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Behavior and thermal environment of Chinook salmon *Oncorhynchus tshawytscha* in the North Pacific Ocean, elucidated from pop-up satellite archival tags

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Abstract Chinook salmon are widely distributed in offshore waters of the North Pacific Ocean, and of great economical and subsistence importance; however, little is known about their oceanic ecology. To address this, we tagged 43 Chinook salmon *Oncorhynchus tshawytscha* (57–100 cm) with pop-up satellite archival tags (PSATs) in the eastern (October– December) and central Bering Sea (August) to provide insights into the oceanic movements, behavior, and thermal environment of this species. The tags retrieved data for up to 260 days and end locations of tagged Chinook salmon spanned from the central Bering Sea ($n = 6$), eastern Bering Sea/ Aleutian Islands ($n = 20$), and the Gulf of Alaska (n = 6). While at liberty, Chinook salmon occupied depths ranging from 0 to 538 m and experienced a thermal environment ranging from −0.6 to 13.5 °C. Overall, mean depths of individual fish ranged from 4.5 to 127.9 m, while median depths ranged from 1.3 to 99.5 m. Although sample sizes were not even among months of the year, Chinook salmon occupied the shallowest and warmest water in May–September and the deepest and coolest water in December–March. Diel depth-specific diving behaviors of Chinook salmon were found in some tag records, but these behaviors appeared to be variable among individuals and plastic in nature within individuals. Results from this study provide insights into movement, diving behavior and the thermal environment of individual Chinook salmon which may have future application in understanding its ecology and developing strategies to further reduce incidental catch of this species.

Keywords Behavior · Depth · Chinook salmon · Ecology · PSATs

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Introduction

Chinook salmon *Oncorhynchus tshawytscha* is an iconic species found throughout the North Pacific Ocean and supports important subsistence, commercial and recreational fisheries (Healey 1991; Quinn 2005; Riddle et al. 2018). In addition to valuable fisheries, Chinook salmon is an important food source for top marine predators including killer whales *Orcinus orca*, and many species of pinnipeds (Ford et al. 1998; Adams et al. 2016; Chasco et al. 2017). For over the past decade, Chinook salmon returns in Alaska have been in decline, which has led to restrictions in both directed fisheries and fisheries where the species is incidentally captured (Gisclair 2009; Stram and Ianelli 2009; ADF&G 2013; Ianelli and Stram 2015; Stram and Ianelli 2015).

Throughout this species' range, anadromous Chinook salmon have variable life histories (reviewed in Healey 1991; Quinn 2005; Riddle et al. 2018). Chinook salmon may rear in freshwater for less than a year (ocean type), or 1–2 years (stream type). After this juvenile rearing phase, anadromous individuals migrate to the ocean where they remain for 1–6 years, before reaching maturity and returning to their natal river to spawn. The spawning migration of Chinook salmon is variable with most northern populations (e.g., Alaska) returning in the spring (i.e., spring run), whereas southern populations may return in the spring, summer (i.e., summer run), or fall (i.e., fall run) months. Chinook salmon are semelparous and die shortly after spawning.

Although information on the basic life history of Chinook salmon is well studied, several large research initiatives are being conducted to improve the understanding of the biology and ecology of Chinook salmon, with the ultimate goal of describing the ongoing/widespread decline in abundance and productivity (ADF&G 2013; Schindler et al. 2013). While many factors may be partially responsible, the species' decline is commonly linked to its oceanic phase, a part of life about which little is known (Schindler et al. 2013). This relative lack of knowledge results from the extensive focus on freshwater juvenile and spawning phases of Chinook salmon, and the high costs and logistical challenges associated with conducting research in the open ocean. Thus information about the ocean migration of Chinook salmon is largely limited to the first year at sea (ocean age 0–1) when individuals are relatively close to shore, despite the fact that individuals may reside in the ocean for up to 6 years (Brodeur et al. 2000; Drenner et al. 2012; Riddle et al. 2018).

The existing information about the oceanic movements, ecology, and habitat occupancy of large growing (e.g., ocean age 2+) Chinook salmon in the North Pacific has been inferred from coded wire tag recoveries, scale pattern analyses, genetic analyses, historic high-seas fisheries, bycatch in other fisheries, limited offshore research programs on other Pacific salmon species, and lab-based research on navigational behaviors of salmon (Myers and Rogers 1988; Myers et al. 2009; Weitkamp 2010; Larson et al. 2013; Putman et al. 2014; Sato et al. 2015). Currently, it is thought that oceanic migrations and spatial distribution of Chinook salmon are largely influenced by life history type (e.g., stream and ocean type), and region of origin. However, there is believed to be large spatial overlap in the stock-specific oceanic distributions of Chinook salmon (Trudel et al. 2009; Weitkamp 2010; Larson et al. 2013). For example, Chinook salmon from many regions, including Russia, Alaska, British Columbia, and the U.S. Pacific Northwest are thought to commonly use the Bering Sea as a summer foraging area (Larson et al. 2013). After feeding there, Chinook salmon from central Alaska to the U.S. Pacific Northwest then make southerly movements to overwinter in the North Pacific Ocean south of the Aleutian Islands or the Gulf of Alaska, whereas Chinook salmon from western Alaska are thought to reside in the Bering Sea year-round (Larson et al. 2013). Although past research has provided these generalized movement patterns, to date, fine-scale movements and habitat occupancy of Chinook salmon in the Bering Sea are not well understood (Walker et al. 2007; Walker and Myers 2009).

Knowledge of several aspects of the oceanic phase of large Chinook salmon, including movement, vertical distribution, and thermal environment may provide important information to address basic and applied research questions. For example, information on this species' migration patterns and their vertical movements can inform life history models that are used to understand population dynamics of fishes (Brodeur et al. 2000; Hinke et al. 2005a). Furthermore, additional information about the ecology and behaviors of large Chinook salmon in the ocean may provide information to help address applied research questions such as quantifying vulnerability to various fishing techniques (e.g., bottom and midwater trawls), and to design spatially explicit fisheries management practices, such as time-area closures, for avoiding bycatch of this species (Smedbol and Wroblewski 2002; Hobday et al. 2010). For example, in some years, Chinook salmon are incidentally captured in significant numbers in the U.S. walleye pollock *Gadus chalcogrammus* trawl fishery in the eastern Bering Sea, which has led to much economic and sociocultural distress among several stakeholders, particularly in rural western Alaska (Gisclair 2009; Stram and Ianelli 2009; Ianelli and Stram 2015; Stram and Ianelli 2015). Given this, the U.S. walleye pollock fishery industry and management agencies are currently seeking to gather information to develop methods and/or regulatory actions to reduce Chinook salmon bycatch.

Pop-up satellite archival tags (PSATs) which record environmental variables while attached to an animal are a method to collect detailed information about the oceanic dispersal, behavior, and habitat occupancy of fish (Arnold and Dewar 2001; Musyl et al. 2011; Thorstad et al. 2013). On a preprogrammed date, the tag releases from the fish, floats to the surface of the water and transmits data to satellites, which are then retrieved by project investigators. Because PSATs do not rely on recapture for data retrieval, they are a fisheries independent method of data collection. Fisheries independent technology is critically important for understanding the oceanic habits of Chinook salmon near western Alaska, because there are currently no offshore directed fisheries or research programs for this species in the Bering Sea. Therefore, the objective of this study was to use PSATs to provide insights into oceanic distribution, movements, behavior, and thermal environment of Chinook salmon in the Bering Sea.

