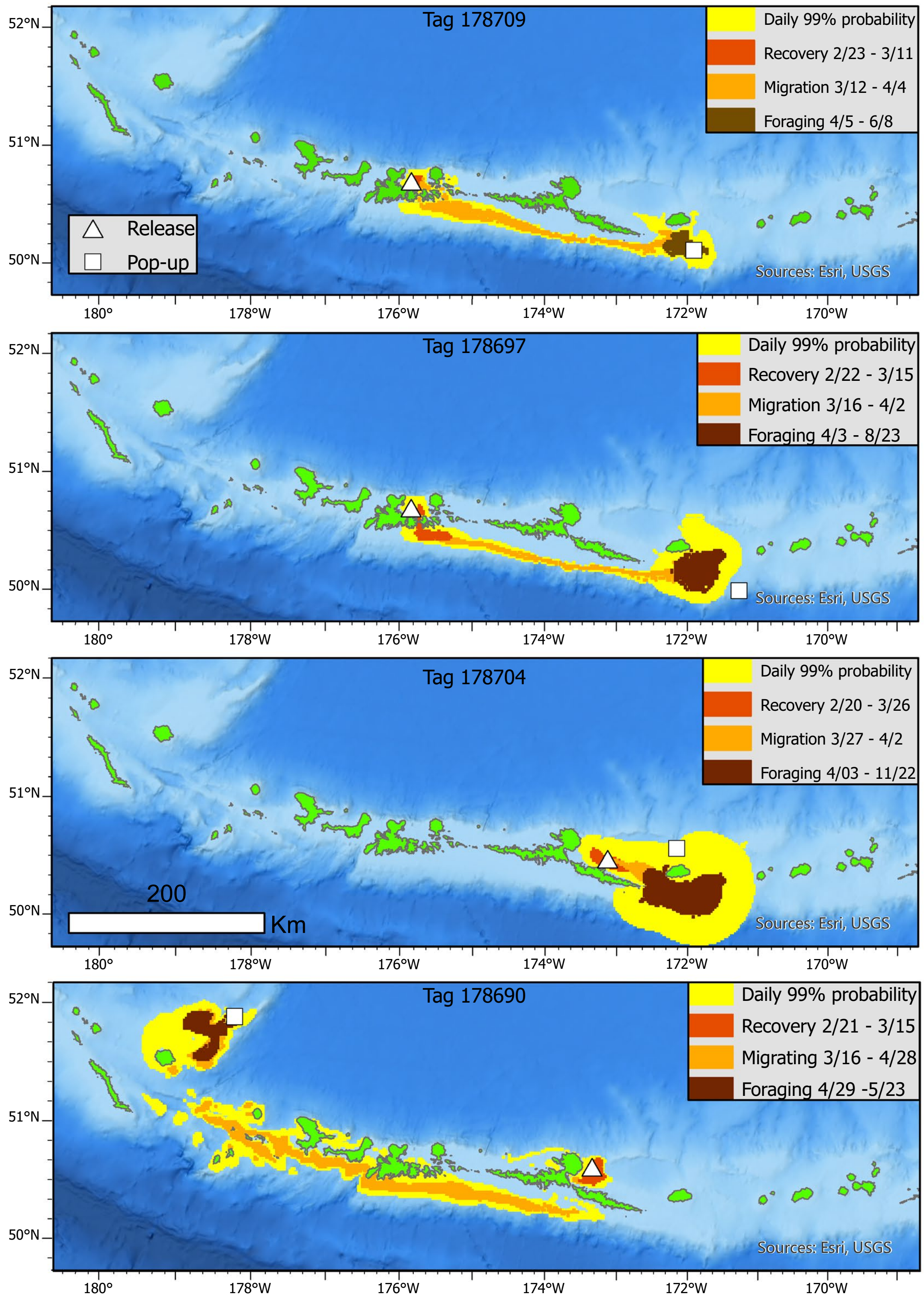

Fig. 10 Recovery/spawning, migration, and summer foraging locations of four Pacific cod based on probability estimates from the geolocation model. Daily 99% probability areas for the entire tagging duration are indicated in yellow. Daily 50% probability areas during recovery/spawning are shown in red, migration in orange, and summer foraging in brown

378 km) from Nazan Bay is almost half the length of the Aleutian Archipelago. Nazan Bay is a well-known large spawning location for Pacific cod, and the movements of these two fish provide insight on how far individuals may travel to reach summer foraging grounds [13]. Shimada et al. [12] also reported some relatively large movements of Pacific cod that were tagged in the Aleutians. Similar to results from this study, they observed a single Pacific cod that was tagged near Adak recaptured near Petrel Bank. They also tagged two Pacific cod near Adak that were recaptured roughly 700 km away in the eastern Bering Sea west of Pribilof Islands 3 and 5 years after they were released. In addition they reported two Pacific cod that were tagged near Unimak Pass recaptured near Seguam Island (~ 500 km) within 250 days.

