

1 **Further examination of the movement, behavior, and predation of Chinook salmon**
2 **in the Bering Sea**

3
4 **Pollock Conservation Cooperative Research Center**

5 **Project Final Report**
6

7
8 Andrew C. Seitz^{1,2}

9 Michael B. Courtney³
10

11
12
13
14 ¹Principal Investigator (acseitz@alaska.edu)

15 ²College of Fisheries and Ocean Sciences, University of Alaska Fairbanks, PO Box 757220,
16 Fairbanks, AK 99775

17
18 ³College of Fisheries and Ocean Sciences, University of Alaska Fairbanks, 17101 Point Lena
19 Loop Road, Juneau, AK 99801
20

21		Table of Contents	
22	Abstract		3
23	Introduction.....		4
24	Methods.....		6
25	Fish capture and tagging		6
26	Tag and data specifications		7
27	Horizontal movements		8
28	Depth and temperature occupancy.....		9
29	Mortality and predation.....		10
30	Results.....		12
31	Summary.....		12
32	Horizontal movement.....		13
33	Depth and temperature occupancy.....		14
34	Mortality and predation.....		16
35	Discussion.....		18
36	Summary.....		18
37	Horizontal movement.....		18
38	Depth and temperature occupancy.....		20
39	Management implications of behavior.....		23
40	Mortality and predation.....		25
41	Conclusion		28
42	Acknowledgments.....		30
43	References.....		31
44	Appendix I		52
45			
46			

47
48
49
50
51
52
53
54
55
56
57
58
59
60
61
62
63
64
65
66
67
68
69

Abstract

While Chinook salmon (*Oncorhynchus tshawytscha*) are widely distributed in offshore waters of the North Pacific Ocean, and of great economical and subsistence importance, 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, thermal environment, and survivorship of Chinook salmon in the northern extent of their range. Tagged Chinook salmon were at liberty for up to 260 days and end locations were in the central Bering Sea (n = 6), eastern Bering Sea/Aleutian Islands (n = 21), 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. While 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. Additionally, PSATs provided evidence of predation on tagged Chinook salmon by salmon sharks (*Lamna ditropis*) (n = 14), marine mammals (n = 2), ectothermic fish(es) (n = 3), and unidentified predators (n = 5) in the Bering Sea and Gulf of Alaska. Information about movement, diving behavior, and thermal environment of individual Chinook salmon may have future application in developing strategies to further reduce incidental catch of this species. Furthermore, high mortality rates in this study suggest that fisheries scientists should consider that late stage mortality by marine apex predators may be shaping this species' abundance and demographics.

70
71
72
73
74
75
76
77
78
79
80
81
82
83
84
85
86
87
88
89
90
91

Introduction

Chinook salmon (*Oncorhynchus tshawytscha*) is an iconic species found throughout the North Pacific Ocean. It supports important subsistence, commercial and recreational fisheries throughout the Gulf of Alaska and Bering Sea. However, Chinook salmon returns in Alaska have been depressed for over a decade. Coupled with these overall declines in abundance, changes in size- and age-structure have been reported throughout the range of the species, with a proportional decrease of older age classes (ocean age 4+) returning to spawning grounds each year (Lewis et al. 2015; Ohlberger et al. 2018; Ruggerone et al. 2016). The depressed abundance and demographic changes have led to severe restrictions on subsistence, commercial and recreational fisheries, particularly in western Alaska (ADF&G 2013; Schindler et al. 2013).

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 this species' biology and ecology, with the ultimate goal of describing the ongoing and 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 stage 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 six years (Brodeur et al. 2000; Drenner et al. 2012; Riddle et al. 2018).

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

109 Pop-up satellite archival tags (PSATs) which record environmental variables while
110 attached to an animal are a method to collect detailed information about the oceanic dispersal,
111 behavior, and habitat occupancy of fishes (Arnold and Dewar 2001; Musyl et al. 2011; Thorstad
112 et al. 2013). On a preprogrammed date, the tag releases from the fish, floats to the surface of the
113 water and transmits data to satellites, which are then retrieved by project investigators. Because
114 PSATs do not rely on recapture for data retrieval, they are a fisheries independent method of data

115 collection. Fisheries independent technology is critically important for understanding the oceanic
116 ecology and behavior of Chinook salmon near western Alaska, because there are currently no
117 offshore directed fisheries or research programs for this species in the Bering Sea. Furthermore,
118 PSATs are also a valuable tool to assess survivorship of tagged fish, because data can be
119 retrieved from individuals that experience mortality (Benson et al. 2018; Lacroix 2014; Nielsen
120 et al. 2018). Therefore, the objective of this study was to use PSATs to provide insights into
121 oceanic distribution, movements, behavior, thermal environment and survivorship of Chinook
122 salmon in the Bering Sea.

123 **Methods**

124 *Fish capture and tagging*

125 Chinook salmon in this study were captured by either hook and line or trawl. For winter
126 sampling, in late October to December in 2013–2015 and 2017, 30 Chinook salmon were
127 captured by hook and line, and tagged and released from a sportfishing vessel, the FV Lucille,
128 near Dutch Harbor, AK in the eastern Bering Sea (Fig. 1). For summer sampling in early August
129 2014 and 2015, 13 Chinook salmon were captured, tagged, and released from the RV Hokko
130 maru in the central Bering Sea (Fig. 1). During this summer sampling, Chinook salmon were
131 captured using a mid-water trawl that contained a live box cod end ($n = 6$) and by hook-and-line
132 ($n = 7$). Based on past genetic analyses, it is likely that we tagged fish from several different
133 stocks, as Chinook salmon captured in the Bering Sea commonly originate from many regions,
134 including Russia, Alaska, British Columbia, and the U.S. Pacific Northwest (Larson et al. 2013).
135 However, the stock-origin of captured fish in this study was unknown. Complete information
136 about tag deployments can be found in Appendix I (Table A1).

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

148 *Tag and data specifications*

149 PSATs used in this study were either the X-tag (n = 22) or HR X-tag (n = 1)
150 manufactured by Microwave Telemetry (<http://www.microwavetelemetry.com>), or MiniPATs (n
151 = 20) manufactured by Wildlife Computers (<https://wildlifecomputers.com/>). In general, while
152 attached to a fish, the tags measured and recorded depth, temperature and ambient light intensity
153 at preprogrammed rates. Tags were programmed to release from the Chinook salmon on
154 preprogrammed dates 0.5–12 months after release into the ocean or if a tag remained at a
155 constant pressure (± 2.5 m depth) for a period of 2–7 days, indicating either death and sinking to
156 the sea floor, or detachment from the fish and floating on the ocean surface. After releasing from
157 the fish, the tags floated to the surface of the sea and transmitted the archived data to satellites
158 (Argos Satellite System). While transmitting, the location of each tag was determined from the

159 Doppler shift of the transmitted radio frequency in successive uplinks received during one
160 satellite pass (Keating 1995). The end locations of tagged fish were considered as the first
161 transmission with an Argos location class ≥ 1 , indicating an accuracy of at least 1.5 km.

162 In this study, X-tags and the HR X-tag recorded data every two minutes, whereas
163 MiniPATs recorded data every 3–15 seconds. However, because of the large amount of data
164 collected by the tags, limited data reception by Argos satellites, and short tag-battery life while
165 transmitting to satellites, only a subset of temperature and depth data were transmitted by the
166 tags. This subset of depth and temperature data was every 15 minutes for X-tags, 2 minutes for
167 the HR X-tag, and 5–10 minutes for MiniPATs. Additionally, daily summaries of minimum and
168 maximum depths and temperature experienced by each tagged fish were provided. For
169 MiniPATs, an onboard algorithm identified daily dawn and dusk events and the corresponding
170 light intensity data were transmitted for post processing. In contrast, X-tags provided daily
171 geolocation estimates of latitude and longitude using the tag manufacturer’s onboard proprietary
172 software during post-processing of transmitted data. The HR X-tag did not provide daily
173 geolocations.

174 *Horizontal movements*

175 To provide insights into horizontal movement of Chinook salmon, minimum
176 displacement of each tagged fish was determined by calculating the great arc circle distance of a
177 non-meandering route that did not pass over land between tagging and end locations, in GIS
178 software (ArcMap 10.1; Environmental Systems Research Institute Inc., Redlands, California).
179 Additionally, for tagged Chinook salmon at liberty for >30 days, individual most likely
180 movement paths were reconstructed using a hidden Markov model (HMM) approach. HMMs are

181 non-parametric state-space models that consist of a two-step forward filter that combines an
182 underlying movement scheme with the data recorded by the tag, and a backward smoothing step,
183 which ensures serial dependency in the time series (Pedersen 2010). The 30 day cut-off was used
184 because the error associated with movement tracks of short duration may exceed the horizontal
185 displacement or may not be informative if the tagged fish remained near the tagging location
186 (Braun et al. 2018; Braun et al. 2015; Musyl et al. 2011). For MiniPATs, Wildlife Computers'
187 proprietary HMM embedded in post-processing software (WC-GPE3, Wildlife Computers 2015)
188 was used, which employs observations of twilight, sea surface temperature (NOAA OI SST V2
189 High Resolution), and bathymetry (ETOP1-Bedrock; <https://www.ngdc.noaa.gov/mgg/global/>) to
190 generate time-discrete and gridded (0.25° by 0.25°) probability distributions to estimate the most
191 likely daily positions (Wildlife Computers 2015). For X-tags, a HMM developed for Atlantic
192 salmon *Salmo salar* was used that generates daily probability distributions on an equidistant grid
193 based on temperature (NOAA OI SST V2 High Resolution), bathymetry (ETOP1-Bedrock;
194 <https://www.ngdc.noaa.gov/mgg/global/>), and a filtered subset of longitude estimates (described
195 in Strøm et al. 2017). Based on these time-series of daily probability distribution, individual
196 migration routes were estimated as the mean of 1000 random tracks sampled through a backward
197 sweep (Thygesen et al. 2009). In both models, a maximum daily swim speed of $100 \text{ km} \cdot \text{day}^{-1}$
198 was assumed and a qualitative comparison revealed similar movement paths when applying the
199 two models.

200 *Depth and temperature occupancy*

201 To provide insights into the behavior and thermal environment of Chinook salmon, each
202 fish's occupied depth and temperature were examined by inspecting time series data from

203 individual tags, and determining minimum, maximum, mean, and median (\pm SD) occupied depths
204 and temperatures. Additionally, the mean (\pm SD) proportion of time that all tagged Chinook
205 salmon spent at depth and temperature intervals was calculated by month and by region. The
206 assignment of data to regions was based on deployment and pop-up locations, as well as dates of
207 changing regions (i.e., central Bering Sea, Bering Sea/Aleutian Islands, Gulf of Alaska), as
208 identified by the HMMs.

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

216 *Mortality and predation*

217 Mortality of tagged fish by predation was inferred from PSAT data, as previous research
218 has identified several types of predation, including by ectothermic and endothermic fishes,
219 marine mammals, and unknown sources, hereafter referred to as “unknown mortality” (e.g.,
220 Béguer-Pon et al. 2012; Lacroix 2014; Wahlberg et al. 2014). In this study, predation was
221 inferred by one or a combination of the following data characteristics: a rapid change in ambient
222 temperature indicating consumption by an endotherm; light sensors recording darkness during
223 periods of day, indicating that the tag was in the stomach of a predator; and/or abrupt changes in
224 depth-based behavior indicating consumption by a predator whose occupied depths were

225 different than those of the free-swimming Chinook salmon prior to predation (e.g., Béguyer-Pon
226 et al. 2012; Lacroix 2014; Strøm 2018). In all of these inferred scenarios of predation, the
227 predators ingested whole, tagged Chinook salmon, including the externally attached PSAT tags.
228 The tags remained in the predators' stomachs, and recorded depth and ambient temperature
229 inside their stomachs. After this period inside the stomachs, the tags were regurgitated or
230 expelled and floated to the surface, triggering them to begin transmitting data to satellites.

231 To identify predators of Chinook salmon, depth-based behavior and internal temperature
232 of predators was qualitatively compared to published observations of large, predatory animals in
233 the North Pacific Ocean. For each predator taxa identified, individual minimum, maximum and
234 mean (\pm SD) occupied depth and visceral temperatures were calculated. To obtain the most
235 accurate readings, only temperature readings taken after tag temperatures became stable were
236 used to calculate mean internal temperatures (Goldman et al. 2004).

237 Unknown mortality was inferred when tag data suggested that tagged fish suddenly sank
238 to the sea floor and remained at a constant depth, until the fail-safe mechanism activated, the tag
239 floated to the surface and transmitted to satellites. In this scenario, it was assumed that mortality
240 was caused by predation, the tagged fish was torn into pieces by a predator and the portion of the
241 carcass with the tag sank to the sea floor, similar to past comparable research (Lacroix 2014;
242 Strøm 2018).