Methods

Fish capture and tagging

Chinook salmon in this study were captured by either hook and line or trawl. For winter sampling, in late October to December in 2013–2015 and 2017, 30 Chinook salmon were captured by hook and line, and tagged and released from a sportfishing vessel, the FV *Lucille*, near Dutch Harbor, AK in the eastern Bering Sea (Fig. 1). For summer sampling in early August 2014 and 2015, 13 Chinook salmon were captured, tagged, and released from the RV *Hokko maru* in the central Bering Sea (Fig. 1). During this summer sampling, Chinook salmon were captured using a mid-water trawl that contained a live box cod end ($n = 6$) and by hook-and-line ($n = 7$). Based on past genetic analyses, it is likely that we tagged fish from several different stocks, as Chinook salmon captured in the Bering Sea commonly originate from many regions, including Russia, Alaska, British Columbia, and the U.S. Pacific Northwest (Larson et al. 2013). However, the stock-origin of captured fish in this study was unknown. Complete information about tag deployments can be found in supplementary material (Table S1).

Immediately after capture, Chinook salmon were examined and deemed appropriate for tagging if they were > 55 cm fork length (FL), had no visible bleeding or large external injuries, nor were fin-clipped (indicating hatchery origin from outside of western Alaska). For tagging, Chinook salmon were carefully removed from the water of the ocean or the live box with a knotless-mesh dipnet and placed in a custom-fabricated tagging cradle that contained flowing sea water. PSATs were attached to Chinook salmon using a "tag backpack" system described in Courtney et al. (2016) and Hedger et al. (2017b). After a PSAT was secured to a fish, it was immediately released headfirst into the ocean. Global Positioning System coordinates at the time of release were used as a fish's tagging location. All fieldwork was conducted under an University of Alaska Fairbanks Institutional Animal Care and Use Committee assurance (495247) and State of Alaska Fisheries Resource Permits (CF-13-110, CF-14-112, CF-15-125, and CF-17-110).

Tag and data specifications

PSATs used in this study were either the X-tag ($n = 22$) or HR X-tag ($n = 1$) manufactured by Microwave Telemetry (http://www.microwavetelemetry.com), or MiniPATs (n = 20) manufactured by Wildlife Computers (https://wildlifecomputers.com/). In general, while attached to a fish, the tags measured and recorded depth, temperature and ambient light intensity at preprogrammed rates. Tags were programmed to release from the Chinook salmon on preprogrammed dates 0.5–12 months after release into the ocean or if a tag remained at a constant pressure (±2.5 m depth) for a period of 2–7 days, indicating either death and sinking to the sea floor, or detachment from the fish and floating on the ocean surface. After releasing from the fish, the tags floated to the surface of the sea and transmitted the archived data to satellites (Argos Satellite System). While transmitting, the location of each tag was determined from the Doppler shift of the transmitted radio frequency in successive uplinks received during one satellite pass (Keating 1995). The end locations of tagged fish were considered as the first transmission with an Argos location class ≥1, indicating an accuracy of at least 1.5 km.

In this study, X-tags and the HR X-tag recorded data every two minutes, whereas MiniPATs recorded data every 3–15 s. However, because of the large amount of data collected by the tags, limited data reception by Argos satellites, and short tag-battery life while transmitting to satellites, only a subset of temperature and depth data were transmitted by the tags. This subset of

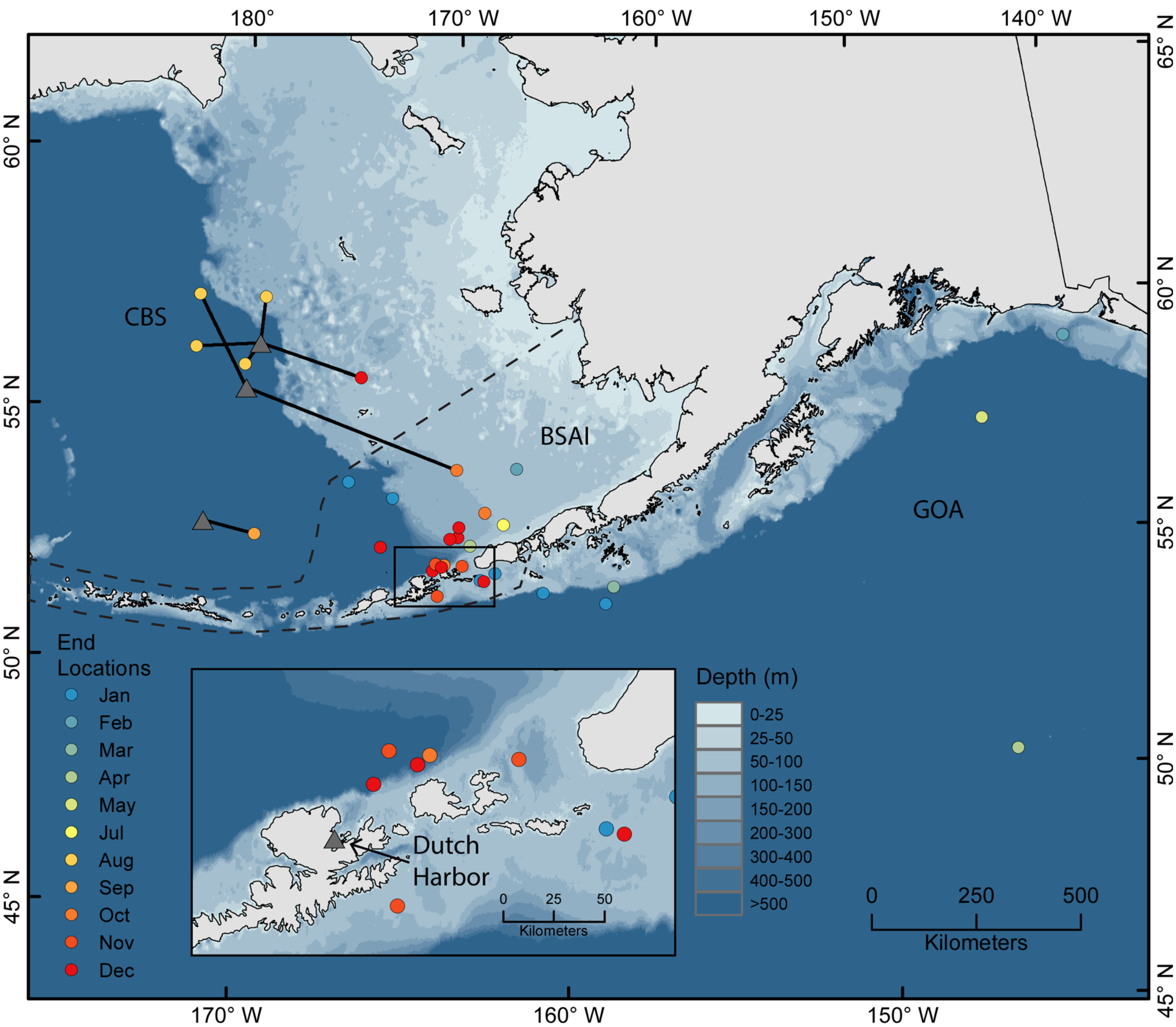


Fig. 1 All tagging locations (triangles) and end locations (circles; n = 32) of pop-up satellite archival tagged Chinook salmon tagged in Dutch Harbor during October to December and in the central Bering Sea (CBS) in August. Solid black lines connect tagging and pop-up locations for interpretive purposes, but do not represent likely movement paths. Aggregations of end locations are delineated (dashed lines) by geographic regions, including the CBS, eastern Bering Sea/Aleutian Islands (BSAI) and Gulf of Alaska (GOA)

depth and temperature data was every 15 min for X-tags, two minutes for the HR X-tag, and 5–10 min for MiniPATs. Additionally, daily summaries of minimum and maximum depths and temperature experienced by each tagged fish were provided. For MiniPATs, an onboard algorithm identified daily dawn and dusk events and the corresponding light intensity data were transmitted for post processing. In contrast, X-tags provided daily geolocation estimates of latitude and longitude using the tag manufacturer's onboard proprietary software during post-processing of transmitted data. The HR X-tag ($n = 1$) did not provide daily geolocations.