The two Pacific cod in our study that each traveled roughly 400 km prior to their scheduled tag pop-up and those Pacific cod with long-distance recaptures reported by Shimada et al. [12] all had to cross over deep passes (> 500 m). Previous research has suggested that in the eastern Bering Sea, Pacific cod spend a majority of their time near the sea floor with minimal daily changes in depth [54, 55]. In the Bering Sea region where the fish were tracked the sea floor is relatively flat, yet the magnitude of daily vertical migrations increased with bathymetric complexity [54]. The Aleutian Island's bathymetry is highly complex with very abrupt changes in depth. Hobson et al. [56] found that Atlantic cod were closely associated with the sea floor, but that vertical movements in the water column increased during hypothesized migration periods. Given the high bathymetric complexity of the Aleutian Islands, it was difficult to determine from depth data alone if a tagged cod was off the bottom. However, based on its time-series depth profile and the depth of Amchitka Pass, the fish that migrated to Petrel Bank had to swim a considerable distance off the bottom. The fish that went to Umnak Island also swam across several deep passes including Amukta Pass that had depths greater than what was recorded for these tagged Pacific cod leading to a conclusion that it too swam off the bottom for considerable distances.

The ability of Pacific cod to spend time swimming off the bottom may not seem to be remarkable, but it is important for understanding population connectivity among the numerous deep passes along the Aleutian Islands. For example, Samalga Pass represents a major biophysical transition in the Aleutian Islands and may limit the gene flow of Pacific cod [2, 6, 44]. Amchitka Pass, the deepest and widest pass, is also considered a potential genetic barrier [6, 57]. The tagging results from this study suggest that Pacific cod can cross these passes, and therefore the passes might present less important genetic barriers for Pacific cod, but instead genetic structure along the Aleutian Islands may be driven by other factors [6]. Spies [6] suggested a migration rate between the Aleutian Islands and the Bering Sea that is far less than 10% per year. This study corroborates the earlier work and indicates that some seasonal movement along the Aleutian Islands.

One of the outstanding questions regarding Pacific cod movement is site fidelity to spawning areas. Nazan Bay has been a major fishing ground during the spawning season and therefore is assumed to be an important spawning location for Pacific cod in the Aleutian Islands. To understand the potential for spawning site fidelity, tagging efforts for this study focused on Nazan Bay during the spawning season for Pacific cod. Unfortunately, all of the scheduled 360-day tags that were released in Nazan Bay area were either recovered early or did not transmit location data, and therefore no data on site fidelity were collected in this area. The only tag that was on a Pacific cod for 360 days popped-up close to where it was originally tagged in Sitkin Sound. Light data suggested that this Pacific cod was a resident fish that did not undertake a large migration between spawning seasons. Since the rest of the tags on migratory Pacific cod popped-up prior to 1 year, it is uncertain as to whether the tagged fish were going to return to their spawning location. The pop-up location and date of the Pacific cod with the third longest days at liberty prior to tag pop-up (270 days), was just north of Umnak Island on November 16th. Interestingly, with the start of spawning season only a few months away, this fish was closer to Unimak Pass, arguably one of the largest known spawning aggregation sites for Pacific cod, than Nazan Bay where it was tagged and released [11–13]. It is unknown whether this fish would have returned to Nazan Bay or remained east of Samalga Pass. Atlantic cod have shown high spawning site fidelity and natal homing in several regions [17, 58, 59]. It would seem likely that Pacific cod in the Aleutian Islands would display the same behavioral traits and additional tagging efforts with deployments longer than a year could help answer this question.

The overall distance moved by Pacific cod in this study aligns with a wide spectrum of fish species behaviors in North Pacific waters, some of which exhibit strong site fidelity and others are considered highly transitory. These movements can vary both seasonally and spatially. Similar to Pacific cod, several rockfish species exhibited a combination of low to high site fidelity off the Oregon coast, with most species showing strong site fidelity and one species exhibiting low site fidelity [60]. This combination of low to high site fidelity within a single fish species has been documented for other fish species and tagging studies. In the Bering Sea, adult walleye pollock (*Gadus chalcogrammus*) between 30 and 50 cm lengths undergo horizontal feeding migrations from 3 to 500 km, but individual movement rates are unknown [61]. In addition, as their diets change, a much smaller proportion (15%) of larger pollock (> 50 cm) participate in these migrations [61]. In the Bering Sea and Aleutian Islands, 22 tagged Greenland turbot (*Reinhardtius hippoglossoides*) traveled between 7.8 and 513.3 km during 19 to 1859 days at liberty with smaller movements occurring in the Aleutian Islands [62]. Additionally, it was suggested that the movement from shallow depths in the summer to deeper depths in the winter may coincide with a return to previously inhabited sites [62]. In the Aleutian Islands, adult sablefish (*Anoplopoma fimbria*) exhibited a general western migration that averages 191 km per year and the distance increased for fish that were tagged in the Aleutians [63]. Similarly, Pacific halibut (*Hippoglossus stenolepis*) tagged near Attu and Atka Islands (Aleutian Islands) traveled up to 166 km, however, none moved away from the island group from which they were tagged [64]. Atka mackerel in the Aleutian Islands also exhibit modest movement rates, in general, tagged fish did not travel distances greater than 20 km, with many tags recovered years later within 5 km of the tagging location [3].