243 Total mortality of Chinook salmon was considered as the sum of mortality ascribed to
244 likely predators and unknown mortality. Total mortality was used in a Kaplan-Meier estimator
245 framework to calculate survivorship rates (\pm 95% confidence intervals) of PSAT tagged Chinook
246 salmon. For this analysis, we used a time-since-release time-scale, in which Chinook salmon

247 entered the model on the day of its deployment, which was considered day 0. Survivorship was
248 then estimated across the monitoring period, and individual fish exited the model upon mortality
249 (predation or unknown), or were right-censored on the pop-up date or the date of prematurely
250 releasing from a Chinook salmon (Benson et al. 2018; Fieberg and DelGiudice 2009). Premature
251 release was assigned when a tag released from a fish and reported to satellites before the
252 programmed release date for unknown reasons, but the tagged Chinook salmon appeared to be
253 alive according to depth data immediately before the tag reported to satellites. Because tags that
254 prematurely released were assumed to detach from live Chinook salmon, censoring these tags
255 provided conservative estimates of survivorship. Additionally, tagged fish that were at-liberty for
256 less than three weeks were removed from survival analyses to avoid any mortality that may have
257 been influenced by capture/tagging processes. A total of 24 tagged Chinook salmon were used in
258 survival analyses.

259 **Results**

260 *Summary*

261 Tagged Chinook salmon were 57–100 cm fork length (72.1 ± 9.7 cm, mean \pm SD) (Table
262 A1). Of the 43 tags deployed, 35 (81.4% of the total 43) reported to satellites, one (2.3% of the
263 total 43) provided an end location but no data, and seven (16.3 % of the total 43) never
264 transmitted and were considered missing (Table A1). Of the 35 tags that successfully transmitted
265 to satellites, four reported on the scheduled pop-up date. The remaining tags reported
266 prematurely: five were premature releases from fish assumed to be alive; 19 had depth,
267 temperature, and light readings associated with predation by a marine predator; and seven were
268 associated with unknown mortality events. Data from these predation/mortality events were

269 removed from depth and temperature analyses. Furthermore, two unknown mortality events
270 occurred immediately after release into the ocean. Because it is likely that these mortality events
271 were due to the capture and tagging process, these records were removed from all analyses.
272 Another tag provided low data return (5% of the hypothetical data that should have been
273 available) and was also excluded from depth and temperature analyses.

274 For individual tags whose data were used in temperature and depth analyses ($n = 32$), the
275 percentage of the complete data records received by Argos satellites varied between 31 and 93%
276 ($74.3 \pm 20.1\%$, mean \pm SD; data resolution = 2–15 min). The number of data sets available for
277 analyses varied seasonally, with most data recorded during October to January.

278 *Horizontal movement*

279 End locations of tagged Chinook salmon were in the central Bering Sea ($n = 6$), eastern
280 Bering Sea/Aleutian Islands ($n = 20$), and the Gulf of Alaska ($n = 6$; Fig. 1). Of the tags deployed
281 in the central Bering Sea during August, end locations and the most likely movement paths of
282 individual fish suggested that they remained in the vicinity of this region or made easterly
283 movements to the eastern Bering Sea by the onset of fall (Fig. 1; Fig. 2). For example, the most
284 likely path of one tagged fish suggested that it occupied the central Bering Sea for the entire
285 duration (August–January; 150 days at liberty) of its deployment (Fig. 2a) while traveling
286 extensively (track length = 2,354 km; minimum dispersal = 256 km). In contrast, one tagged
287 Chinook salmon migrated easterly to the eastern Bering Sea shelf by early September, and
288 reported 545 km away in late-October while traveling less extensively (Fig. 2b; track length =
289 980 km).

290 For Chinook salmon tagged during the winter near Dutch Harbor, AK, end locations and
291 most likely movement paths demonstrated that the majority remained in the southeastern Bering
292 Sea/Aleutian Islands, regardless of their time at liberty (Fig. 1, Fig. 3). For example, the most
293 likely path of one tagged Chinook salmon that was at liberty for 260 days suggested that this fish
294 remained in the eastern Bering Sea Shelf from its deployment in November to its pop-up date in
295 July (Fig. 3b; track length = 2,581 km). In contrast to the Chinook salmon tagged in the eastern
296 Bering Sea/Aleutian Islands that remained in these waters during the deployment period, six fish
297 migrated eastward to the Gulf of Alaska (Fig. 1, Fig. 3a, Fig. 4). Based on their most likely
298 movement paths, five of these tagged fish exited the Bering Sea during the months of December
299 and January (Fig. 4a, c; tracks lengths = 2,123–2,345 km), while one fish exited the Bering Sea
300 in late March (Fig. 4b; track length = 2,937 km). The most likely movement paths of these fish
301 suggested that the migration of five of these fish followed the continental shelf (Fig. 4c), while
302 one individual transited through and occupied offshore basin waters of the Gulf of Alaska (Fig.
303 4a).

304 *Depth and temperature occupancy*

305 While at liberty, Chinook salmon occupied depths ranging from 0 to 538 m and
306 experienced a thermal environment ranging from -0.6 to 13.5°C (Fig. 5). Overall mean depths of
307 individual fish ranged from 4.5 to 127.9 m (53.0 ± 30.4 m; grand mean \pm SD), while median
308 depths ranged from 1.3 to 99.9 m (48.3 ± 31.4 , grand median \pm SD; Table A1). Although sample
309 sizes were not even among months of the year, in general, Chinook salmon occupied the
310 shallowest and warmest water in May–September and the deepest and coolest water in
311 December–March (Fig. 5b, c).

312 While Chinook salmon occupied waters of the central Bering Sea during late summer and
313 early fall they were highly surface oriented (Fig. 2, Fig. 5a). Individual maximum depths ranged
314 from 38 to 285 meters, with mean and median depths of individual fish ranging from 4.4 to 45.6
315 m (15.1 ± 14.4 m; grand mean \pm SD) and 1.3 to 48.4 m (4.0 ± 16.8 m; grand median \pm SD),
316 respectively. Overall, these tagged fish, generally experienced a stratified (~ 4 – 11°C) thermal
317 environment from August to September (Fig. 2). By mid-October, diving depths increased as
318 waters became increasingly isothermal (~ 4 – 6°C) (Fig. 2a).

319 While occupying waters of the eastern Bering Sea/Aleutian Islands from November to
320 July, fish spent approximately 45% of their time within the upper 50 m of the water column (Fig.
321 5a). Overall mean and median occupied depths of individual fish ranged from 18.2 to 97.2 m
322 (59.1 ± 24.1 m; grand mean \pm SD) and 6.7 to 105.0 m (61.1 ± 28.5 ; grand median \pm SD),
323 respectively. Diving behavior varied substantially among individual tagged fish, but most
324 occupied depths near the surface daily, and dives to >80 m were common, with maximum depths
325 ranging from 76 to 427 m. In contrast to these general behaviors, one tagged fish occupied
326 depths of 0 to 50 m for nearly its entire tag deployment from early-October to mid-February (Fig
327 3c) and four other tagged fish remained exclusively at ~ 50 – 150 m deep during their times at
328 liberty during November–January. In the eastern Bering Sea/Aleutian Islands, tagged fish
329 generally experienced a stratified thermal environment of ~ 5 – 10°C from early June to mid-
330 November, after which their thermal environment became increasing isothermal (~ 4 – 6°C) from
331 early-November to late-May.

332 In general, tagged Chinook salmon occupied deeper water while in the Gulf of Alaska
333 from January to May (maximum depths ranged from 76 to 538) compared to those in the eastern

334 Bering Sea/Aleutian Islands during the same season (Fig. 5a). When present in the Gulf of
335 Alaska, individual mean and median depths were 29.6–139.5 m (71.1 ± 38.3 m; grand mean \pm
336 SD), and 22.5 to 123.7 m (70.2 ± 37.3 m; grand median \pm SD) respectively, and tagged fish
337 experienced a thermal environment ranging from 2.8–9.4°C.

338 For individual tagged fish, diel differences in depth distributions were detected in 19 of
339 32 tag records (median paired difference range 2.1–106.8 m; $\alpha = 0.05$). However, these
340 differences were not consistent. Qualitative analyses documented that some Chinook salmon
341 occupied deeper waters and exhibited greater diving activity during the day compared to periods
342 of night ($n = 9$), others demonstrated the opposite behavior ($n=10$), and finally others displayed
343 no diel trends ($n = 13$). Some tagged fish switched among behaviors on time scales of days to
344 months during their time at-liberty (Fig. 6). Visually identified diel patterns of depth occupation
345 showed no qualitatively consistent association with geographic area, season, or even month, as
346 behaviors of tagged fish occupying similar regions during the same season varied widely.

347 *Mortality and predation*

348 Mortality of Chinook salmon was relatively common in the central and eastern Bering
349 Sea, near the Aleutian Islands, and in the western Gulf of Alaska (Fig. 7). Survivorship of
350 Chinook salmon ($n = 24$ used in survival analyses) for the monitoring period of 25 to 260 days
351 was 0.18 (0.06–0.55, 95% confidence interval; Fig. 8).

352 Based on known visceral temperatures and species distribution (Anderson and Goldman
353 2001; Goldman et al. 2004), 14 predation events were attributed to salmon sharks *Lamna ditropis*
354 5–143 (38 ± 39 , mean \pm SD) days after tag deployment (Table A1). This inference was based on
355 temperature readings rapidly increasing above ambient water of ~ 4 – 11 °C to 20–26°C then

356 stabilizing at $\sim 25^{\circ}\text{C}$. Most likely, the only place in the Bering Sea where the ambient
357 temperature is consistently $20\text{--}26^{\circ}\text{C}$, even at depths >0 m, is in the stomach of a salmon shark
358 (Anderson and Goldman 2001; Goldman et al. 2004; Goldman and Musick 2008). While PSATs
359 were in the stomach of salmon sharks for $1.1\text{--}5.6$ days (2.6 ± 1.4 mean \pm SD), mean and maximum
360 visceral temperatures of individuals were $21.5\text{--}28.4^{\circ}\text{C}$ and $23.6\text{--}29.4^{\circ}\text{C}$, respectively (Table A1,
361 Fig. 9a–f). The range of depths occupied by salmon sharks was $0\text{--}307$ m. In general, most
362 salmon sharks demonstrated deep diving behavior during the day, and shallow water occupancy
363 with little diving behavior at night (Fig. 9a–f). In contrast, one salmon shark remained
364 exclusively at the ocean surface ($\sim 0\text{--}1$ m) while the PSAT was in its stomach for 1.1 days (Table
365 A1).

366 Two predation events were attributed to marine mammals 26–30 days after tag
367 deployment (Table A1; Fig. 9g, h). This inference was based on temperature readings rapidly
368 increasing from ambient water temperatures of $5\text{--}7^{\circ}\text{C}$ to $36\text{--}38^{\circ}\text{C}$ (Austin et al. 2006; Gales and
369 Renouf 1993; Kuhn and Costa 2006). While the tags were in the stomach of marine mammals for
370 $1.8\text{--}2.2$ days, mean and maximum visceral temperatures of individuals were $34.8\text{--}37.4^{\circ}\text{C}$ and
371 $36.0\text{--}38.2^{\circ}\text{C}$, respectively (Table A1; Fig. 9g,h). For one marine mammal predator, dives to 10
372 meters were common during the first six hours, after which the predator remained mostly at a
373 depth of 0 m, indicating occupation of shallow water or possibly land (Fig. 9g). In the other
374 marine mammal predation event, the animal spent most of its time within the first 10 m of the
375 water column, but dives to $\sim 60\text{--}120$ m during daytime were common (Fig. 9h).

376 Three predation events were attributed to ectothermic fish(es), 13–67 days (43 ± 27 ,
377 mean \pm SD) after release (Table A1; Fig. 9i,j). Unlike the predation events attributed to

378 endotherms, no observable differences in ambient temperatures were found before and after
379 consumption of the tagged Chinook salmon. However, abrupt changes in depth occupation that
380 coincided with the tags' light sensor indicating darkness for several days were evident (Fig. 9i,j).
381 Behaviors of ectothermic predators varied (Table A1). For example, one ectothermic predator
382 occupied a wide range of depths of 0 to 274 m (Figure 9i), while the other two ectothermic
383 predators exhibited benthic behaviors by remaining at depth windows of ~60–80 m and ~400–
384 480 m (Table A1; Figure 9j).

385 **Discussion**

386 *Summary*

387 The current study provides detailed insights into the movements, behaviors, habitat
388 occupancy, and natural mortality of Chinook salmon on continuous time scales spanning 0.5–8.5
389 months. While the information collected in this study is qualitative, it highlights the efficacy of
390 PSATs for studying Chinook salmon, and provides information to basic and applied questions
391 that have eluded scientists until now.