Data analyses

To classify the individual fate of tagged Chinook salmon, time-series data for each tag's entire time at liberty were plotted and visually examined. Premature release of a tag from a live fish was inferred when depth and temperature records suggested the tagged fish was alive immediately before the tag detached from the fish before the pre-programmed date and read a constant depth of 0 m for days before transmitting data. Predation was inferred from anomalous depth (i.e., abrupt change in depth-based behavior), temperature (abrupt increase above ambient) and/or light intensity readings (complete darkness during periods of daytime), and is presented in detail in a companion manuscript (Seitz et al. 2019). Similar to past research, these anomalous readings were interpreted as consumption of a tagged fish by an endothermic or ectothermic predator, after which the tag was expelled, floated to the surface of the ocean and transmitted data (e.g., Béguer-Pon et al. 2012; Lacroix 2014; Wahlberg et al. 2014; Strøm et al. 2019). Unknown mortality was inferred when a tag had a constant depth > 0 m, which is interpreted as the fish being killed and subsequently all or part of it sinking to the sea floor before the tag detached from the carcass, floated to the surface and transmitted data to satellites.

To provide insights into horizontal movement of Chinook salmon, minimum displacement of each tagged fish was determined by calculating the great arc circle distance of a non-meandering route that did not pass over land between tagging and end locations, in GIS software (ArcMap 10.1; Environmental Systems Research Institute Inc., Redlands, California). Additionally, for tagged Chinook salmon at liberty for >30 days, individual most likely movement paths were reconstructed using a hidden Markov model (HMM) approach. HMMs are non-parametric state-space models that consist of a two-step forward filter that combines an underlying movement scheme with the data recorded by the tag, and a backward smoothing step, which ensures serial dependency in the time series (Pedersen 2010). The 30 day cut-off was used because the error associated with movement tracks of short duration may exceed the horizontal displacement or may not be informative if the tagged fish remained near the tagging location (Musyl et al. 2011; Braun et al. 2015; Braun et al. 2018). For MiniPATs, Wildlife Computers' proprietary HMM embedded in postprocessing software (WC-GPE3, Wildlife Computers 2015) was used, which employs observations of twilight, sea surface temperature (NOAA OI SST V2 High Resolution), and bathymetry (ETOP1-Bedrock; https://www.ngdc.noaa.gov/mgg/global/) to generate time-discrete and gridded (0.25° by 0.25°) probability distributions to estimate the most likely daily positions (Wildlife Computers 2015). For X-tags, a HMM developed for Atlantic salmon *Salmo salar* was used that generates daily probability distributions on an equidistant grid based on temperature (NOAA OI SST V2 High Resolution), bathymetry (ETOP1-Bedrock; https://www.ngdc.noaa.gov/mgg/global/), and a filtered subset of longitude estimates (described in Strøm et al. 2017). Based on these time-series of daily probability distribution, individual migration routes were estimated as the mean of 1000 random tracks sampled through a backward sweep (Thygesen et al. 2009). In both models, a maximum daily swim speed of 100 km·day^{-1} was assumed and a qualitative comparison revealed similar movement paths when applying the two models.

To provide insights into the behavior and thermal environment of Chinook salmon, each fish's occupied depth and temperature were examined by inspecting time series data, and by determining minimum, maximum, mean, median (±SD) occupied depths and temperatures. Additionally, the mean (±SD) proportion of time that that all tagged Chinook salmon spent at depth and temperature intervals was calculated by month and by each region. The assignment of data to regions was based on deployment and pop-up locations, as well as dates of changing regions (i.e., central Bering Sea, Bering Sea/Aleutian Islands, Gulf of Alaska), as identified by the HMMs.

To examine potential diel differences in the occupied depths of Chinook salmon, daily night (nocturnal), day (diurnal) and twilight (sun 0–18° below earth's horizon) periods were determined for each tag record (http://aa.usno.navy.mil/data/docs/RS_OneDay.php). Subsequently, the depths occupied during each of these periods were visually examined for qualitative differences. During some time periods for individual fish, periods of diel behaviors were evident, so to quantitatively examine differences between diel depth distributions for each tag record, a Wilcoxon signed rank test using paired diel means for each day was used ($\alpha = 0.05$).

Results

Summary

Tagged Chinook salmon were 57–100 cm fork length (72.1 ± 9.7 cm, mean ± SD) and were at liberty up to 260 days (Table S1). Of the 43 tags deployed, 35 (81.4% of the total 43) reported to satellites, one (2.3% of the total 43) provided an end location but no data, and seven (16.3% of the total 43) never transmitted and were considered missing (Table S1). Of the 35 tags that successfully transmitted to satellites, four reported on the scheduled pop-up date. The remaining tags reported prematurely: five were premature releases from fish assumed to be alive; 19 had depth, temperature, and light readings associated with predation by a marine predator; and seven were associated with unknown mortality events (described in Seitz et al. 2019). Data from these predation/mortality events were removed from all analyses and as such, only data from before mortality events were used for movement, behavior and temperature analyses. Furthermore, two of the seven unknown mortality events occurred immediately after release into the ocean. Because it is likely that these mortality events were due to the capture and tagging process, these records were removed from all analyses. Another tag provided low data return (5% of the hypothetical data that should have been available) and was also excluded from analyses.

For individual tags whose data were used in aggregated analyses ($n = 32$), the percentage of the complete data records received by Argos satellites varied between 31 and 93% (74.3 ± 20.1%, mean ± SD; data resolution = 2–15 min). The number of data sets available for analyses varied seasonally, with most data recorded during October to January (Fig. 2).

Horizontal movement

End locations of tagged Chinook salmon were in the central Bering Sea ($n = 6$), eastern Bering Sea/Aleutian Islands ($n = 20$), and the Gulf of Alaska (n = 6; Fig. 1). Of the tags deployed in the central Bering Sea during August, end locations and the most likely movement paths of individual fish suggested that they remained in the vicinity of this region or made easterly movements to the eastern Bering Sea by the onset of fall (Fig. 1; Fig. 3a, c). For example, the most likely path of one tagged fish suggested that it occupied the central Bering Sea for the entire duration (August–January; 150 days at liberty) of its deployment (Fig. 3a) while traveling extensively (track length = 2354 km; minimum dispersal = 256 km). In contrast, one tagged Chinook salmon migrated easterly to the eastern Bering Sea shelf by early September, and reported 545 km away in late-October while traveling less extensively (Fig. 3b; track length = 980 km).