Early mortality

The tagged Pacific cod in this study had a high post-tagging mortality rate which was surprising, as other Pacific cod tagging studies have had very high tag recovery rates (20–40%), suggesting that tagging mortality was low in these earlier studies [11, 27]. Although we were not able to determine the cause post-tagging mortality, we speculate that is related to internal injuries from their capture and release as compared to tag attachment procedures. Pacific cod have a closed swim bladder (physoclistous) and due to the depths in which the Pacific cod in this study were caught, they all experienced some level of barotrauma as a result of rapid decompression [27, 65]. Pacific cod with external injuries such as bloated eyes, everted stomachs, swollen coelomic cavities, or subcutaneous gas bubbles were not used for this study. However, internal injuries could not be assessed. Based on the depth profiles of the Pacific cod that survived, and the work conducted by Nichol et al. [27] and Ferter et al. [65], the fish from this study likely all had ruptured swim bladders. A number of Pacific cod in this study and in Nichol et al. [27] were able to overcome this injury during a recuperation period during which ruptured swim bladders sealed and individuals were able to secrete gas back into the swim bladder [65]. It seems plausible that the fish in this study that died suffered from a separate injury such as air embolisms or other damage to internal organs rather than from ruptured swim bladders.

Ferter et al. [65] found that for Atlantic cod, the probability of gas bubbles in blood approaches 100% for cod that have been caught in depths as shallow as 60 m. They found that "quick release after capture is of utmost importance as prolonged surface holding exacerbates barotrauma effects (e.g., blockage of blood flow because of gas embolisms)." In this study, time on the boat was not a significant indicator of whether a Pacific cod would survive. However, all of the holding times during this study were relatively long (average = 192 min, minimum = 19 min), during which time the fish may have suffered additional barotrauma injuries.

One factor that had a significant influence on survival was fish length. Larger Pacific cod were more likely to die, and all Pacific cod over 90 cm died. It is unknown why size affected survivorship. One possibility is the reproductive state of the Pacific cod that were targeted affected survival. Since it was spawning season, all fish likely had enlarged gonads. Peregrin et al. [66] found that for pink snapper (*Chrysophrys auratus*) reproductive stage was an important predictor of barotrauma. Immature, resting, and spent fish generally incurred fewer injuries. They attributed this difference in injury rate to the available space in the coelomic cavity. It is possible that the larger Pacific cod that were tagged had less room in their coelomic cavity and thus sustained more injuries than smaller fish. Although not statistically significant, Pacific cod that were caught with a trawl net were generally more likely to die in comparison to those brought up in a pot irrespective of size. The commercial tows of Pacific cod were long (~ 6 h.), and although the most recently caught fish (top of net) were chosen, how much time they had spent in the net was unknown. All of the fish were likely exhausted after having struggled during the haul back and emptying of the net. The combination of this energy depletion along with barotrauma meant that 43% of the tagged fish caught in trawl gear did not survive in comparison to a 30% tagging mortality rate on the pot vessel. The ability to detect a significant difference between gear types may have been partially due to the insufficient sample size.

The tagging operations themselves were relatively short and they were not considered to be a major contributor to mortality although they likely added additional stress. Subsequent research conducted by the authors (unpublished data) on Pacific cod with PSATs with a similar tag attachment in the northern Bering Sea found no immediate tagging mortality ($n = 40$). Fish were smaller, came from less than 50 m depth, were caught with hook and line, and released within 10 min of capture. Based on these findings, future research should plan on returning fish to depth as fast as possible and continue to experiment with other means of capture, such as hook and line.

Researchers should avoid tagging Pacific cod greater than 90 cm until there is a better understanding of their high mortality rate.