392 *Horizontal movement*

393 Most Chinook salmon tagged in the eastern Bering Sea/Aleutian Islands during winter
394 resided in this area throughout the winter months. Furthermore, there was a tendency for fish
395 tagged in the central Bering Sea during summer to make southerly movements to the eastern
396 Bering Sea at the onset of fall. The affinity for tagged fish to occupy the eastern Bering Sea
397 highlights the importance of these waters as overwintering habitat for Chinook salmon (Larson et
398 al. 2013; Walker and Myers 2009). The importance of this region is likely a result of its high
399 productivity that is stimulated by the northward transport of well-mixed nutrient-rich waters

400 through the Aleutian passes to the eastern Bering Sea shelf (Stabeno et al. 2001; Stabeno et al.
401 2016; Stabeno et al. 1999). Although the factors that shape the overwintering spatial distribution
402 of Chinook salmon are complex (Myers et al. 2016), the seasonal movements documented in this
403 study likely reflect behaviors to maximize growth, by maximizing interactions with suitable prey
404 fields and minimizing metabolic costs by seeking cool waters in times of low prey availability
405 (Davis et al. 2009a; Riddle et al. 2018; Walker and Myers 2009).

406 The variation in movement distances and directions of individual tagged fish between
407 tagging and end locations is likely explained by an interaction between the time of year of
408 tagging and the stock-of-origin of each tagged fish. Based on genetic analyses, Chinook Salmon
409 captured in the Bering Sea commonly originate from Russia, Alaska, British Columbia, and the
410 U.S. Pacific Northwest (Larson et al. 2013). It is thought that immature individuals from these
411 regions utilize similar foraging areas in the central and eastern Bering Sea during summer
412 (Larson et al. 2013). After feeding, Chinook salmon natal to central Alaska to the Pacific
413 Northwest migrate south to overwinter in the North Pacific Ocean south of the Aleutian Islands
414 and the Gulf of Alaska (Healey 1991; Larson et al. 2013; Myers et al. 2009). In contrast,
415 Chinook salmon from western Alaska are thought to reside in the Bering Sea year-round. While
416 present in these waters, fish from western Alaskan are thought to summer in the central Bering
417 Sea shelf and basin, and overwinter above the eastern Bering Sea shelf. Given the differences in
418 movement patterns among fish from different stocks and that we likely tagged fish from several
419 stocks, it is probable that the tagged Chinook salmon that left the Bering Sea during winter were
420 natal to a river outside of western Alaska. Specifically, the fish whose tags reported from the
421 central Gulf of Alaska may have been swimming back to their natal rivers in British Columbia or
422 the U.S. Pacific Northwest, based on their direction of travel. The corollary that fish that

423 remained in the Bering Sea were from western Alaska is not necessarily true, as many of the tags
424 were attached to these fish for short durations. As such, these tag deployments did not coincide
425 with times that Chinook salmon were likely to move from the Bering Sea to the Gulf of Alaska,
426 and therefore it is difficult to speculate on their natal rivers.

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

439 *Depth and temperature occupancy*

440 Chinook salmon occupied a broad range of depths, with pronounced seasonal shifts. The
441 pattern of shallow water occupancy during the summer followed by a transition to deeper, cooler,
442 and isothermal waters during winter is corroborated by previous research in the Bering Sea and
443 off the coast of Oregon and California using electronic archival tags (Hinke et al. 2005a; Walker
444 and Myers 2009). Thus, these changes in depth distribution appear to be conserved across the

445 range of Chinook salmon and likely reflect seasonal changes in stratification of the water
446 column, and the distribution and abundance of prey that occur throughout the North Pacific Ocean
447 (Hinke et al. 2005a; Stabeno et al. 2001; Walker and Myers 2009). Similarly, changes in the
448 stratification of the water column has been suggested to shape the foraging behavior of other
449 pelagic fish species, such as Atlantic salmon and Atlantic bluefin tuna *Thunnus thynnus* (Hedger
450 et al. 2017a; Strøm et al. 2018; Walli et al. 2009). For example, electronic archival tags have
451 documented a preference for Atlantic bluefin tuna to conduct short and shallow dives when
452 waters are strongly stratified, and also to spend less time above the thermocline when water is
453 weakly stratified (Walli et al. 2009). This behavior has been proposed as a behavior to maximize
454 encounters with prey, which may be densely aggregated in surface waters during times of high
455 stratification.

456 Chinook salmon are opportunistic foragers, and as such, the seasonal changes in patterns
457 of occupied depths and temporal diving behaviors may reflect changes in diet and/or flexible
458 foraging strategies. During the summer months in the Bering Sea, when tagged fish were found
459 to occupy relatively shallow waters, Chinook salmon diets are typically composed of forage
460 fishes, including juvenile walleye pollock and Pacific sandlance *Ammodytes hexapterus*, as well
461 as invertebrates including several species of zooplankton and cephalopods that typically inhabit
462 relatively shallow water (Davis et al. 2005; Davis et al. 2009b). In contrast, during the winter,
463 Chinook salmon diets switch almost exclusively to cephalopods, including master armhook squid
464 *Beryteuthis magister* and shortarm gonate squid *Gonatus kamtschaticus*, which are typically
465 patchily distributed and occur at high densities at greater depths (Arkhipkin et al. 1998; Davis et
466 al. 2009a). Flexible feeding strategies have been documented for many pelagic fish species, and

467 this plasticity is likely important for Chinook salmon which may migrate across large geographic
468 areas during this species' oceanic phase (Strøm et al. 2018; Walli et al. 2009).

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

479 Chinook salmon in this study experienced a wide range of temperatures while occupying
480 waters of the Bering Sea and Gulf of Alaska. As a result, Chinook salmon may not necessarily
481 seek out waters of similar temperatures among different oceanographic regions. These results
482 corroborate previous research in the Bering Sea in which Chinook salmon were found to occupy
483 a broad range of temperatures that appeared to follow seasonal changes of the North Pacific
484 Ocean (Walker and Myers 2009). These collective observations are in direct contrast to behavior
485 patterns found in the southern end of this species' range, off the coast of Oregon and northern
486 California, where Chinook salmon appeared to seasonally adjust their vertical position in the
487 water to almost exclusively occupy a narrow range of water temperatures (8–12°C) during all
488 seasons of the year (Hinke et al. 2005a). Differences in habitat occupation by Chinook salmon in

489 the northern and southern portions of this species' range likely reflect a complex relationship
490 among fish behavior, temperature regimes, and prey resource abundance and distribution.

491 *Management implications of behavior*

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

507 Understanding the vertical distribution of Chinook salmon provides further information
508 about the susceptibility of Chinook salmon to incidental capture in groundfish fisheries.
509 Although occupied depths of individual Chinook salmon were highly variable, they spent the
510 majority of their time within the top 75 m of the water column while in the eastern Bering Sea.

511 These results support past analyses on the depth distribution of this species in the eastern Bering
512 Sea tabulated from bycatch records in which ~85% of Chinook salmon bycatch was from fishing
513 at depths of 25 to 75 m (January–February) (Walker et al. 2007). Given that acoustic and trawl
514 survey data from the eastern Bering Sea shelf documents that approximately ~90% of the adult
515 (>30 cm) walleye pollock biomass, independent of bottom depth, is located within 50 m of the
516 seafloor (Honakalehto and McCarthy 2015; Honkalehto et al. 2018), our results indicate that
517 focusing trawl tows to within 50 m of the seafloor and below a depth of ~75 m could reduce
518 Chinook salmon bycatch. However, further research is needed as our results and corresponding
519 interpretations differ from changing fishing strategies of the walleye pollock Catcher/Processor
520 sector, that reports a decrease in Chinook salmon bycatch when shifting fishing efforts from
521 depths >~230 m to shallower waters (Madsen and Haflinger 2016).

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

533 *Mortality and predation*

534 PSATs provided estimates of low late marine survival rates of large Chinook salmon, and
535 a preliminary glimpse into natural mortality of this species caused by sharks, marine mammals,
536 and ectothermic fish(es). Most notably, this study provides evidence that salmon shark predation
537 may be a substantial source of oceanic mortality of large immature and maturing Chinook
538 salmon. Predation by salmon sharks occurred during both the summer and winter, and
539 throughout a wide range including the central and eastern Bering Sea, and near the Aleutian
540 Islands. The potentially frequent incidence of salmon shark predation on Chinook salmon is
541 corroborated by a previous estimate that salmon sharks have the capacity to consume a
542 considerable proportion of Pacific salmon *Oncorhynchus* spp. residing in the Bering Sea and
543 Gulf of Alaska on an annual basis (Nagasawa 1998).

544 Interestingly, there was evidence that salmon sharks occupy the Bering Sea during the
545 winter, where ambient water temperatures were ~4–6°C. While salmon sharks previously have
546 been found to occupy subarctic environments of the North Pacific Ocean, including the Bering
547 Sea, most research suggests that they make southerly movements out of these cold habitats by
548 the onset of winter (Goldman and Musick 2008; Weng et al. 2005; Weng et al. 2008). In
549 contrast, results from this study suggest that not all salmon sharks leave the Bering Sea during
550 the winter. While the overall abundance of salmon sharks in the eastern North Pacific is poorly
551 understood, anecdotal reports suggest that this species has rebounded substantially since the
552 cessation of the high seas drift gillnet fishery (1992) and Canadian flying squid fishery (1987)
553 (Goldman and Musick 2008; Okey et al. 2007). Further protective measures which have been
554 facilitated through amendments to the Magnuson-Stevens Conservation and Management Act

555 (1976), including the Shark Finning Prohibition Act of 2000, and the Shark Conservation Act of
556 2010, likely have attributed to increases in salmon shark productivity in recent years. With the
557 current warming of the Bering Sea (Stabeno et al. 2007), the known endothermy (Goldman et al.
558 2004), a possibly expanding niche (Weng et al. 2005), and likely increases in abundance of
559 salmon sharks in the north Pacific Ocean (Okey et al. 2007), future research is important to
560 understand the role of this predator in the mortality of Pacific salmon. An understanding of this
561 predator-prey relationship will have implications for appropriate science-based management for
562 both predator and prey.

563 Unlike predation by salmon sharks, that have unique internal temperatures, identifying
564 the species of marine mammal and ectothermic fish(es) predators is much more speculative. In
565 the case of one marine mammal, based on its occupation of 0 m for an extended period (~31 hr),
566 we speculate that it may have been a species of pinniped, as this group regularly hauls out on
567 land (Call et al. 2007; Lander et al. 2011; Trites and Porter 2002). Specifically, Stellar sea lions
568 *Eumetopias jubatus* frequently occur in the area of the predation event and are known to be
569 principle predators of Chinook salmon (Adams et al. 2016; Chasco et al. 2017). In the other case
570 of marine mammal predation, the predator consumed the largest tagged Chinook salmon in this
571 study (100 cm FL), and was found to frequently dive to ~60–120 m during daylight hours. Based
572 on this evidence, it is probable that predation occurred by a resident killer whale *Orcinus orca*.
573 Killer whales are distributed adjacent to the Aleutian Islands, and are known to not only be
574 principle predators of Chinook salmon (Adams et al. 2016; Chasco et al. 2017; Ford et al. 1998),
575 but also have been shown to consume proportionally more of the largest and oldest Chinook
576 salmon than are available in their environment (Ford and Ellis 2006).

577 In the cases of predation by ectothermic fish(es), predator identification is speculative at
578 best. Based on depth-based behaviors after ingestion of the tagged Chinook salmon, predation
579 was likely from large deep-dwelling fish species, such as a Pacific halibut *Hippoglossus*
580 *stenolepis* (Seitz et al. 2011) or sleeper shark *Somniosus pacificus* (Hulbert et al. 2006).
581 Unfortunately, the depth-based behavior of both species is qualitatively similar, making species
582 identification of the predator challenging (Hulbert et al. 2006; Loher and Seitz 2006; Seitz et al.
583 2011).

584 In this study, we assumed that unknown mortality events were attributed to predation,
585 similar to past and comparable research (Lacroix 2014; Strøm 2018). In this study, 4/5 of these
586 events occurred 60–156 days after tag deployment, and Chinook salmon behaviors immediately
587 before death was indistinguishable from the behavior of other tagged fish that were assumed to
588 be healthy. Given this, we believe that the assumption of predation is justified, and that is not
589 likely that these tagged fish simply died and sank to the seafloor as a result of being unhealthy,
590 nor that these events are likely attributable to capture and tagging effects. If these events are
591 attributed to predation, based on feeding strategies and gape limitations, the most probable
592 predator is either a species of pinniped or a resident killer whale. Pinnipeds are known to tear
593 apart prey before consuming them (Hocking et al. 2016; Hocking et al. 2017), while killer
594 whales are known to roll after capture of prey and also to carry and share salmon prey, during
595 which time they are torn to pieces (Ford and Ellis 2006). However, the overall high frequency of
596 predation events attributed to salmon sharks may suggest that unknown mortality was at least
597 partially caused by individuals of this species, which either did not consume the entire tagged
598 fish, or immediately detached or expelled the PSAT during the predation event.