For Chinook salmon tagged during the winter near Dutch Harbor, AK, end locations and most likely movement paths demonstrated that the majority remained in the southeastern Bering Sea/Aleutian Islands, regardless of their time at liberty (Fig. 1, Fig. 4). For example, the most likely path of one tagged Chinook salmon that was at liberty for 260 days suggested that this fish remained in the eastern Bering Sea Shelf from its deployment in November to its pop-up date in July (Fig. 5b; track length = 2581 km). In contrast to the Chinook salmon tagged in the eastern Bering Sea/Aleutian Islands that remained in these waters during the deployment period, six fish migrated eastward to the Gulf of Alaska (Figs.1, 4a, 5). Based on their most likely movement paths, five of these tagged fish exited the Bering Sea during the months of December and January (Fig. 5a, c; tracks lengths = 2123–2345 km), while one fish exited the Bering Sea in late March (Fig. 5b; track length = 2937 km). The most likely movement paths of these fish suggested that the migration of five of these fish followed the continental shelf (Fig. 5c), while one individual transited through and occupied offshore basin waters of the Gulf of Alaska (Fig. 5a).

Depth and temperature occupancy

While at liberty, Chinook salmon occupied depths ranging from 0 to 538 m and experienced a thermal environment ranging from −0.6 to 13.5 °C (Fig. 2). Overall mean depths of individual fish ranged from 4.5 to 127.9 m (53.0 ± 30.4 m; grand mean ± SD), while median depths ranged from 1.3 to 99.5 m (48.3 ± 31.4, grand median ± SD; Table S1). Although sample sizes were not even among months of the year, in general, Chinook salmon occupied the shallowest and warmest water in May–September and the deepest and coolest water in December–March (Fig. 2b, c).

While Chinook salmon occupied waters of the central Bering Sea during late summer and early fall they were highly surface oriented (Figs. 2a and 3). Individual maximum depths ranged from 38 to 285 m, with mean and median depths of individual fish ranging from 4.4 to 45.6 m (15.1 ± 14.4 m; grand mean ± SD) and 1.3 to 48.4 m (4.0 ± 16.8 m; grand median ± SD), respectively. Overall, these tagged fish, generally experienced a stratified thermal environment from August to September (Fig. 3a). By mid-October, diving depths increased as waters became increasingly isothermal (Fig. 3a).

While occupying waters of the eastern Bering Sea/Aleutian Islands from November to July, fish spent approximately 45% of their time within the upper 50 m of the water column (Fig. 2a). Overall mean and median occupied depths of individual fish ranged from 18.2 to 97.2 m (59.1 ± 24.1 m; grand mean ± SD) and 6.7 to 105.0 m (61.1 ± 28.5;

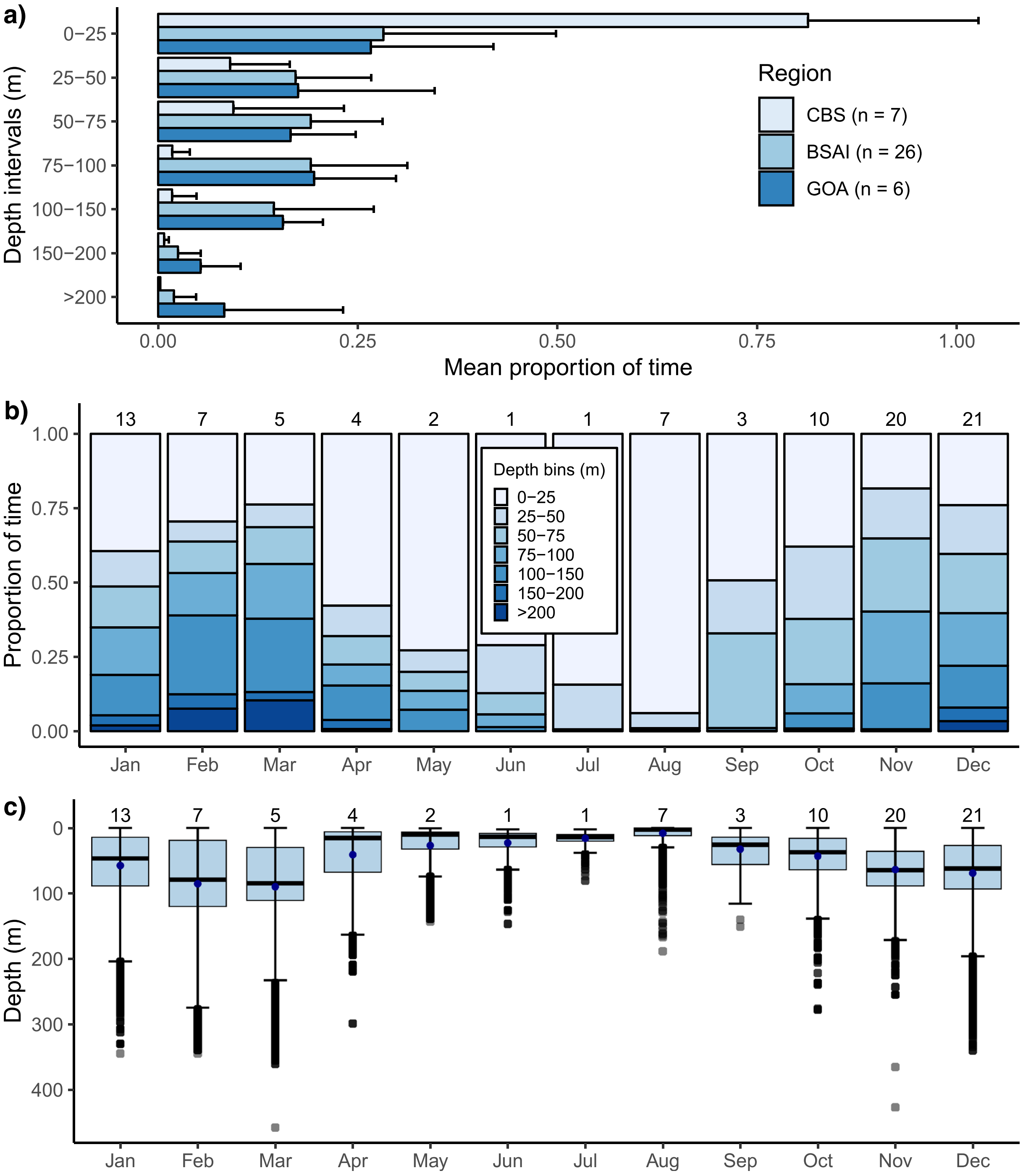


Fig. 2 **a** Aggregated regional mean proportion of time spent at discrete depth bins of Chinook salmon tagged with pop-up satellite archival tags in the Bering Sea. **b** Aggregated monthly proportion of time spent in discrete depth bins, and (**c**) seasonal trends in depth distribution. For plot (**a**), whiskers represent the standard deviation of individual means. For boxplots (**c**), median diving depths are solid lines, means are blue dots, and boxes represent the first and third quartiles. Whiskers represent the largest observation less than or equal to the box, plus or minus 1.5 times the inter-quartile range, and black dots represent outliers. The number of unique PSATs used for analyses are noted in each respective panel. CBS = central Bering Sea, BSAI = Bering Sea/Aleutian Islands, GOA = Gulf of Alaska