Cause of early pop-ups

Nine PSATs that popped-up early (i.e., before their scheduled release) from either mrPATs or MiniPATs did not transmit sufficient data to understand the cause of these early pop-ups. The early pop-ups could be the result of immediate tagging mortality, delayed mortality because of capture and release stressors, gear failure of the 'tag backpack', tag failure, or they could be the result of predation. Five of these PSATs popped-up within a similar time frame as the Pacific cod with MiniPAT tags that were determined to have died due to tagging procedures. Thus, at least a portion of these unknown early releases may be attributed to tagging mortality. High mortality rates of externally tagged fish have been recorded in several studies and temperature and depth information have been used to indicate predation of tagged fish by marine mammals [67–71]. Stomach temperatures of marine mammals are significantly warmer than the surrounding water, so the only explanation for the increase in tag temperatures for two of these early releases to 38 °C along with rapid ascent to shallow water was that they were predated by a marine mammal [72, 73]. In the Aleutian Islands, the only marine mammals that forage on adult Pacific cod are Steller sea lions (*Eumetopias jubatus*) and killer whales (*Orcinus orca*) [74]. If our tags were ingested by a killer whale we would have expected to see more changes in depth as the whale continued to dive [75]. We hypothesize that the near constant depth on the surface was indicative of a sea lion that had hauled out Furthermore, Kuhn et al. [73] found that it took a California sea lion's, *Zalophus californianus*, stomach on average 93 min to return to its normal temperatures after consuming 4 kg of food which is a comparable weight and warming time observed in this study. Since three Pacific cod in this study had likely been predated upon by a marine mammal, it is also possible that some portion of the unknown early releases met a similar fate.

Our three stationary tags were programmed to release from the bottom after 360 days, yet they all popped-up early; 172, 199 and 259 days after deployment. The exact cause of their early pop-up is unknown since they were not recovered, but we believe that it was most likely due to a failure in the mooring system as compared to a problem with the MiniPAT. The 'weakest' link in the mooring was the 180-kg monofilament loop with a copper crimp. It is possible that the monofilament was somehow abraded or that the copper crimp corroded. This monofilament loop has been replaced with stainless steel wire or spectra line on subsequent moorings placed by the authors. Another possibility is that the mooring landed into or close to rocky bottom and the braided rope that connected the float to the weight was abraded as currents moved it back and forth across a rock. We attempted to minimize this issue by surrounding the bottom section of the rope with a rubber hose, but on future deployments in possible rocky areas, we intend to investigate other materials.

Conclusions

This study provided important initial insights into the seasonal movement patterns of Pacific cod in the Aleutian Islands. Most tracked Pacific cod (77%) undertook migrations in the middle of March (64–394 km) from their winter spawning areas to summer foraging areas, but a few individuals remained in their capture location suggesting a partial migration strategy. Their ability to cross deep passes that were previously seen as potential barriers to movement has expanded our understanding of population connectivity. Future research should focus on refining winter capture procedures, deploying tags for a full year to obtain information about return migration, and releasing tags in different regions within the Aleutian Islands study area.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40317-021-00250-2.

Additional file 1. Information on the length, tag type, release date, and release location for all tagged Pacific cod , as well as the pop-up date, reason for early pop-up (FIS = caught by commercial fisher, MML = marine mammal predation, UNK = unknown), location, days at liberty, distance between release and pop-up, and number of transmissions from MiniPATs.

Acknowledgements

We want to thank Jerry Downing of the B&N Fisheries Company and Captain Dan Carney of the FV *Ocean Explorer* and crew for providing their vessel and expertise in fishing for Pacific cod. We also want to thank Captain Todd Hoppe and crew of the FV *Deliverance* for offering time on their vessel and providing fishing expertise. We would like to thank the captain, crew, and observers onboard the FV *Seafreeze Alaska*, FV *Seafreeze America* and FV *Katie Ann*, for returning tags which provided invaluable information. Finally, we thank Ingrid Spies, Steve Barbeaux, and Wayne Palsson at the AFSC and two anonymous reviewers for their thoughtful comments on the manuscript.

Authors' contributions

All authors contributed to the design of the research. DB, SM, and DF conducted field work. DB and JN performed analysis and wrote the paper. SM, DF, and KR conducted review and editing. All authors read and approved the final manuscript.

Funding

Funding for this research came from the North Pacific Research Board (NBRP) Project # 1810 and the generous donations of multiple fishing companies (Aleutian Spray Fisheries, Adak Community Development Corporation, United States Seafoods, O'Hara Corporation, Ocean Peace Inc., B&N Fisheries Company, Golden Harvest Alaska Seafoods, American Seafood Corp) organized by John Gauvin.