599 It is important to acknowledge that relatively large external tags, such as PSATs, have the
600 potential to induce capture/tagging and/or post-tagging effects, thus biasing this study's results.
601 Specifically, externally attached tags can negatively affect the swimming performance of fishes
602 (e.g., Methling et al. 2011), therefore increasing a fish's susceptibility to predation (e.g.,
603 Cosgrove et al. 2015). While literature on the effects of towing PSATs on the swimming
604 performance and survival of Chinook salmon does not exist, it has been qualitatively examined
605 for PSAT-tagged adult Atlantic salmon (Hedger et al. 2017b) and suggests that PSATs have
606 minimal effects on its behavior, marine survival, and geographical distribution during its ocean
607 migration. Furthermore, while the literature is scarce on similar sized fish, minimal impacts of
608 PSATs on the metabolic cost of transport of juvenile sandbar sharks *Carcharhinus plumbeus* of
609 similar sizes to the Chinook salmon in this study have been reported (Lynch et al. 2017). Even if
610 PSATs increased the vulnerability of Chinook salmon to predation, the findings in this study
611 indicate that predators may be spatially and temporally widespread and co-occur with Chinook
612 salmon during all periods of the year.

613 Understanding the potential impact of low oceanic survival of large immature and
614 maturing Chinook salmon is important, as it has become dogma that processes in the nearshore
615 environment during the early marine phase of Pacific salmon life history largely govern adult
616 population dynamics. As a corollary, it is widely assumed that the risk of mortality decreases
617 dramatically after the critical periods of ocean entry and first ocean winter, the marine
618 environment is relatively safe thereafter, and that effects in this 'late' marine stage have minimal
619 impacts on population characteristics, including dynamics and life history traits (Beamish and
620 Mahnken 2001). Recently, changes in age- and size-structure, including a proportional decrease
621 of older age classes of spawning Chinook salmon has been documented throughout this species'

622 range (Lewis et al. 2015; Ruggerone et al. 2016; Siegel et al. 2018). While size-selective harvest
623 of Chinook salmon may be driving these observed changes, researchers have hypothesized that
624 additional factors including environmental conditions in the ocean and density dependent effects
625 may be may be increasing late ocean mortality, and may be responsible for the decline of older
626 age classes of Chinook salmon returning spawning grounds (Lewis et al. 2015; Ohlberger et al.
627 2018; Ruggerone et al. 2016). The low survival rate of tagged Chinook salmon in this study
628 provides evidence of relatively common ‘late ocean’ mortality. We hypothesize that large apex
629 predators provide a specific mechanism of this mortality, ultimately contributing to the
630 proportional decrease of older age classes of Chinook salmon returning to the spawning grounds
631 each year. Similarly, predation by porbeagle sharks *Lamna nasus* and Atlantic bluefin tuna
632 *Thunnus thynnus* on the large oceanic life stage of imperiled Atlantic salmon has been
633 hypothesized as an important factor hindering the recovery of stocks from Canadian rivers
634 (Lacroix 2014).

635 **Conclusion**

636 In conclusion, compared to traditional approaches, the current study provides
637 unprecedented insight into movement, behavior, thermal environment, and survivorship of
638 individual Chinook salmon. While information collected in this study is qualitative, it provides
639 information useful for revisiting assumptions about the ecology of Chinook salmon, and provides
640 information which may have future application in understanding its ecology and developing
641 strategies to further reduce incidental catch of this species. Furthermore, high mortality rates in
642 this study suggest that fisheries scientists should consider that late stage mortality by marine
643 apex predators may be shaping this species’ abundance and demographics.

644
645
646
647
648
649
650
651
652
653
654
655
656
657
658
659

Acknowledgments

This project was supported by the Arctic-Yukon-Kuskokwim Sustainable Salmon Initiative and the Pollock Conservation Cooperative Research Center at the University of Alaska Fairbanks. Additional in-kind support was provided by National Marine Fisheries Service Alaska Science Center, NETS Seattle, and the Fisheries Research Agency of Japan. We thank Dave Magone, Mark Evans, Debbie Brown, Parker Bradley, Nicholas Smith, Kristin Neuneker, and Nate Cathcart for their help during winter tagging operations. We thank John Strøm, Audun Rikardsen, and Kaitlyn Manishin for insights into data analyses and reporting. We thank Shigehiko Urawa and Shunpei Sato of the Hokkaido National Fisheries Research Institute, and the captain and crew of the R/V Hokko maru for their help and generosity during summer tagging fieldwork. Koji Tamura of NETS Seattle enabled us to transport a 750 lb. metal box across the Pacific Ocean, not once, but twice. Finally, we thank Robert Walker and Kate Myers, both retired, of the former University of Washington High-Seas Salmon Research Program and Jim Murphy of the National Oceanic and Atmospheric Administration for their valuable insights into all phases of this research project.

660
661
662
663
664
665
666
667
668
669
670
671
672
673
674
675
676
677
678
679
680
681
682

References

Adams, J., I. C. Kaplan, B. Chasco, K. N. Marshall, A. Acevedo-Gutiérrez, and E. J. Ward. 2016. A century of Chinook salmon consumption by marine mammal predators in the Northeast Pacific Ocean. *Ecological Informatics* 34:44-51.

ADF&G. 2013. Chinook salmon stock assessment and research plan, 2013. Alaska Department of Fish and Game, Special Publication No. 13-01, Anchorage, Alaska.

Anderson, S. D., and K. J. Goldman. 2001. Temperature measurements from salmon sharks, *Lamna ditropis*, in Alaskan waters. *Copeia* 2001(3):794-796.

Arkhipkin, A. I., V. A. Bizikov, and A. V. Verkhunov. 1998. Distribution and growth in juveniles of the squid *Berryteuthis magister* (Cephalopoda, Gonatidae) in the western Bering Sea. *Sarsia* 83(1):45-54.

Arnold, G., and H. Dewar. 2001. Electronic tags in marine fisheries research: a 30-year perspective. Pages 7-64 in J. R. Sibert, and J. L. Nielsen, editors. *Electronic tagging and tracking in marine fisheries*. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Arostegui, M. C., T. E. Essington, and T. P. Quinn. 2017. Interpreting vertical movement behavior with holistic examination of depth distribution: a novel method reveals cryptic diel activity patterns of Chinook salmon in the Salish Sea. *Animal Biotelemetry* 5(2).

Austin, D., W. D. Bowen, J. I. McMillan, and D. J. Boness. 2006. Stomach temperature telemetry reveals temporal patterns of foraging success in a free-ranging marine mammal. *Journal of Animal Ecology* 75(2):408-420.

Beamish, R. J., and C. Mahnken. 2001. A critical size and period hypothesis to explain natural regulation of salmon abundance and the linkage to climate and climate change. *Progress in Oceanography* 49(1-4):423-437.

683 Béguer-Pon, M., J. Benchetrit, M. Castonguay, K. Aarestrup, S. E. Campana, M. J. W.
684 Stokesbury, and J. J. Dodson. 2012. Shark predation on migrating adult American eels
685 (*Anguilla rostrata*) in the Gulf of St. Lawrence. PLoS One 7(10):e46830.

686 Benson, J. F., S. J. Jorgensen, J. B. O'Sullivan, C. Winkler, C. F. White, E. Garcia-Rodriguez, O.
687 Sosa-Nishizaki, and C. G. Lowe. 2018. Juvenile survival, competing risks, and spatial
688 variation in mortality risk of a marine apex predator. Journal of Applied Ecology
689 55(6):2888-2897.

690 Braun, C. D., B. Galuardi, and S. R. Thorrold. 2018. HMMoce: An R package for improved
691 geolocation of archival-tagged fishes using a hidden Markov method. Methods in
692 Ecology and Evolution 9(5):1212-1220.

693 Braun, C. D., G. B. Skomal, S. R. Thorrold, and M. L. Berumen. 2015. Movements of the reef
694 manta ray (*Manta alfredi*) in the Red Sea using satellite and acoustic telemetry. Marine
695 biology 162(12):2351-2362.

696 Brodeur, R. D., W. T. Peterson, G. W. Boehlert, E. Casillas, M. H. Schiewe, M. B. Eldridge, S.
697 T. Lindley, J. H. Helle, and W. R. Heard. 2000. A coordinated research plan for estuarine
698 and ocean research on Pacific salmon. Fisheries 25(6):7-16.

699 Call, K. A., B. S. Fadely, A. Greig, and M. J. Rehberg. 2007. At-sea and on-shore cycles of
700 juvenile Steller sea lions (*Eumetopias jubatus*) derived from satellite dive recorders: a
701 comparison between declining and increasing populations. Deep Sea Research Part II:
702 Topical Studies in Oceanography 54(3-4):298-310.

703 Chasco, B., I. C. Kaplan, A. Thomas, A. Acevedo-Gutiérrez, D. Noren, M. J. Ford, M. B.
704 Hanson, J. Scordino, S. Jeffries, S. Pearson, K. N. Marshall, and E. J. Ward. 2017.
705 Estimates of Chinook salmon consumption in Washington State inland waters by four

706 marine mammal predators from 1970 to 2015. Canadian Journal of Fisheries and Aquatic
707 Sciences 74(8):1173-1194.

708 Computers, W. 2015. Data portal's location processing (GPE3 & FastLoc-GPS) user guide.
709 Wildlife Computes, Inc., Redmond, Washington.

710 Cosgrove, R., I. Arregui, H. Arrizabalaga, N. Goni, and J. D. Neilson. 2015. Predation of pop-up
711 satellite archival tagged albacore (*Thunnus alalunga*). Fisheries Research 162:48-52.

712 Courtney, M. B., B. S. Scanlon, A. H. Rikardsen, and A. C. Seitz. 2016. Utility of pop-up
713 satellite archival tags to study the summer dispersal and habitat occupancy of Dolly
714 Varden in Arctic Alaska. Arctic 69(2):137-146.

715 Davis, N. D., M.-a. Fukuwaka, J. L. Armstrong, and K. W. Myers. 2005. Salmon food habits
716 studies in the Bering Sea, 1960 to present. North Pacific Anadromous Fish Commission
717 Technical Report 6:24-28.

718 Davis, N. D., K. W. Myers, and W. J. Fournier. 2009a. Winter food habits of Chinook salmon in
719 the eastern Bering Sea. North Pacific Anadromous Fish Commission Bulletin 5:243-253.

720 Davis, N. D., A. V. Volkov, A. Y. Efimkin, N. A. Kuznetsova, J. L. Armstrong, and O. Sakai.
721 2009b. Review of BASIS salmon food habits studies. North Pacific Anadromous Fish
722 Commission Bulletin 5:197-208.

723 Drenner, S. M., T. D. Clark, C. K. Whitney, E. G. Martins, S. J. Cooke, and S. G. Hinch. 2012. A
724 synthesis of tagging studies examining the behaviour and survival of anadromous
725 salmonids in marine environments. PLoS One 7(3):e31311.

726 Fieberg, J., and G. D. DelGiudice. 2009. What time is it? Choice of time origin and scale in
727 extended proportional hazards models. Ecology 90(6):1687-1697.

728 Ford, J. K. B., and G. M. Ellis. 2006. Selective foraging by fish-eating killer whales *Orcinus*
729 *orca* in British Columbia. Marine Ecology Progress Series 316:185-199.

730 Ford, J. K. B., G. M. Ellis, L. G. Barrett-Lennard, A. B. Morton, R. S. Palm, and K. C. Balcomb
731 III. 1998. Dietary specialization in two sympatric populations of killer whales (*Orcinus*
732 *orca*) in coastal British Columbia and adjacent waters. Canadian Journal of Zoology
733 76:1456-1471.

734 Gales, R., and D. Renouf. 1993. Detecting and measuring food and water intake in captive seals
735 using temperature telemetry. The Journal of Wildlife Management 57(3):514-519.

736 Gisclair, B. R. 2009. Salmon bycatch management in the Bering Sea Walleye pollock fishery:
737 Threats and opportunities for western Alaska. Pages 799-816 in C. C. Krueger, and C. E.
738 Zimmerman, editors. Pacific salmon: Ecology and management of westem Alaska's
739 populations American Fisheries Society, Symposium 70, Bethesda, Maryland.

740 Goldman, K. J., S. D. Anderson, R. J. Latour, and J. A. Musick. 2004. Homeothermy in adult
741 salmon sharks, *Lamna ditropis*. Environmental Biology of Fishes 71(4):403-411.