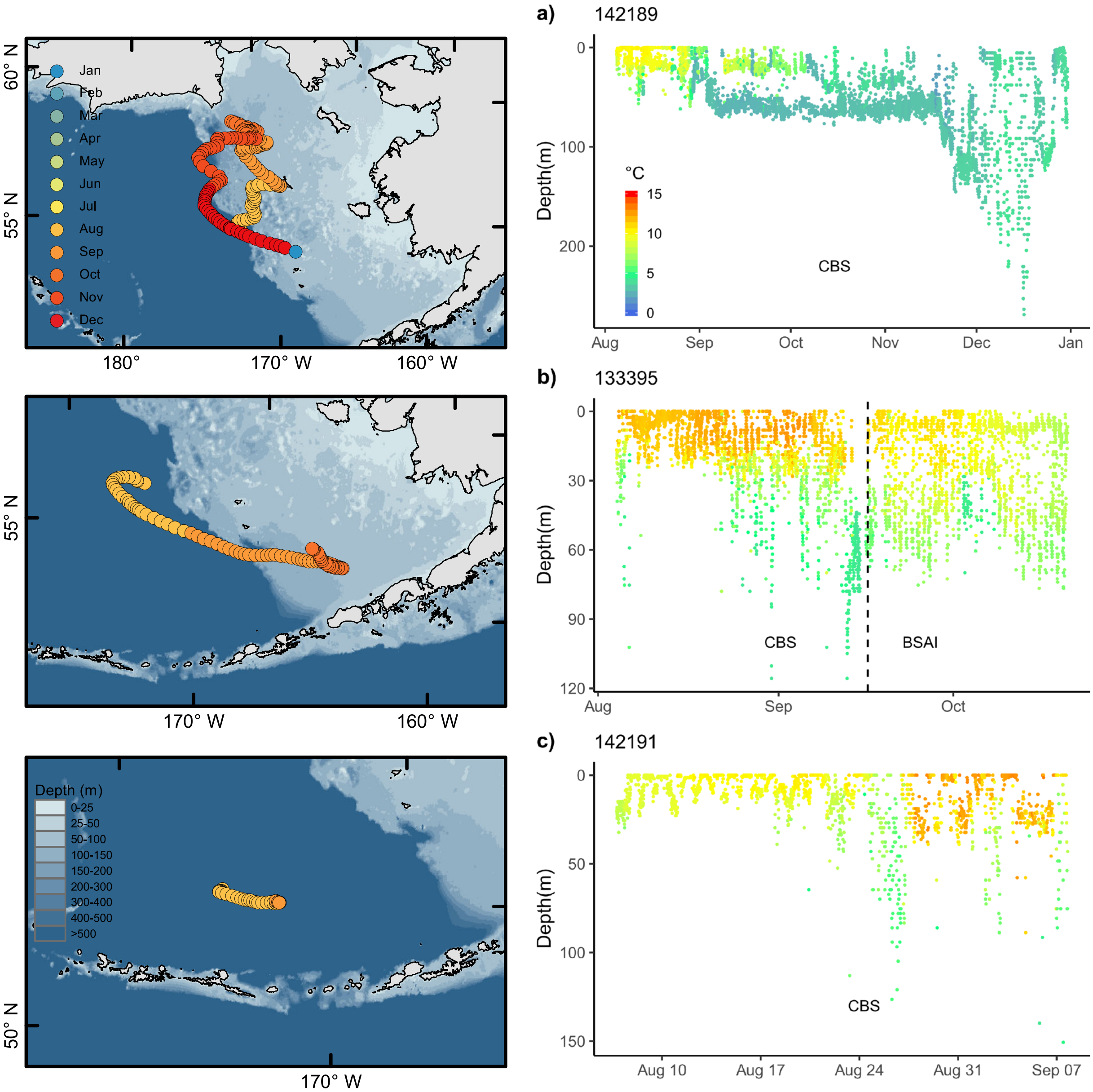
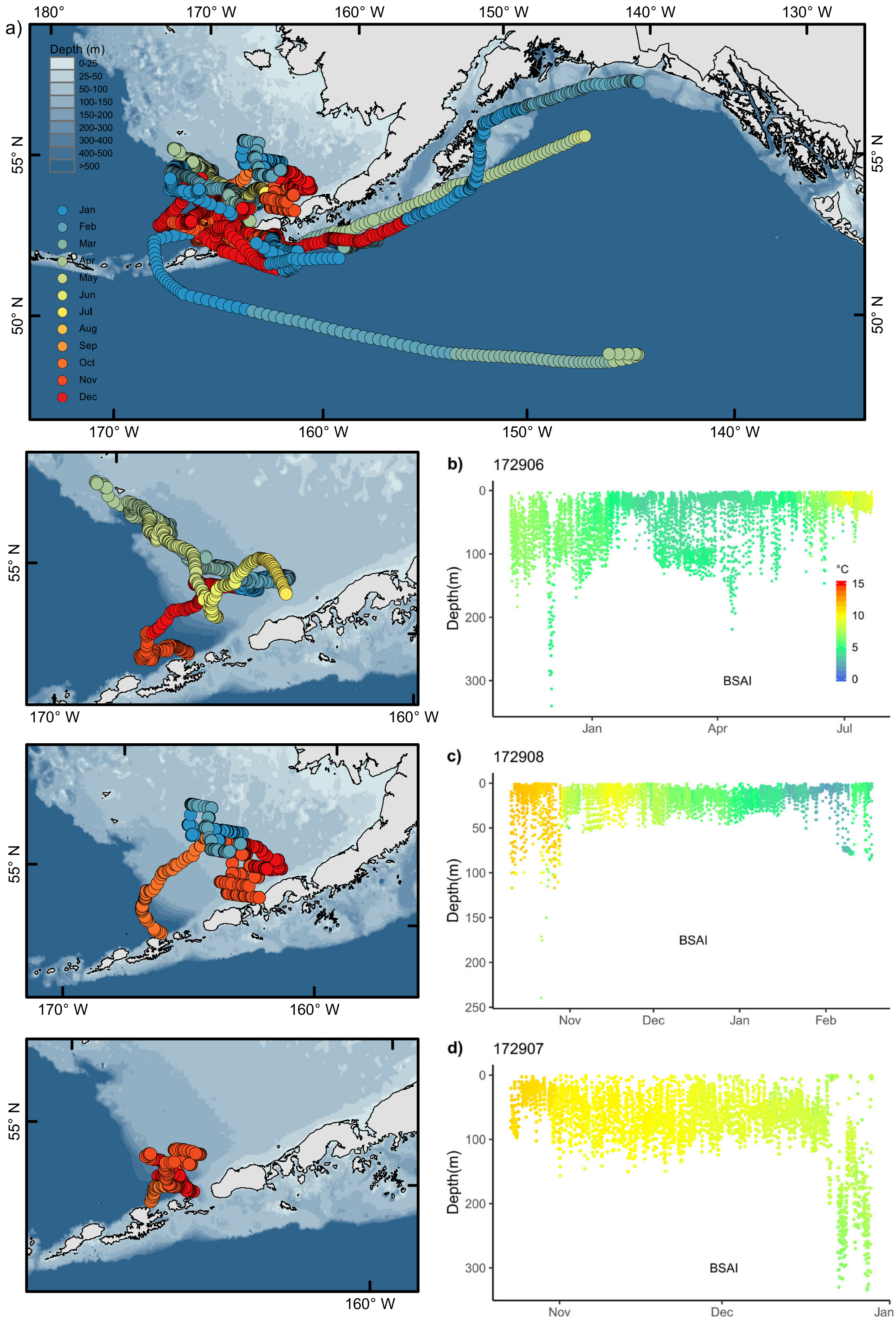