Availability of data and materials
The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate
NMFS Animal Care and Use Policy (04-112) is currently limited to research on free-living marine mammals, seabirds, and sea turtles and does not cover research on captive or wild fish. However, every effort was made to follow accepted standards and ensure the ethical treatment of captured fish including guidelines from the U.S. Government Principles for the Utilization and Care of Vertebrate Animals Used in Testing, Research and Training (https://olaw.nih.gov/policies-laws/gov-principles.htm) and the American Fisheries Society Guidelines for the Use of Fishes in Research (https://fisheries.org/docs/policy_useoffishes.pdf; Chapter V).

Consent for publication
Not applicable.

Competing interests
The authors declare that they have no competing interests.

Author details
[1]National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Alaska Fisheries Science Center, 7600 Sand Point Way Northeast, Seattle, WA 98115, USA. [2]Pacific States Marine Fisheries Commission, 205 SE Spokane Street, Suite 100, Portland, OR 97202, USA. [3]Kingfisher Marine Research, LLC, 1102 Wee Burn Dr., Juneau, AK 99801, USA. [4]Adak Community Development Corporation, PO Box 771, Port Townsend, WA 98636, USA. [5]Lynker Technologies, LLC, 202 Church Street SE #536, Leesburg, VA 20175, USA.

Received: 11 March 2021 Accepted: 21 June 2021
Published online: 07 July 2021

References

1. Stabeno PJ, Schumacher JD, Ohtani K. The physical oceanography of the Bering Sea. In: Dynamics of the Bering Sea. Fairbanks: University of Alaska Sea Grant; 1999. p. 1–28.
2. Logerwell E, Aydin K, Barbeaux S, Brown E, Conners M, Lowe S, Orr J, Ortiz I, Reuter R, Spencer P. Geographic patterns in the demersal ichthyofauna of the Aleutian Islands. Fish Oceanogr. 2005;14:93–112.
3. McDermott SF, Fritz L, Haist V. Estimating movement and abundance of Atka mackerel (*Pleurogrammus monopterygius*) with tag–release–recapture data. Fish Oceanogr. 2005;14:113–30.
4. Laman EA, Kotwicki S, Rooper CN. Correlating environmental and biogenic factors with abundance and distribution of Pacific ocean perch (*Sebastes alutus*) in the Aleutian Islands. Alaska Fish Bull. 2015;113(3):270–89.
5. Cunningham KM, Canino MF, Spies IB, Hauser L. Genetic isolation by distance and localized fjord population structure in Pacific cod (*Gadus macrocephalus*): limited effective dispersal in the northeastern Pacific Ocean. Can J Fish Aquat Sci. 2009;66(1):153–66.
6. Spies I. Landscape genetics reveals population subdivision in Bering Sea and Aleutian Islands Pacific cod. Trans Am Fish Soc. 2012;141(6):1557–73.
7. Grant WS, Ståhl G. Evolution of Atlantic and Pacific cod: loss of genetic variation and gene expression in Pacific cod. Evolution. 1988;42(1):138–46.
8. Smirnova M, Orlova SY, Orlov A. The population genetic organization of Pacific cod *Gadus macrocephalus* in the North Pacific based on microsatellite analysis. J Ichthyol. 2019;59(4):555–65.
9. Drinan DP, Gruenthal KM, Canino MF, Lowry D, Fisher MC, Hauser L. Population assignment and local adaptation along an isolation-by-distance gradient in Pacific cod (*Gadus macrocephalus*). Evol Appl. 2018;11(8):1448–64.
10. National Marine Fisheries Service. Fisheries of the United States, 2018. NOAA Current Fishery Statistics No. 2018. U.S. Department of Commerce; 2020. https://www.fisheries.noaa.gov/national/commercial-fishing/fisheries-united-states-2018.
11. Rand KM, Munro P, Neidetcher SK, Nichol DG. Observations of seasonal movement from a single tag release group of Pacific cod in the eastern Bering Sea. Mar Coast Fish. 2014;6(1):287–96.
12. Shimada AM, Kimura DK. Seasonal movements of Pacific cod, *Gadus macrocephalus*, in the eastern Bering Sea and adjacent waters based on tag-recapture data. Fish Bull. 1994;92:800–16.