742 Goldman, K. J., and J. A. Musick. 2008. Biology and ecology of the salmon shark, *Lamna*
743 *ditropis*. Pages 95-104 in C. M.D., P. E.K., and B. E.A., editors. Sharks of the open
744 ocean: biology, fisheries and conservation. Blackwell Scientific, Maldon, Massachusetts.

745 Healey, M. C. 1991. Life history of chinook salmon (*Oncorhynchus tshawytscha*). Pages 313-
746 393 in C. Groot, and L. Margolis, editors. Pacific salmon life histories. University of
747 British Columbia Press, Vancouver, British Columbia.

748 Hedger, R. D., A. H. Rikardsen, J. F. Strøm, D. A. Righton, E. B. Thorstad, and T. F. Næsje.
749 2017a. Diving behaviour of Atlantic salmon at sea: effects of light regimes and
750 temperature stratification. Marine Ecology Progress Series 574:127-140.

751 Hedger, R. D., A. H. Rikardsen, and E. B. Thorstad. 2017b. Pop-up satellite archival tag effects
752 on the diving behaviour, growth and survival of adult Atlantic salmon *Salmo salar* at sea.
753 Journal of Fish Biology 90(1):294-310.

754 Hinke, J. T., D. G. Foley, C. Wilson, and G. M. Watters. 2005a. Persistent habitat use by
755 Chinook salmon *Oncorhynchus tshawytscha* in the coastal ocean. Marine Ecology
756 Progress Series 304:207-220.

757 Hinke, J. T., G. M. Watters, G. W. Boehlert, and P. Zedonis. 2005b. Ocean habitat use in autumn
758 by Chinook salmon in coastal waters of Oregon and California. Marine Ecology Progress
759 Series 285:181-192.

760 Hobday, A. J., J. R. Hartog, T. Timmiss, and J. Fielding. 2010. Dynamic spatial zoning to
761 manage southern bluefin tuna (*Thunnus maccoyii*) capture in a multi-species longline
762 fishery. Fisheries Oceanography 19(3):243-253.

763 Hocking, D. P., E. M. G. Fitzgerald, M. Salverson, and A. R. Evans. 2016. Prey capture and
764 processing behaviors vary with prey size and shape in Australian and subantarctic fur
765 seals. Marine Mammal Science 32(2):568-587.

766 Hocking, D. P., M. A. Ladds, D. J. Slip, E. M. G. Fitzgerald, and A. R. Evans. 2017. Chew,
767 shake, and tear: prey processing in Australian sea lions (*Neophoca cinerea*). Marine
768 Mammal Science 33(2):541-557.

769 Honakalehto, T., and A. McCarthy. 2015. Results of the acoustic-trawl survey of walleye pollock
770 (*Gadus chalcogrammus*) on the U.S. and Russian Bering Sea Shelf in June - August 2014
771 (DY1407). Alaska Fisheries Science Center, National Marine Fisheries Service, Seattle,
772 Washington.

773 Honkalehto, T., A. McCarthy, and N. Lauffenburger. 2018. Results of the acoustic-trawl survey
774 of walleye pollock (*Gadus chalcogrammus*) on the U.S. Bering Sea shelf in June -
775 August 2016 (DY1608). Alaska Fisheries Science Center, National Marine Fisheries
776 Service, Seattle, Washington.

777 Hulbert, L. B., M. F. Sigler, and C. R. Lunsford. 2006. Depth and movement behaviour of the
778 Pacific sleeper shark in the north-east Pacific Ocean. *Journal of Fish Biology* 69(2):406-
779 425.

780 Ianelli, J. N., and D. L. Stram. 2015. Estimating impacts of the pollock fishery bycatch on
781 western Alaska Chinook salmon. *ICES Journal of Marine Science* 72(4):1159-1172.

782 Keating, K. A. 1995. Mitigating elevation-induced errors in satellite telemetry locations. *The*
783 *Journal of Wildlife Management* 59(4):801-808.

784 Kuhn, C. E., and D. P. Costa. 2006. Identifying and quantifying prey consumption using stomach
785 temperature change in pinnipeds. *Journal of Experimental Biology* 209(22):4524-4532.

786 Lacroix, G. L. 2014. Large pelagic predators could jeopardize the recovery of endangered
787 Atlantic salmon. *Canadian Journal of Fisheries and Aquatic Sciences* 71(3):343-350.

788 Lander, M. E., D. S. Johnson, J. T. Sterling, T. S. Gelatt, and B. S. Fadely. 2011. Diving
789 behaviors and movements of juvenile steller sea lions (*Eumetopias jubatus*) captured in
790 the central Aleutian Islands, April 2005. Alaska Fisheries Science Center, National
791 Marine Fisheries Service,, NMFS-AFSC-218, Seattle, Washington.

792 Larson, W. A., F. M. Utter, K. W. Myers, W. D. Templin, J. E. Seeb, C. M. Guthrie III, A. V.
793 Bugaev, and L. W. Seeb. 2013. Single-nucleotide polymorphisms reveal distribution and
794 migration of Chinook salmon (*Oncorhynchus tshawytscha*) in the Bering Sea and North
795 Pacific Ocean. *Canadian Journal of Fisheries and Aquatic Sciences* 70(1):128-141.

796 Lewis, B., W. S. Grant, R. E. Brenner, and T. Hamazaki. 2015. Changes in size and age of
797 Chinook salmon *Oncorhynchus tshawytscha* returning to Alaska. PLoS One
798 10(6):e0130184.

799 Loher, T., and A. Seitz. 2006. Seasonal migration and environmental conditions of Pacific
800 halibut *Hippoglossus stenolepis*, elucidated from pop-up archival transmitting (PAT)
801 tags. Marine Ecology Progress Series 317:259-271.

802 Lynch, S. D., B. J. Marcek, H. M. Marshall, P. G. Bushnell, D. Bernal, and R. W. Brill. 2017.
803 The effects of pop-up satellite archival tags (PSATs) on the metabolic rate and swimming
804 kinematics of juvenile sandbar shark *Carcharhinus plumbeus*. Fisheries Research
805 186:205-215.

806 Madsen, S., and K. Haflinger. 2016. Chinook salmon bycatch reduction incentive plan. Report
807 to National Marine Fisheries Service.

808 Methling, C., C. Tudorache, P. V. Skov, and J. F. Steffensen. 2011. Pop up satellite tags impair
809 swimming performance and energetics of the European eel (*Anguilla anguilla*). PLoS
810 One 6(6):e20797.

811 Murphy, J. M., and W. R. Heard. 2001. Chinook salmon data storage tag studies in Southeast
812 Alaska, 2001. North Pacific Anadromous Fish Commission Document 555:1-21.

813 Murphy, J. M., and W. R. Heard. 2002. Chinook salmon data storage tag studies in Southeast
814 Alaska, 2002. North Pacific Anadromous Fish Commission Document 632:1-16.

815 Musyl, M. K., M. L. Domeier, N. Nasby-Lucas, R. W. Brill, L. M. McNaughton, J. Y. Swimmer,
816 M. S. Lutcavage, S. G. Wilson, B. Galuardi, and J. B. Liddle. 2011. Performance of pop-
817 up satellite archival tags. Marine Ecology Progress Series 433:1-28.

818 Myers, K. W., J. R. Irvine, E. A. Logerwell, S. Urawa, S. V. Naydenko, A. V. Zavolokin, and N.
819 D. Davis. 2016. Pacific salmon and steelhead: life in a changing winter ocean. North
820 Pacific Anadromous Fish Commission Bulletin 6:113-138.

821 Myers, K. W., R. V. Walker, N. D. Davis, J. L. Armstrong, and M. E. Kaeriyama. 2009. High
822 seas distribution, biology, and ecology of Arctic–Yukon–Kuskokwim salmon: direct
823 information from high seas tagging experiments, 1954–2006. C. C. Krueger, and C. E.
824 Zimmerman, editors. Pacific salmon: Ecology and management of western Alaska's
825 populations volume 70. American Fisheries Society, Bethesda, Maryland.

826 Nagasawa, K. 1998. Predation by salmon sharks (*Lamna ditropis*) on Pacific salmon
827 (*Oncorhynchus* spp.) in the North Pacific Ocean. North Pacific Anadromous Fish
828 Commission Bulletin 1:419-433.

829 NPFMC. 2008. Draft environmental impact statement for Bering Sea/Aleutian Islands Chinook
830 salmon bycatch management. North Pacific Fisheries Management Council, Anchorage,
831 Alaska.

832 NPFMC. 2016. Bering Sea Chinook salmon and chum salmon bycatch management measures
833 North Pacific Fishery Management Council, Anchorage, Alaska.

834 Ohlberger, J., E. J. Ward, D. E. Schindler, and B. Lewis. 2018. Demographic changes in
835 Chinook salmon across the Northeast Pacific Ocean. *Fish and Fisheries* 19(3):533-546.

836 Okey, T. A., B. A. Wright, and M. Y. Brubaker. 2007. Salmon shark connections: North Pacific
837 climate change, indirect fisheries effects, or just variability? *Fish and Fisheries* 8(4):359-
838 366.

839 Pedersen, M. W. 2010. Hidden Markov modelling of movement data from fish. Technical
840 University of Denmark, Kongens Lyngby, Denmark.

841 Quinn, T. P. 2005. The behavior and ecology of Pacific salmon and trout. University of
842 Washington Press, Seattle, Washington.

843 Riddle, B. E., R. D. Brodeur, A. V. Bugaev, P. Moran, J. M. Murphy, J. A. Orsi, M. Trudel, L.
844 A. Weitkamp, B. K. Wells, and A. C. Wertheimer. 2018. Ocean ecology of Chinook
845 salmon. Pages 555-696 in R. J. Beamish, editor. The ocean ecology of Pacific salmon and
846 trout. America Fisheries Society, Bethesda, Maryland.

847 Ruggerone, G. T., B. M. Connors, B. A. Agler, L. I. Wilson, and D. C. Gwinn. 2016. Growth,
848 age at maturation, and survival of Yukon, Kuskokwim, and Nushagak Chinook salmon.
849 Final report to Arctic-Yukon Kuskokwim Sustainable Salmon Initiative, Anchorage,
850 Alaska.

851 Schindler, D., C. Krueger, P. Bisson, M. Bradford, B. Clark, J. Conitz, K. Howard, M. Jones, J.
852 Murphy, and K. Myers. 2013. Arctic-Yukon-Kuskokwim Chinook salmon research
853 action plan: Evidence of decline of Chinook salmon populations and recommendations
854 for future research. Prepared for the AYK Sustainable Salmon Initiative., Anchorage,
855 Alaska.

856 Seitz, A. C., T. Loher, B. L. Norcross, and J. L. Nielsen. 2011. Dispersal and behavior of Pacific
857 halibut *Hippoglossus stenolepis* in the Bering Sea and Aleutian Islands region. Aquatic
858 Biology 12(3):225-239.

859 Smedbol, R. K., and J. S. Wroblewski. 2002. Metapopulation theory and northern cod population
860 structure: interdependency of subpopulations in recovery of a groundfish population.
861 Fisheries Research 55(1-3):161-174.

862 Stabeno, P. J., N. A. Bond, N. B. Kachel, S. A. Salo, and J. D. Schumacher. 2001. On the
863 temporal variability of the physical environment over the south-eastern Bering Sea.
864 Fisheries Oceanography 10(1):81-98.

865 Stabeno, P. J., N. A. Bond, and S. A. Salo. 2007. On the recent warming of the southeastern
866 Bering Sea shelf. Deep Sea Research Part II: Topical Studies in Oceanography 54(23-
867 26):2599-2618.

868 Stabeno, P. J., S. L. Danielson, D. G. Kachel, N. B. Kachel, and C. W. Mordy. 2016. Currents
869 and transport on the eastern Bering Sea shelf: An integration of over 20 years of data.
870 Deep Sea Research Part II: Topical Studies in Oceanography 134:13-29.

871 Stabeno, P. J., J. D. Schumacher, and K. Ohtani. 1999. The physical oceanography of the Bering
872 Sea. Pages 1-28 *in* T. L. Thomas, and K. Ohtani, editors. Dynamics of the Bering Sea: a
873 summary of physical, chemical, and biological characteristics, and a synopsis of research
874 on the Bering Sea. University of Alaska Sea Grant, Fairbanks, Alaska.

875 Stram, D. L., and J. N. Ianelli. 2009. Eastern Bering Sea pollock trawl fisheries: variation in
876 salmon bycatch over time and space. Pages 827-850 *in* C. C. Krueger, and C. E.
877 Zimmerman, editors. Pacific salmon: Ecology and management of western Alaska's
878 populations. American Fisheries Society, Symposium 70, Bethesda, Maryland.

879 Stram, D. L., and J. N. Ianelli. 2015. Evaluating the efficacy of salmon bycatch measures using
880 fishery-dependent data. ICES Journal of Marine Science 72(4):1173-1180.