Fig. 3 Most likely paths produced by a hidden Markov model (left) and temperature at depth (right) of three tagged Chinook salmon in the central Bering Sea in August 2015 that were at liberty >30 days. Tag identification numbers are noted in respective panels and correspond to those given in Table S1. Vertical dashed lines in depth and temperature time series represent the time of transition between geographic regions. CBS = central Bering Sea, BSAI=Bering Sea/Aleutian Islands

grand median ± SD), respectively. Diving behavior varied substantially among individual tagged fish, but most occupied depths near the surface daily, and dives to >80 m were common, with maximum depths ranging from 81 to 480 m. In contrast to these general behaviors, one tagged fish occupied depths of 0 to 50 m for nearly its entire tag deployment from early-October to mid-February

Fig. 4 **a** Most likely movement paths produced by a hidden Markov model for Chinook salmon ($n = 18$) tagged in the eastern Bering Sea/Aleutian Islands (BSAI) that were at liberty for at least 30 days. **b**, **c**, **d**) Examples of individual most likely movement paths (left) and temperature at depth (right) of Chinook salmon which were inferred to have remained in the eastern Bering Sea. Tag identification numbers are noted in respective panels and correspond to those given in Table S1 ▶


a)
180°
170° W
160° W
150° W
140° W
130° W
Depth (m)
0-25
25-50
50-100
100-150
150-200
200-300
300-400
400-500
>500
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
55° N
50° N
b)
172906
Depth(m)
°C
15
10
5
0
BSAI
Jan
Apr
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Dec
Jan
170° W
160° W

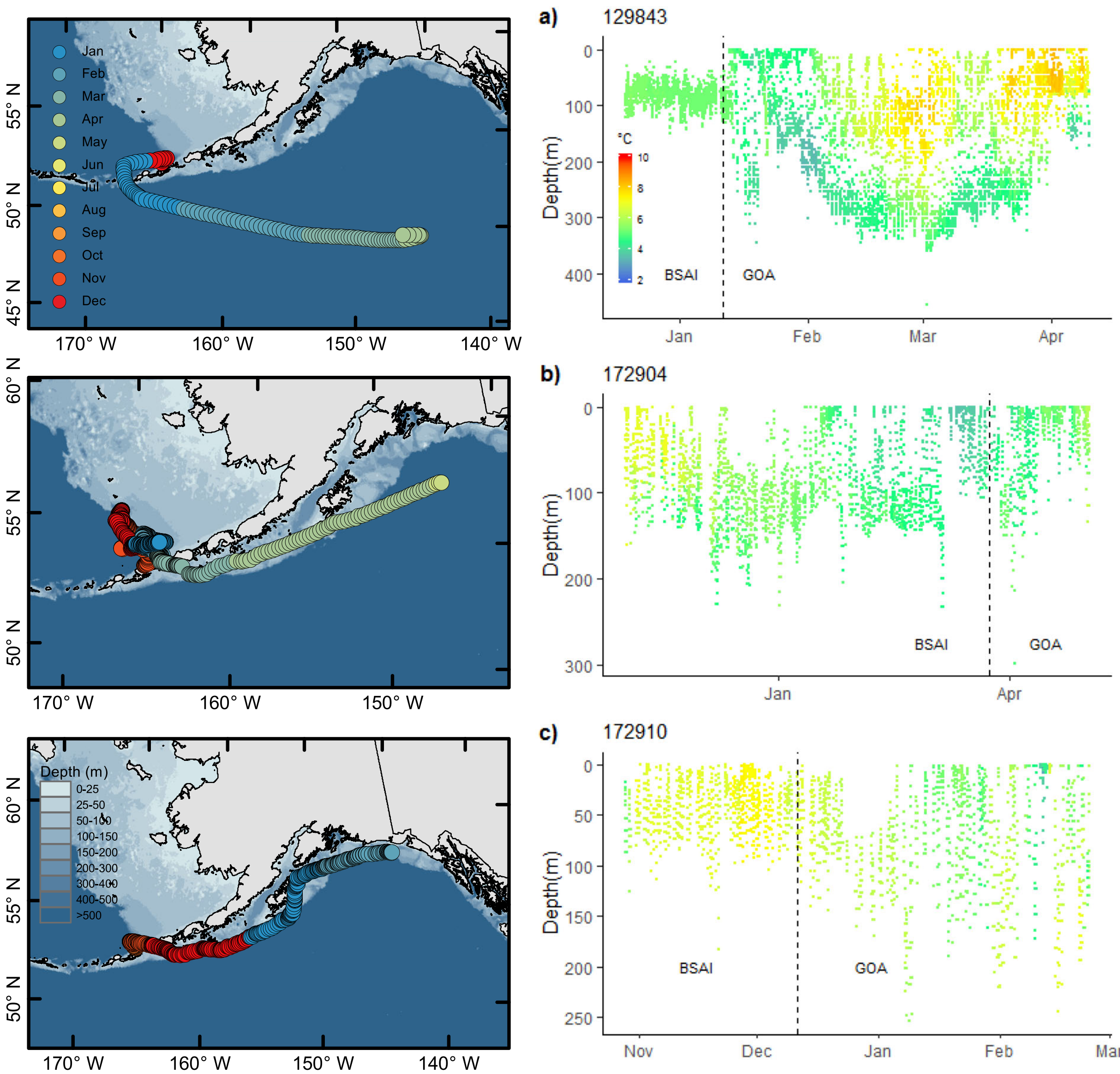

Fig. 5 Most likely paths produced by a hidden Markov model (left) and temperature at depth (right) of tagged Chinook salmon whose tags reported in the Gulf of Alaska (GOA). Tag identification numbers are noted in respective panels and correspond to those given in Table S1. Vertical dashed lines in depth and temperature time series represent the time of transition between geographic regions. BSAI = Bering Sea/Aleutian Islands

(Fig. 4c) and four other tagged fish remained exclusively at ~50–150 m deep during their times at liberty during November–January. In the eastern Bering Sea/Aleutian Islands, tagged fish generally experienced a stratified thermal environment of ~5–10 °C from early June to mid-November, after which their thermal environment became increasing isothermal (~4–6 °C) from early-November to late-May.

In general, tagged Chinook salmon occupied deeper water while in the Gulf of Alaska from January to May (maximum depths ranged from 76 to 538) compared to those in the eastern Bering Sea/Aleutian Islands during the same season. When present in the Gulf of Alaska, individual mean and median depths were 29.6–139.5 m (71.1 ± 38.3 m; grand mean ± SD), and 22.5 to 123.7 m (70.2 ± 37.3 m; grand median ± SD) respectively, and tagged fish experienced a thermal environment ranging from 2.8–9.4 °C.

For individual tagged fish, diel differences in depth distributions were detected in 19 of 32 tag records (median paired difference range 2.1–106.8 m; $\alpha = 0.05$). However, these differences were not consistent as nine tagged fish had deeper mean depths during the day compared to night, while the opposite was true for 10 individuals. Qualitative analyses documented that some Chinook salmon occupied deeper waters and exhibited greater diving activity during the day compared to periods of night, others demonstrated the opposite behavior, and finally others displayed no diel trends. Some tagged fish switched among behaviors on time scales of days to months during their time at-liberty (Fig. 6). However, visually identified diel patterns of depth occupation showed no qualitatively consistent association with geographic area, season, or even month, as behaviors of tagged fish occupying similar regions during the same season varied widely.