13. Neidetcher SK, Hurst TP, Ciannelli L, Logerwell EA. Spawning phenology and geography of Aleutian Islands and eastern Bering Sea Pacific cod (*Gadus macrocephalus*). Deep Sea Res II. 2014;109:204–14.
14. Lewandoski SA, Bishop MA, McKinzie MK. Evaluating Pacific cod migratory behavior and site fidelity in a fjord environment using acoustic telemetry. Can J Fish Aquat Sci. 2018;75(11):2084–95.
15. Thorsteinsson V, Pálsson ÓK, Tómasson GG, Jónsdóttir IG, Pampoulie C. Consistency in the behaviour types of the Atlantic cod: repeatability, timing of migration and geo-location. Mar Ecol Prog Ser. 2012;462:251–60.
16. Robichaud D, Rose GA. Migratory behaviour and range in Atlantic cod: inference from a century of tagging. Fish Fish. 2004;5(3):185–214.
17. Svedäng H, Righton D, Jonsson P. Migratory behaviour of Atlantic cod *Gadus morhua*: natal homing is the prime stock-separating mechanism. Mar Ecol Prog Ser. 2007;345:1–12.
18. Neuenfeldt S, Righton D, Neat F, Wright P, Svedäng H, Michalsen K, Subbey S, Steingrund P, Thorsteinsson V, Pampoulie C. Analysing migrations of Atlantic cod *Gadus morhua* in the north-east Atlantic Ocean: then, now and the future. J Fish Biol. 2013;82(3):741–63.
19. Thompson GG, Spies IB, Palsson W. Assessment of the Pacific cod stock in the Aleutian Islands. North Pacific Fisheries Management Council; 2019. https://www.fisheries.noaa.gov/resource/data/2019-assessment-pacific-cod-stock-aleutian-islands.
20. Chittenden CM, Ådlandsvik B, Pedersen OP, Righton D, Rikardsen AH. Testing a model to track fish migrations in polar regions using pop-up satellite archival tags. Fish Oceanogr. 2013;22(1):1–13.
21. Courtney MB, Scanlon BS, Rikardsen AH, Seitz ACJA. Utility of pop-up satellite archival tags to study the summer dispersal and habitat occupancy of Dolly Varden in Arctic Alaska. Artic. 2016;69(2):137–46.
22. Hedger R, Rikardsen A, Thorstad E. Pop-up satellite archival tag effects on the diving behaviour, growth and survival of adult Atlantic salmon *Salmo salar* at sea. J Fish Biol. 2017;90(1):294–310.
23. Nielsen JK, Rose CS, Loher T, Drobny P, Seitz AC, Courtney MB, Gauvin J. Characterizing activity and assessing bycatch survival of Pacific halibut with accelerometer pop-up satellite archival tags. Anim Biotelem. 2018;6(1):10.
24. Pedersen MW, Righton D, Thygesen UH, Andersen KH, Madsen H. Geolocation of North Sea cod (*Gadus morhua*) using hidden Markov models and behavioural switching. Can J Fish Aquat Sci. 2008;65(11):2367–77.
25. Thygesen UH, Pedersen MW, Madsen H. Geolocating fish using hidden Markov models and data storage tags. In: Nielsen J, Arrizabalaga H, Fragoso N, Hobday A, Lutcavage M, Sibert J, editors. Tagging and tracking of marine animals with electronic devices. Netherlands: Springer; 2009. p. 277–93.
26. Nielsen J, Mueter F, Adkison M, Loher T, McDermott S, Seitz A. Effect of study area bathymetric heterogeneity on parameterization and performance of a depth-based geolocation model for demersal fishes. Ecol Model. 2019;402:18–34.
27. Nichol D, Chilton E. Recuperation and behaviour of Pacific cod after barotrauma. ICES J Mar Sci. 2006;63(1):83–94.
28. Zimmermann M, Prescott M, Rooper CN. Smooth sheet bathymetry of the Aleutian Islands. NOAA Tech Memo NMFS-AFSC-250. US Department of Commerce; 2013.
29. Hill RD, Braun MJ. Geolocation by light level. In: Electronic tagging and tracking in marine fisheries. Dordrecht: Springer; 2001. p. 315–30.
30. Seitz AC, Norcross BL, Wilson D, Nielsen JL. Evaluating light-based geolocation for estimating demersal fish movements in high latitudes. Fish Bull. 2006;104(4):571–9.
31. Braun CD, Galuardi B, Thorrold SR. HMMoce: an R package for improved geolocation of archival-tagged fishes using a hidden Markov method. Methods Ecol Evol. 2018;9(5):1212–20.
32. Le Bris A, Fisher JA, Murphy HM, Galbraith PS, Castonguay M, Loher T, Robert D. Migration patterns and putative spawning habitats of Atlantic halibut (*Hippoglossus hippoglossus*) in the Gulf of St. Lawrence