881 Strøm, J. F. 2018. Ocean migration of Atlantic salmon. Ph.D Disertation. UiT The Arctic
882 University of Norway, Tromsø, Norway.

883 Strøm, J. F., E. B. Thorstad, G. Chafe, S. H. Sørbye, D. Righton, A. H. Rikardsen, and J. Carr.
884 2017. Ocean migration of pop-up satellite archival tagged Atlantic salmon from the
885 Miramichi River in Canada. *ICES Journal of Marine Science* 74(5):1356-1370.

886 Strøm, J. F., E. B. Thorstad, R. D. Hedger, and A. H. Rikardsen. 2018. Revealing the full ocean
887 migration of individual Atlantic salmon. *Animal Biotelemetry* 6(1):2.

888 Thorstad, E. B., A. H. Rikardsen, A. Alp, and F. Økland. 2013. The use of electronic tags in fish
889 research—an overview of fish telemetry methods. *Turkish Journal of Fisheries and*
890 *Aquatic Sciences* 13:881-896.

891 Thygesen, U. H., M. W. Pedersen, and H. Madsen. 2009. Geolocating fish using hidden Markov
892 models and data storage tags. Pages 277-293 in J. L. Nielsen, and coeditors, editors.
893 *Tagging and tracking of marine animals with electronic devices*. Springer, Netherlands.

894 Trites, A. W., and B. T. Porter. 2002. Attendance patterns of Steller sea lions (*Eumetopias*
895 *jubatus*) and their young during winter. *Journal of Zoology* 256(4):547-556.

896 Wahlberg, M., H. Westerberg, K. Aarestrup, E. Feunteun, P. Gargan, and D. Righton. 2014.
897 Evidence of marine mammal predation of the European eel (*Anguilla anguilla* L.) on its
898 marine migration. *Deep Sea Research Part I: Oceanographic Research Papers* 86:32-38.

899 Walker, R. V., and K. W. Myers. 2009. Behavior of Yukon River Chinook salmon in the Bering
900 Sea as inferred from archival tag data. *North Pacific Anadromous Fish Commission*
901 *Bulletin* 5:121-130.

902 Walker, R. V., V. V. Sviridov, S. Urawa, and T. Azumaya. 2007. Spatio-temporal variation in
903 vertical distributions of Pacific salmon in the ocean. *North Pacific Anadromous Fish*
904 *Commission Bulletin* 4:193-201.

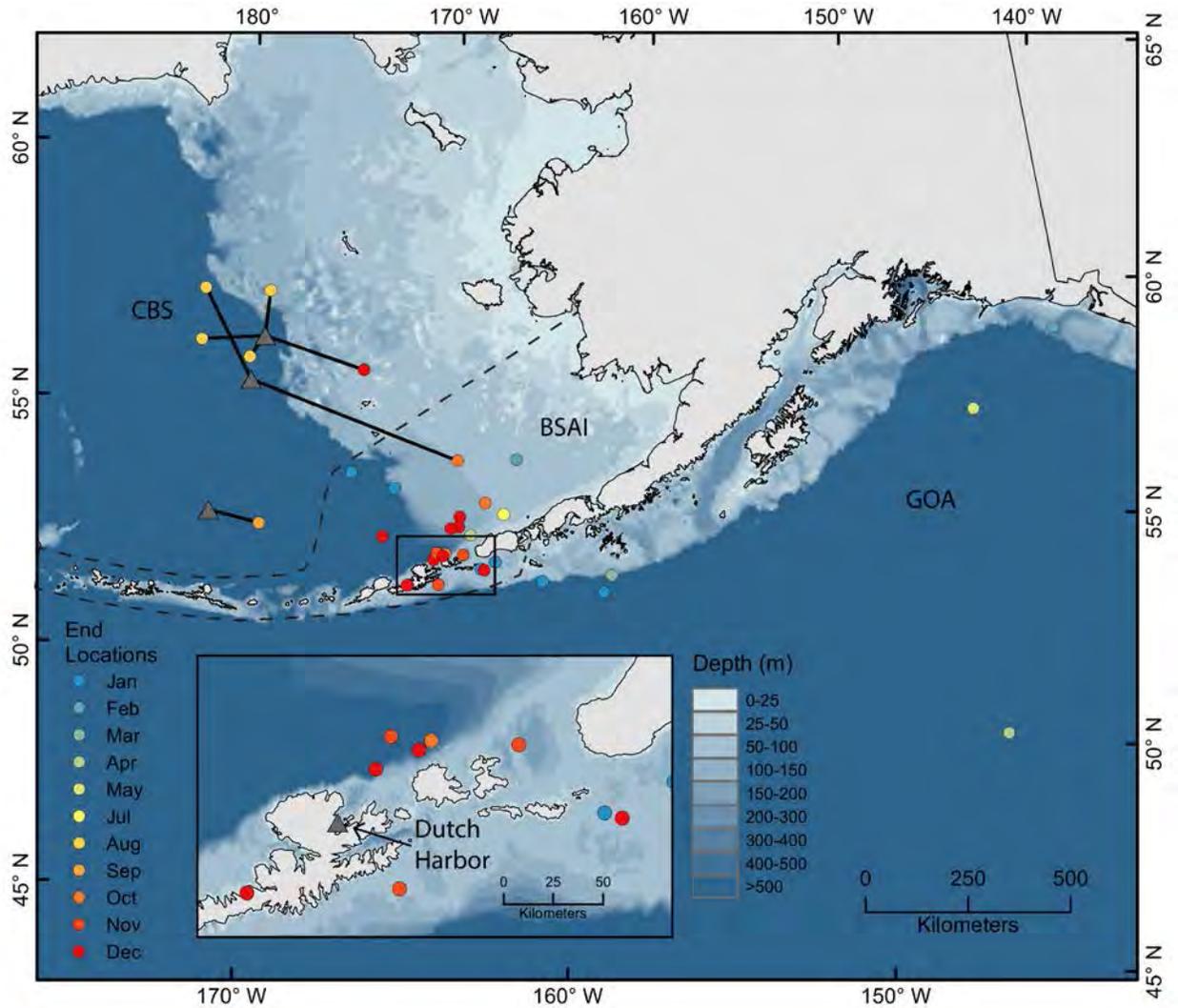
905 Walli, A., S. L. Teo, A. Boustany, C. J. Farwell, T. Williams, H. Dewar, E. Prince, and B. A.
906 Block. 2009. Seasonal movements, aggregations and diving behavior of Atlantic bluefin
907 tuna (*Thunnus thynnus*) revealed with archival tags. PLoS One 4(7):e6151.

908 Weng, K. C., P. C. Castilho, J. M. Morrissette, A. M. Landeira-Fernandez, D. B. Holts, R. J.
909 Schallert, K. J. Goldman, and B. A. Block. 2005. Satellite tagging and cardiac physiology
910 reveal niche expansion in salmon sharks. Science 310(5745):104-106.

911 Weng, K. C., D. G. Foley, J. E. Ganong, C. Perle, G. L. Shillinger, and B. A. Block. 2008.
912 Migration of an upper trophic level predator, the salmon shark *Lamna ditropis*, between
913 distant ecoregions. Marine Ecology Progress Series 372:253-264.

914 Wilson, S. G., and B. A. Block. 2009. Habitat use in Atlantic bluefin tuna *Thunnus thynnus*
915 inferred from diving behavior. Endangered Species Research 10:355-367.