Discussion

The current study provides detailed insights into the individual movements, behaviors, and thermal environment of multiple Chinook salmon on continuous time scales spanning 0.5–8.5 months. While in the ocean, dependent on season and geographic location, Chinook salmon displayed a wide range of vertical movement patterns, which can be used to make inference about the oceanic ecology of this species. Furthermore, information on the spatial distribution of Chinook salmon may be used to address important management issues in the North Pacific Ocean.

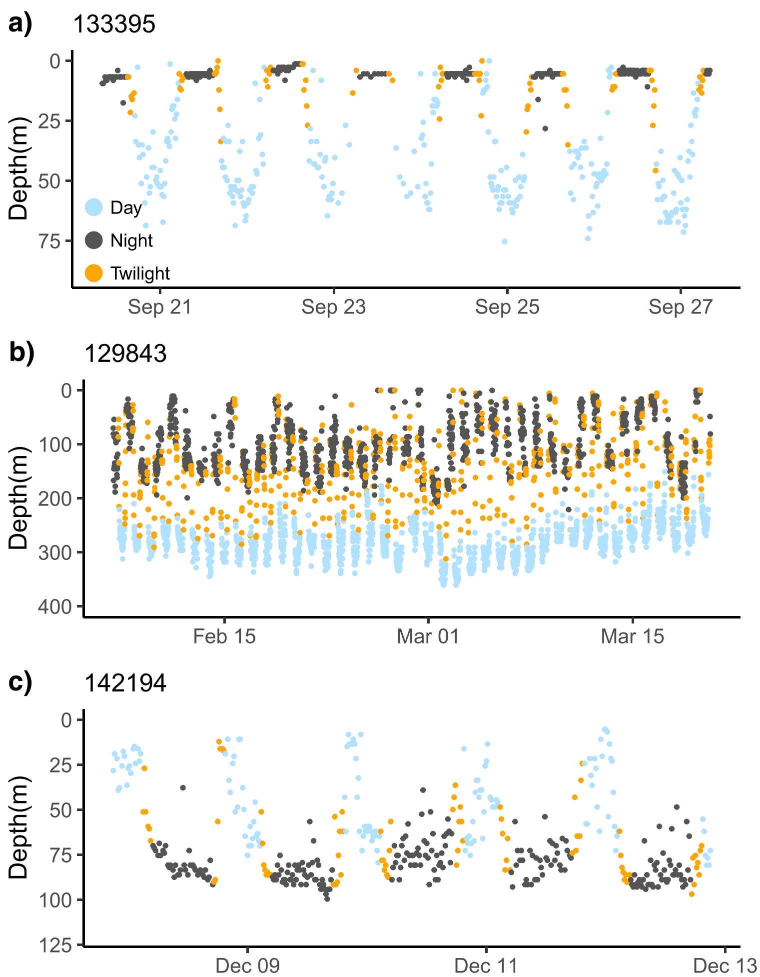

Fig. 6 Zoomed examples of differences in diel depth occupation in which the tagged Chinook salmon occupied deeper depths during the daytime (**a**, **b**) or nighttime (**c**). Tag identification numbers are noted in respective panels and correspond to those given in Table S1

Horizontal movement

Most Chinook salmon tagged in the eastern Bering Sea/ Aleutian Islands during winter resided in this area throughout the winter months. Furthermore, there was a tendency for fish tagged in the central Bering Sea during summer to make southerly movements to the eastern Bering Sea at the onset of fall. The affinity for tagged fish to occupy the eastern Bering Sea highlights the importance of these waters as overwintering habitat for Chinook salmon (Walker and Myers 2009; Larson et al. 2013). The importance of this region is likely a result of its high productivity that is stimulated by the northward transport of well-mixed nutrient-rich waters through the Aleutian passes to the eastern Bering Sea shelf (Stabeno et al. 1999; Stabeno et al. 2001; Stabeno et al. 2016). Although the factors that shape the overwintering spatial distribution of Chinook salmon are complex (Myers et al. 2016), the seasonal movements documented in this study likely reflect behaviors to maximize growth, by maximizing interactions with suitable prey fields and minimizing metabolic costs by seeking cool waters in times of low prey availability (Davis et al. 2009a; Walker and Myers 2009; Riddle et al. 2018).

The variation in movement distances and directions of individual tagged fish between tagging and end locations is likely explained by an interaction between the time of year of tagging and the stock-of-origin of each tagged fish. Based on genetic analyses, Chinook Salmon captured in the Bering Sea commonly originate from Russia, Alaska, British Columbia, and the U.S. Pacific Northwest (Larson et al. 2013). It is thought that immature individuals from these regions utilize similar foraging areas in the central and eastern Bering Sea during summer (Larson et al. 2013). After feeding, Chinook salmon natal to central Alaska to the Pacific Northwest migrate south to overwinter in the North Pacific Ocean south of the Aleutian Islands and the Gulf of Alaska (Healey 1991; Myers et al. 2009; Larson et al. 2013). In contrast, Chinook salmon from western Alaska are thought to reside in the Bering Sea year-round. While present in these waters, fish from western Alaskan are thought to summer in the central Bering Sea shelf and basin, and overwinter above the eastern Bering Sea shelf. Given the differences in movement patterns among fish from different stocks and that we likely tagged fish from several stocks, it is probable that the tagged Chinook salmon that left the Bering Sea during winter were natal to a river outside of western Alaska. Specifically, the fish whose tags reported from the central Gulf of Alaska may have been swimming back to their natal rivers in British Columbia or the U.S. Pacific Northwest, based on their direction of travel. The corollary that fish that remained in the Bering Sea were from western Alaska is not necessarily true, as many of the tags were attached to these fish for short durations. As such, these tag deployments did not coincide with times that Chinook salmon were likely to move from the Bering Sea to the Gulf of Alaska, and therefore it is difficult to speculate on their natal rivers.

Based on most likely movement paths of individual tagged fish, Chinook salmon that feed in the Bering Sea, but are natal to more southerly rivers, may initiate their return migration in the middle of winter, ~4–7 months prior to freshwater river entry. To date, little information exists about the timing and duration of the return migration of Chinook salmon to their natal rivers, although it is thought that it is less directed and longer in duration compared to that of other salmonids such as chum salmon *O. keta* and sockeye salmon *O. nerka* (Quinn 2005).This assumed type of return migration to natal rivers by Chinook salmon is thought to reflect intense foraging behaviors on the homeward migration (Quinn 2005). The depth records showing regular, oscillatory diving behavior, which has been inferred as foraging behavior for many pelagic fish species (e.g.,Wilson and Block 2009), and relatively short daily travel of individual Chinook salmon transiting across the Gulf of Alaska support this assumed return migratory behavior of intense feeding while transiting.