revealed by geolocation of pop-up satellite archival tags. ICES J Mar Sci. 2018;75(1):135–47.
33. Nielsen JK, Hooge PN, Taggart SJ, Seitz AC. Characterizing Pacific halibut movement and habitat in a marine protected area using net squared displacement analysis methods. Mar Ecol Prog Ser. 2014;517:229–50.
34. Van Der Kooij J, Righton D, Strand E, Michalsen K, Thorsteinsson V, Svedäng H, Neat FC, Neuenfeldt S. Life under pressure: insights from electronic data-storage tags into cod swimbladder function. ICES J Mar Sci. 2007;64(7):1293–301.
35. Le Bris A, Fréchet A, Galbraith PS, Wroblewski JS. Evidence for alternative migratory behaviours in the northern Gulf of St Lawrence population of Atlantic cod (*Gadus morhua* L.). ICES J Mar Sci. 2013;70(4):793–804.
36. Meager JJ, Fernö A, Skjæraasen JE. The behavioural diversity of Atlantic cod: insights into variability within and between individuals. Rev Fish Biol Fish. 2018;28(1):153–76.
37. Chapman B, Hulthén K, Brodersen J, Nilsson PA, Skov C, Hansson LA, Brönmark C. Partial migration in fishes: causes and consequences. J Fish Biol. 2012;81(2):456–78.
38. Chapman BB, Brönmark C, Nilsson JÅ, Hansson LA. The ecology and evolution of partial migration. Oikos. 2011;120(12):1764–75.
39. Paul A, Paul J, Smith R. Consumption, growth and evacuation in the Pacific cod, *Gadus macrocephalus*. J Fish Biol. 1990;37(1):117–24.
40. Urban D. Food habits of Pacific cod and walleye pollock in the northern Gulf of Alaska. Mar Ecol Prog Ser. 2012;469:215–22.
41. Comeau L, Campana S, Chouinard G. Timing of Atlantic cod (*Gadus morhua* L.) seasonal migrations in the southern Gulf of St Lawrence: interannual variability and proximate control. ICES J Mar Sci. 2002;59(2):333–51.
42. Siceloff L, Howell WH. Fine-scale temporal and spatial distributions of Atlantic cod (*Gadus morhua*) on a western Gulf of Maine spawning ground. Fish Res. 2013;141:31–43.
43. Neat FC, Bendall V, Berx B, Wright PJ, Ó Cuaig M, Townhill B, Schön PJ, Lee J, Righton D. Movement of Atlantic cod around the British Isles: implications for finer scale stock management. J Appl Ecol. 2014;51(6):1564–74.
44. Ladd C, Hunt GL Jr, Mordy CW, Salo SA, Stabeno PJ. Marine environment of the eastern and central Aleutian Islands. Fish Oceanogr. 2005;14:22–38.
45. Mordy CW, Stabeno PJ, Ladd C, Zeeman S, Wisegarver DP, Salo SA, Hunt JRGL. Nutrients and primary production along the eastern Aleutian Island Archipelago. Fish Oceanogr. 2005;14:55–76.
46. Rand KM, Lowe SA. Defining essential fish habitat for Atka mackerel with respect to feeding within and adjacent to Aleutian Islands trawl exclusion zones. Mar Coast Fish. 2011;3(1):21–31.
47. Rand K, Beauchamp D, Lowe S. Longitudinal growth differences and the influence of diet quality on Atka mackerel of the Aleutian Islands, Alaska: using a bioenergetics model to explore underlying mechanisms. Mar Coast Fish. 2010;2(1):362–74.
48. Jahncke J, Coyle K, Hunt GL Jr. Seabird distribution, abundance and diets in the eastern and central Aleutian Islands. Fish Oceanogr. 2005;14:160–77.
49. Yang M-S. Diet changes of Pacific cod (*Gadus macrocephalus*) in Alaska between 1980 and 1995. Fish Bull. 2004;102(2):400–5.
50. Livingston PA. Interannual trends in Pacific cod, *Gadus macrocephalus*, predation on three commercially important crab species in the eastern Bering Sea. Fish Bull. 1989;87(4):807–27.
51. Poltev YN, Stominok DY. Feeding habits the Pacific cod *Gadus macrocephalus* in oceanic waters of the northern Kuril Islands and Southeast Kamchatka. Russ J Mar Biol. 2008;34(5):316–24.
52. Yang M-S. The trophic role of Atka mackerel, *Pleurogrammus monopterygius*, in the Aleutian Islands area. Fish Bull. 1999;97(4):1047–57.
53. Cooper D, McDermott S. Seasonal, small-scale distribution of Atka mackerel in the Aleutian Islands, Alaska, with respect to reproduction. Mar Coast Fish. 2011;3(1):10–20.
54. Nichol D, Kotwicki S, Zimmermann M. Diel vertical migration of adult Pacific cod *Gadus macrocephalus* in Alaska. J Fish Biol. 2013;83(1):170–89.