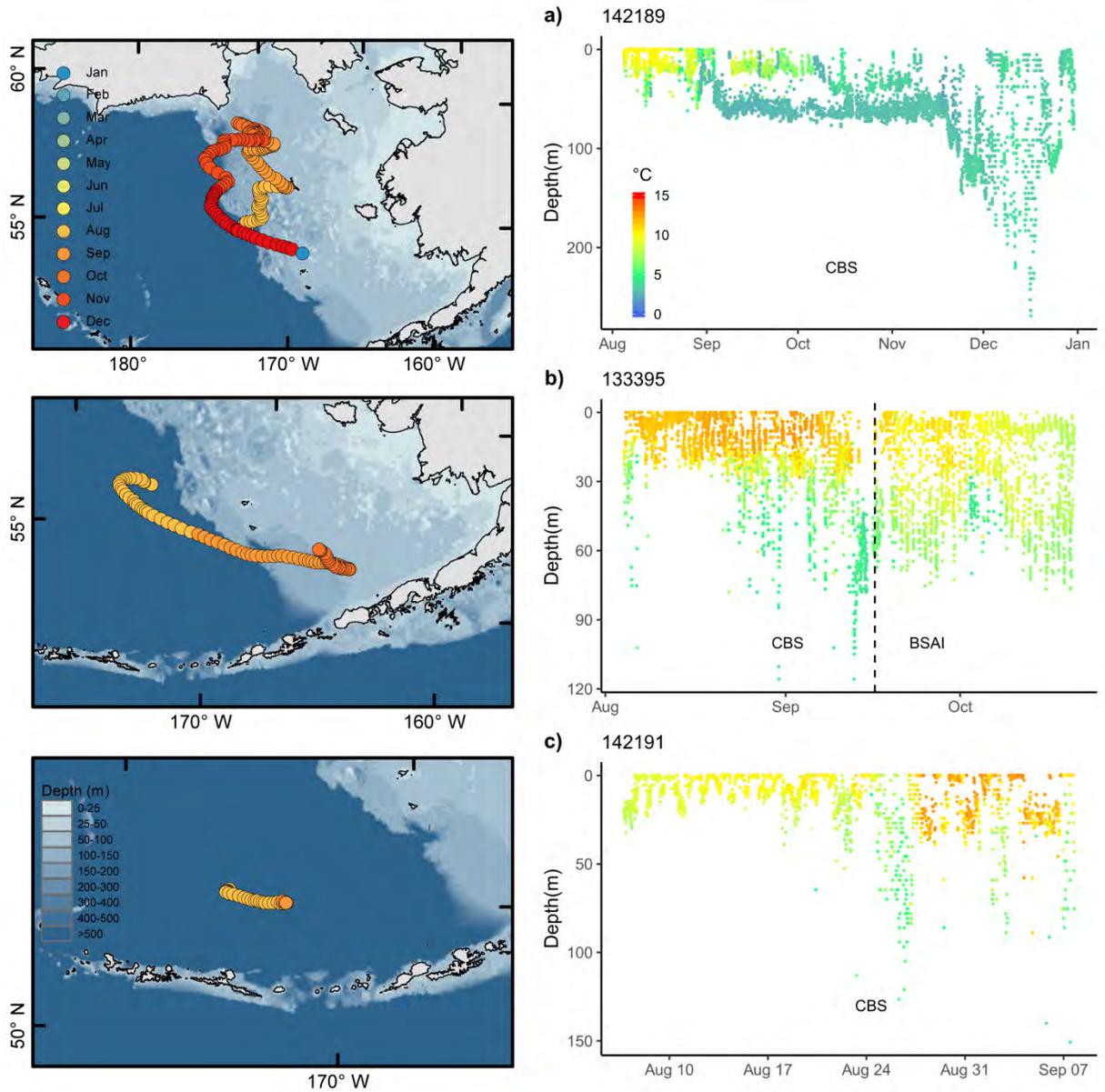
916



917

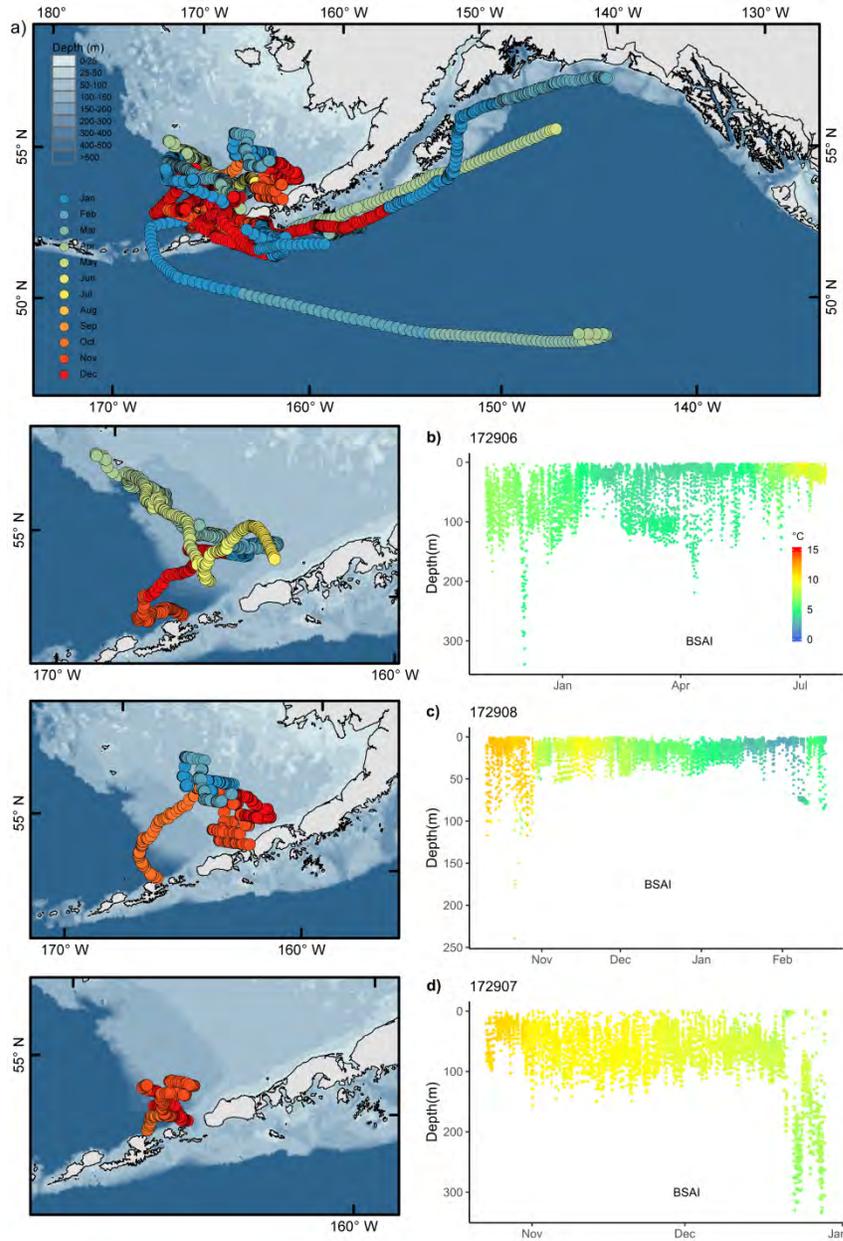
918 Figure 1. All tagging locations (triangles) and end locations (circles; n = 33) of pop-up satellite
 919 archival tagged Chinook salmon in the Bering Sea tagged in Dutch Harbor, AK during October
 920 to December and in the central Bering Sea (CBS) in August. Solid black lines connect tagging
 921 and pop-up locations (CBS tag deployments) for interpretive purposes, but do not represent
 922 likely movement paths. Aggregations of end locations are delineated (dashed lines) by
 923 geographic regions, including the CBS, eastern Bering Sea/Aleutian Islands (BSAI) and Gulf of
 924 Alaska (GOA).

925



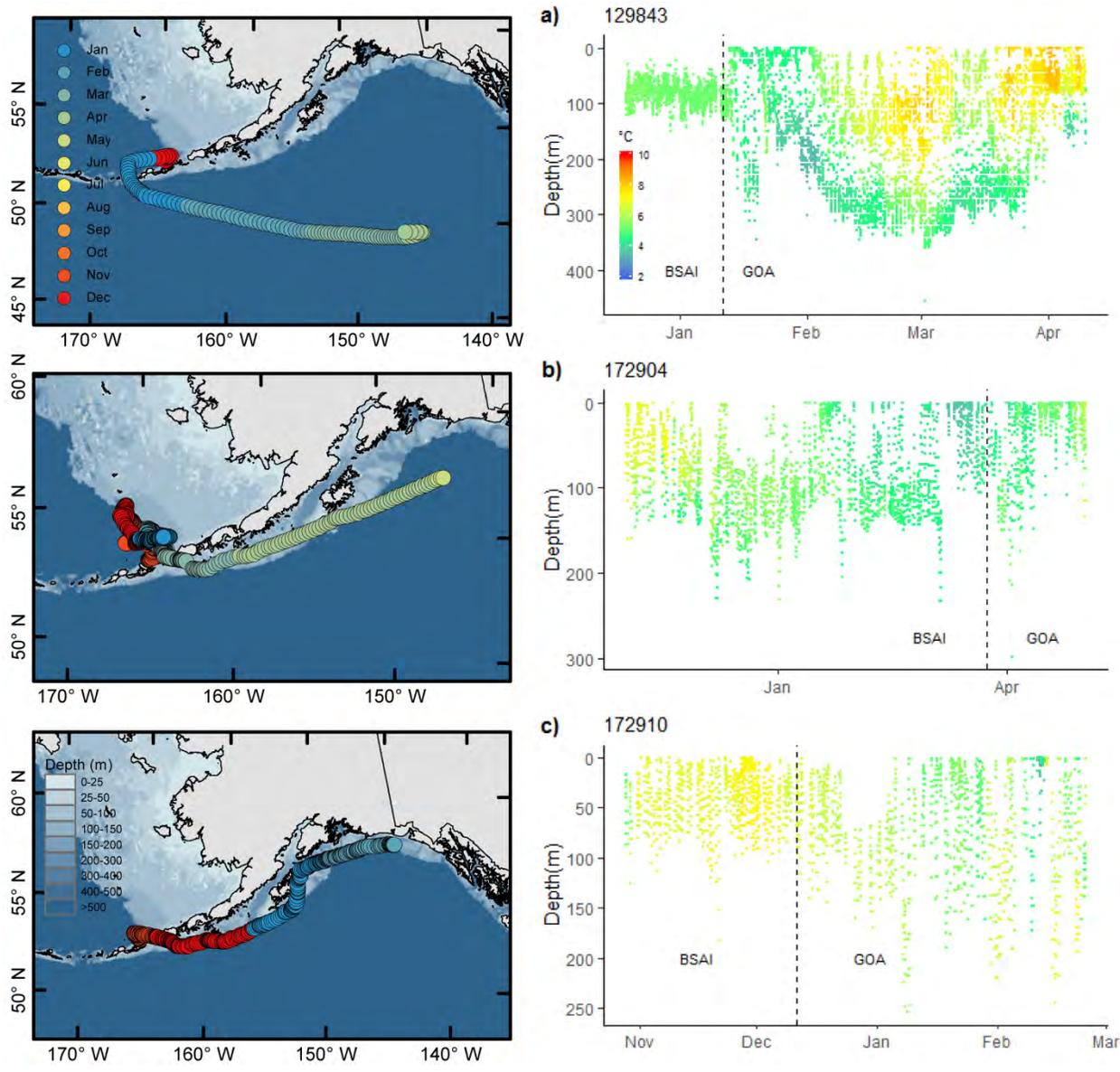
926

927 Figure 2. Most likely paths produced by a hidden Markov model (left) and temperature at depth
 928 (right) of three tagged Chinook salmon in the central Bering Sea (CBS) in August 2015 that were
 929 at liberty >30 days. Tag identification numbers are noted in respective panels and correspond to
 930 those given in Table A1. Vertical dashed lines in depth and temperature time series represent the
 931 time of transition between geographic regions. BSAI=Bering Sea/Aleutian Islands.



932

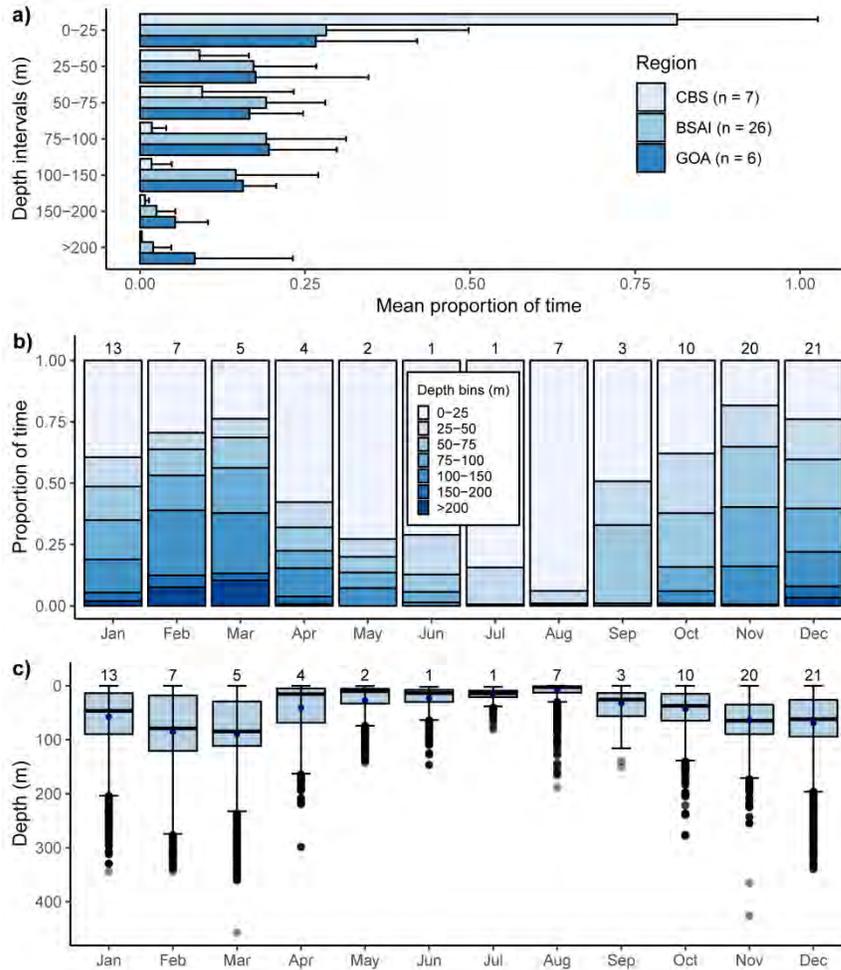
933 Figure 3. a) Most likely movement paths produced by a hidden Markov model for all Chinook
 934 salmon (n = 18) tagged in the eastern Bering Sea/Aleutian Islands (BSAI) that were at liberty for
 935 at least 30 days. b, c, d) Examples of three individual most likely movement paths (left) and
 936 temperature at depth (right) of Chinook salmon tagged in the BSAI. Tag identification numbers
 937 are noted in respective panels and correspond to those given in Table A1.



938

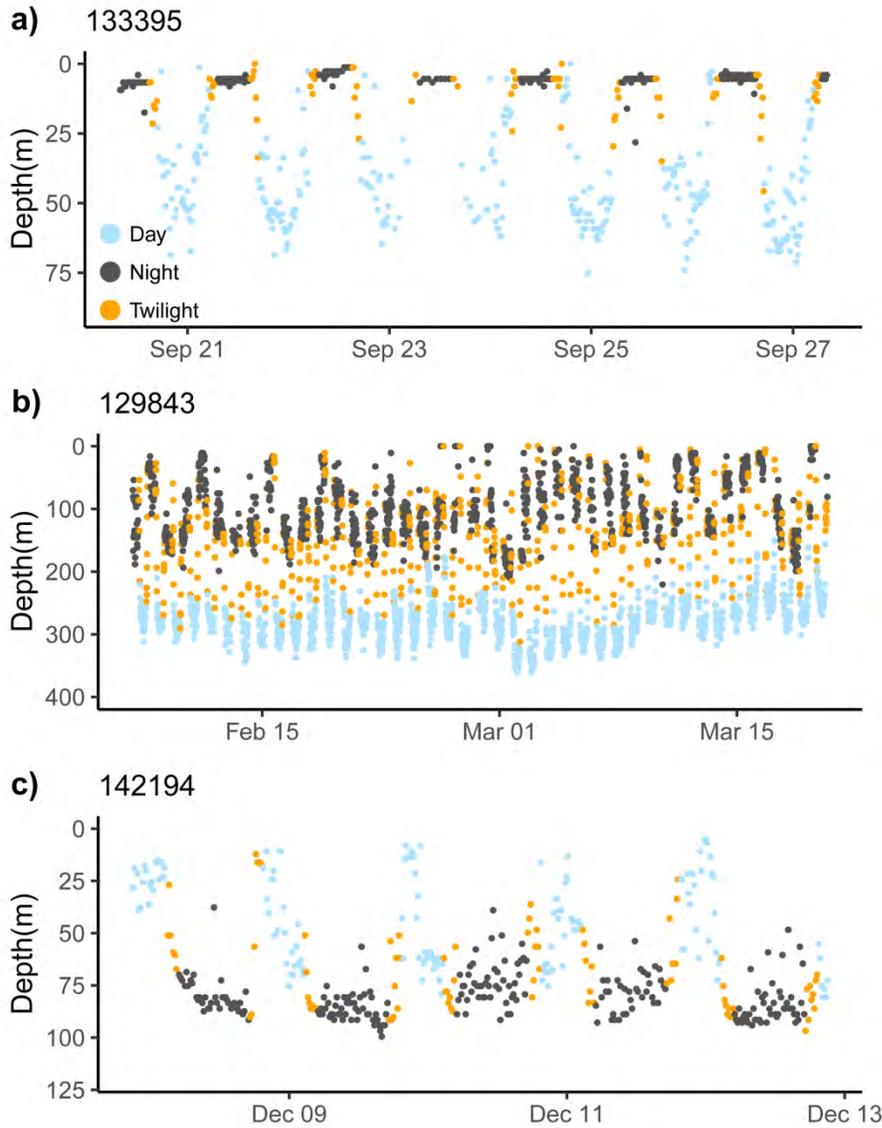
939 Figure 4. Most likely paths produced by a hidden Markov model (left) and temperature at depth
 940 (right) of tagged Chinook salmon whose tags reported in the Gulf of Alaska (GOA). Tag
 941 identification numbers are noted in respective panels and correspond to those given in Table A1.
 942 Vertical dashed lines in depth and temperature time series represent the time of transition
 943 between geographic regions. BSAI=Bering Sea/Aleutian Islands.