Depth and temperature occupancy

Chinook salmon occupied a broad range of depths, with pronounced seasonal shifts. The pattern of shallow water occupancy during the summer followed by a transition to deeper, cooler, and isothermal waters during winter is corroborated by previous research in the Bering Sea and off the coast of Oregon and California using electronic archival tags (Hinke et al. 2005a; Walker and Myers 2009). Thus, these changes in depth distribution appear to be conserved across the range of Chinook salmon and likely reflect seasonal changes in stratification of the water column, and the distribution and abundance of prey that occur throughout the North Pacific Ocean (Stabeno et al. 2001; Hinke et al. 2005a; Walker and Myers 2009). Similarly, changes in the stratification of the water column has been suggested to shape the foraging behavior of other pelagic fish species, such as Atlantic salmon and Atlantic bluefin tuna *Thunnus thynnus* (Walli et al. 2009; Hedger et al. 2017a; Strøm et al. 2018;). For example, electronic archival tags have documented a preference for Atlantic bluefin tuna to conduct short and shallow dives when waters are strongly stratified, and also to spend less time above the thermocline when water is weakly stratified (Walli et al. 2009). This behavior has been proposed as a behavior to maximize encounters with prey, which may be densely aggregated in surface waters during times of high stratification.

Chinook salmon are opportunistic foragers, and as such, the seasonal changes in patterns of occupied depths and temporal diving behaviors may reflect changes in diet and/or flexible foraging strategies. During the summer months in the Bering Sea, when tagged fish were found to occupy relatively shallow waters, Chinook salmon diets are typically composed of forage fishes, including juvenile walleye pollock and Pacific sandlance *Ammodytes hexapterus*, as well as invertebrates including several species of zooplankton and cephalopods that typically inhabit relatively shallow water (Davis et al. 2005; Davis et al. 2009b). In contrast, during the winter, Chinook salmon diets switch almost exclusively to cephalopods, including master armhook squid *Berryteuthis magister* and shortarm gonate squid *Gonatus kamtschaticus,* which are typically patchily distributed and occur at high densities at greater depths (Arkhipkin et al. 1998; Davis et al. 2009a). Flexible feeding strategies have been documented for many pelagic fish species, and this plasticity is likely important for Chinook salmon which may migrate across large geographic areas during this species' oceanic phase (Walli et al. 2009; Strøm et al. 2018).

In general, diel depth-specific diving behaviors of Chinook salmon appeared to be variable both within and among individuals, and did not appear to be related to the season of the year. The variable and discontinuous occurrence of diel diving behaviors are similar to that of the only other electronic tagged Chinook salmon ($n = 3$) in the central Bering Sea (Walker and Myers 2009; Walker unpublished data) and Southeast Alaska (Murphy and Heard 2001; Murphy and Heard 2002). Further south, studies on Chinook salmon off the coast of Oregon, California, and the Salish Sea have all suggested that the presence/absence of diel vertical behaviors is correlated to multiple factors, including season and geographic location (Hinke et al. 2005b; Arostegui et al. 2017), which may be driven by foraging, thermoregulation, and/or predator avoidance.

Chinook salmon in this study experienced a wide range of temperatures while occupying waters of the Bering Sea and Gulf of Alaska. As a result, Chinook salmon may not necessarily seek out waters of similar temperatures among different oceanographic regions. These results corroborate previous research in the Bering Sea in which Chinook salmon were found to occupy a broad range of temperatures that appeared to follow seasonal changes of the North Pacific Ocean (Walker and Myers 2009). These collective observations are in direct contrast to behavior patterns found in the southern end of this species' range, off the coast of Oregon and northern California, where Chinook salmon appeared to seasonally adjust their vertical position in the water to almost exclusively occupy a narrow range of water temperatures (8–12 °C) during all seasons of the year (Hinke et al. 2005a). Differences in habitat occupation by Chinook salmon in the northern and southern portions of this species' range likely reflect population-specific responses to the geomagnetic field (Putman et al. 2014), and a complex relationship among fish behavior, temperature regimes, and prey resource abundance and distribution.

Management implications

Information on the spatial distribution of Chinook salmon obtained from this study may be used to address important management issues in the North Pacific Ocean, including understanding this species' susceptibility to incidental catch in groundfish fisheries. One of world's largest groundfish fisheries, that for walleye pollock in the Bering Sea/Aleutian Islands, is composed of two seasons, spanning ~June to October and ~January to April. It is known that the majority of the Chinook salmon bycatch occurs in the fall (September to October) and winter (January to March) periods on the eastern Bering Sea continental shelf break and slope (Stram and Ianelli 2009); however, it is currently not understood whether locations of these incidental catches reflect distribution patterns (e.g., aggregations or concentrations) of Chinook salmon in the Bering Sea, or are simply related to where the majority of the fishing effort occurs (Stram and Ianelli 2009; Walker and Myers 2009). End locations and most likely movement paths of tagged fish in this study demonstrate that Chinook salmon commonly used waters in and adjacent to areas of high incidental catches of this species (NPFMC 2008; NPFMC 2016) providing evidence that spatial patterns in incidental catch reflect general distribution patterns of this species.

Understanding the vertical distribution of Chinook salmon provides further information about the susceptibility of Chinook salmon to incidental capture in groundfish fisheries. Although occupied depths of individual Chinook salmon were highly variable, they spent the majority of their time within the top 75 m of the water column while in the eastern Bering Sea. These results support past analyses on the depth distribution of this species in the eastern Bering Sea tabulated from bycatch records in which ~85% of Chinook salmon bycatch was from fishing at depths of 25 to 75 m (January–February) (Walker et al. 2007). Given that acoustic and trawl survey data from the eastern Bering Sea shelf documents that approximately~90% of the adult (>30 cm) walleye pollock biomass, independent of bottom depth, is located within 50 m of the seafloor (Honakalehto and McCarthy 2015; Honkalehto et al. 2018), our results indicate that focusing trawl tows to within 50 m of the seafloor and below a depth of ~75 m could reduce Chinook salmon bycatch. However, further research is needed as our results and corresponding interpretations differ from changing strategies of the walleye pollock Catcher/Processor sector, that reports a reduction in fishing efforts at depths >~230 m to shallower waters to specifically avoid Chinook salmon (Madsen and Haflinger 2016).

Furthermore, past research has indicated that the bycatch rate for Chinook salmon relative to walleye pollock catches was lower during night time trawls, and that bycatch might be reduced if fishing efforts were concentrated during those time periods rather than mid-day fishing efforts (Stram and Ianelli 2009). Our results do not corroborate these generalizations, and in contrast, do not show any consistent patterns (e.g., diel) in depth occupancy. Given the lack of consistent diel behaviors of Chinook salmon in this study, there may be no simple solutions for avoiding bycatch of Chinook salmon in groundfish fisheries, in relation to fishing during certain times of the day. However, additional deployments of PSATs on Chinook salmon in the eastern Bering Sea would likely lead to a better understanding of trends in daily depth occupation of individual Chinook salmon, that ultimately may further aid management strategies to reduce incidental catch of this species.

Conclusion

In conclusion, compared to traditional approaches, the current study provides unprecedented insight into movement, behavior and thermal environment of individual Chinook salmon. This information is valuable for understanding the oceanic life stage, filling knowledge gaps in the life cycle of Chinook salmon. However, it is important to note that this study had a relatively small sample size of fish from unknown stocks-of-origin. Because different stocks of Chinook salmon are known to demonstrate different spatial distribution and behavioral patterns, it is highly unlikely that we have provided comprehensive descriptions of the patterns and variability in the distribution, behavior and thermal environment of Chinook salmon in the northern portion of this species' range. Further investigations with larger sample sizes, broadened geographic scope and genetic analyses to determine area of origin will be invaluable to improve our understanding of the oceanic ecology of Chinook salmon, and may inform future management considerations by subsistence, recreational and commercial users, as well as biological resource managers.

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