55. Nichol DG, Honkalehto T, Thompson GG. Proximity of Pacific cod to the sea floor: using archival tags to estimate fish availability to research bottom trawls. Fish Res. 2007;86(2–3):129–35.
56. Hobson VJ, Righton D, Metcalfe JD, Hays GC. Vertical movements of North Sea cod. Mar Ecol Prog Ser. 2007;347:101–10.
57. Hunt GL, Stabeno PJ. Oceanography and ecology of the Aleutian Archipelago: spatial and temporal variation. Fish Oceanogr. 2005;14:292–306.
58. Robichaud D, Rose G. Multiyear homing of Atlantic cod to a spawning ground. Can J Fish Aquat Sci. 2001;58(12):2325–9.
59. Dean MJ, Hoffman WS, Zemeckis DR, Armstrong MP. Fine-scale diel and gender-based patterns in behaviour of Atlantic cod (*Gadus morhua*) on a spawning ground in the Western Gulf of Maine. ICES J Mar Sci. 2014;71(6):1474–89.
60. Hannah RW, Rankin PS. Site fidelity and movement of eight species of Pacific rockfish at a high-relief rocky reef on the Oregon coast. N Am J Fish Manag. 2011;31(3):483–94.
61. Kotwicki S, Buckley TW, Honkalehto T, Walters G. Variation in the distribution of walleye pollock (*Theragra chalcogramma*) with temperature and implications for seasonal migration. Fish Bull. 2005;103(4):574–87.
62. Siwicke KA, Coutré K. Periodic movements of Greenland turbot *Reinhardtius hippoglossoides* in the eastern Bering Sea and Aleutian Islands. Fish Res. 2020;229:105612.
63. Hanselman DH, Heifetz J, Echave KB, Dressel SC. Move it or lose it: movement and mortality of sablefish tagged in Alaska. Can J Fish Aquat Sci. 2015;72(2):238–51.
64. Seitz AC, Loher T, Nielsen JL. Seasonal movements and environmental conditions experienced by Pacific halibut along the Aleutian Islands, examined by pop-up satellite tags. Seattle: International Pacific Halibut Commission; 2008.
65. Ferter K, Weltersbach MS, Humborstad O-B, Fjelldal PG, Sambraus F, Strehlow HV, Vølstad JH. Dive to survive: effects of capture depth on barotrauma and post-release survival of Atlantic cod (*Gadus morhua*) in recreational fisheries. ICES J Mar Sci. 2015;72(8):2467–81.
66. Peregrin LS, Butcher PA, Broadhurst MK, Millar RB. Angling-induced barotrauma in snapper *Chrysophrys auratus*: are there consequences for reproduction? PLoS ONE. 2015;10(3):e0119158.
67. Seitz AC, Courtney MB, Evans MD, Manishin K. Pop-up satellite archival tags reveal evidence of intense predation on large immature Chinook salmon (*Oncorhynchus tshawytscha*) in the North Pacific Ocean. Can J Fish Aquat Sci. 2019;999:1–8.
68. Luo J, Ault JS, Ungar BT, Smith SG, Larkin MF, Davidson TN, Bryan DR, Farmer NA, Holt SA, Alford AS. Migrations and movements of Atlantic tarpon revealed by two decades of satellite tagging. Fish Fish. 2020;21(2):290–318.
69. Wahlberg M, Westerberg H, Aarestrup K, Feunteun E, Gargan P, Righton D. Evidence of marine mammal predation of the European eel (*Anguilla anguilla* L.) on its marine migration. Deep Sea Res I Oceanogr Res Pap. 2014;86:32–8.
70. Strøm JF, Rikardsen AH, Campana SE, Righton D, Carr J, Aarestrup K, Stokesbury MJ, Gargan P, Javierre PC, Thorstad EB. Ocean predation and mortality of adult Atlantic salmon. Sci Rep. 2019;9(1):1–11.
71. Kerstetter DW, Polovina J, Graves JE. Evidence of shark predation and scavenging on fishes equipped with pop-up satellite archival tags. Fish Bull. 2004;102(4):750.
72. Austin D, Bowen W, McMillan J, Boness D. Stomach temperature telemetry reveals temporal patterns of foraging success in a free-ranging marine mammal. J Anim Ecol. 2006;75(2):408–20.
73. Kuhn CE, Costa DP. Identifying and quantifying prey consumption using stomach temperature change in pinnipeds. J Exp Biol. 2006;209(22):4524–32.
74. Tollit D, Fritz L, Joy R, Miller K, Schulze A, Thomason J, Walker W, Zeppelin T, Gelatt T. Diet of endangered Steller sea lions (*Eumetopias jubatus*) in the Aleutian Islands: new insights from DNA detections and bioenergetic reconstructions. Can J Zool. 2017;95(11):853–68.
75. Baird RW, Hanson MB, Dill LM. Factors influencing the diving behaviour of fish-eating killer whales: sex differences and diel and interannual variation in diving rates. Can J Zool/Rev Can Zool. 2005;83(2):257–67.

Publisher's Note