944



945

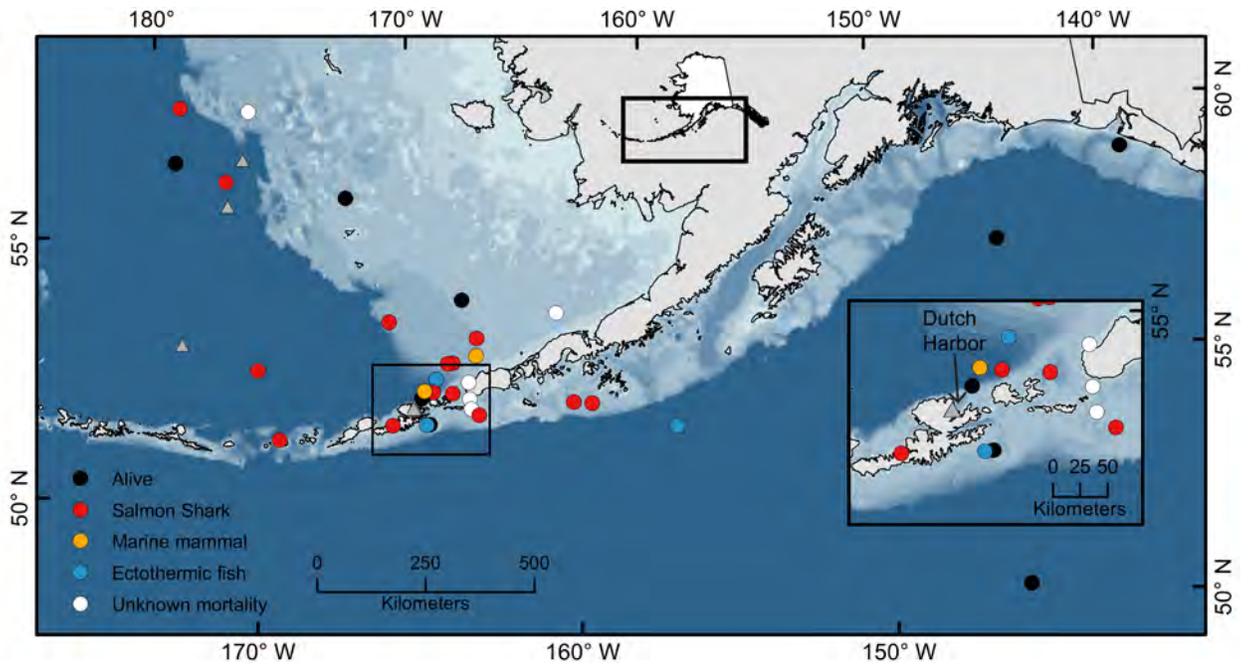
946 Figure 5. (a) Aggregated regional mean proportion of time spent at discrete depth bins of
 947 Chinook salmon tagged with pop-up satellite archival tags in the Bering Sea. (b) Aggregated
 948 monthly proportion of time spent in discrete depth bins, and (c) seasonal trends in depth
 949 distribution. For plot (a), whiskers represent the standard deviation. For boxplots (c), median
 950 diving depths are solid lines, means are blue dots, and boxes represent the first and third
 951 quartiles. Whiskers represent the largest observation less than or equal to the box, plus or minus
 952 1.5 times the interquartile range, and black dots represent outliers. The number of unique PSATs
 953 used for analyses are noted in each respective panel. CBS=central Bering Sea, BSAI=Bering
 954 Sea/Aleutian Islands, GOA=Gulf of Alaska.



955

956 Figure 6. Zoomed examples of differences in diel depth occupation in which the tagged Chinook
 957 salmon occupied deeper depths during the daytime (a, b) or nighttime (c). Tag identification
 958 numbers are noted in respective panels and correspond to those given in Table A1.

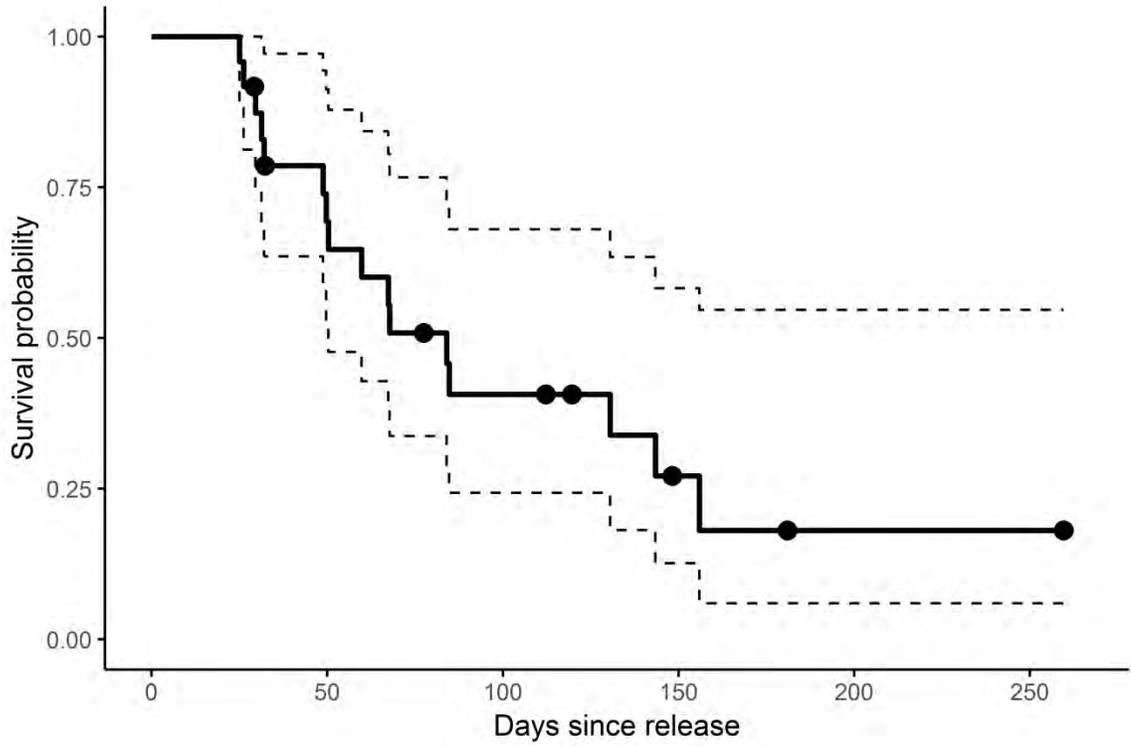
959



960

961 Figure 7. End locations of PSATs attached to Chinook salmon (n =33) in the central and eastern
 962 Bering Sea. Colors indicate inferred fates of individual tagged Chinook salmon. Specifically,
 963 “alive” refers to Chinook salmon that were inferred to be alive when their PSAT popped-up and
 964 reported to satellites, while it is inferred that the remaining fish were consumed by various
 965 predators. Gray triangles denote tag deployment locations.

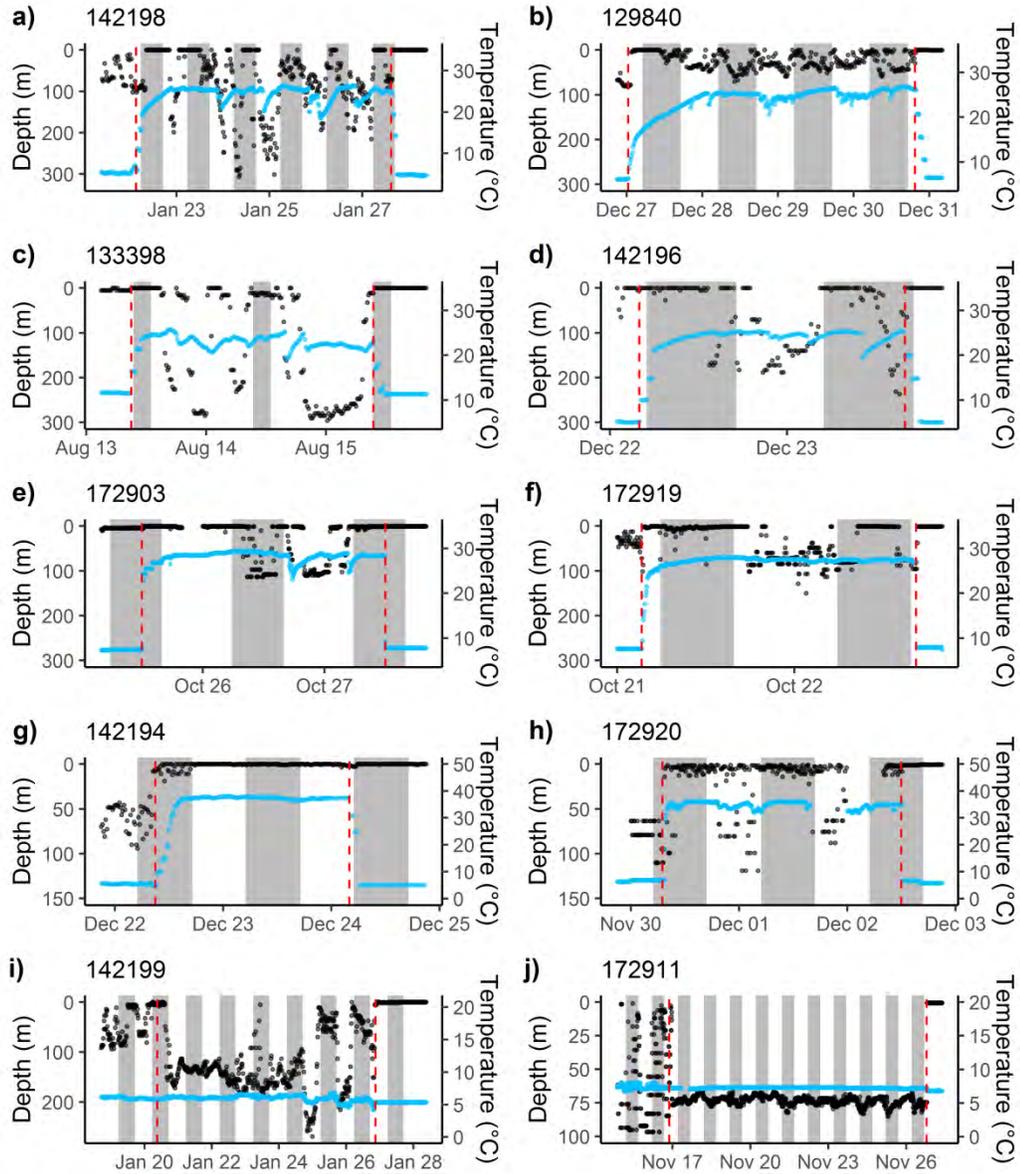
966



967

968 Figure 8. Kaplan-Meier survival probabilities (solid line) and 95% confidence intervals (dashed
 969 lines) of tagged Chinook salmon ($n = 24$) for the monitoring period (25–262 days) of this study.
 970 Solid circles denote tagged fish inferred to be alive (i.e., censored individuals) at the time of
 971 PSAT reporting.

972



973

974 Figure 9. Examples of tagged Chinook salmon predation by salmon sharks (a–f), marine
 975 mammals (g, h), and ectothermic fish(es) (i, j). Black circles denote depth measured by the tag
 976 and blue circles denote temperature. Red dashed lines denote estimated times of predator
 977 consumption and subsequent expulsion of PSATs. Gray shaded regions represent periods of
 978 night. Tag identification numbers are noted in respective panels and correspond to those in Table
 979 A1.

981 Table A1. Deployment information for pop-up satellite archival tags attached to 43 Chinook salmon in the Bering Sea.

Tag ID	Tag type	Fork length (cm)	Deployment date (GMT)	End date (GMT)	Data days ^a	Resolution (min)	Percent data retrieved	Depth (m) ^b	Temperature (°C) ^b	Depth range (m)	Temperature range (°C)	Displacement (km)	Track length (km)	Pop-up reason ^c
129843	Xtag	85	12/19/2013	4/10/2014	112	15	84	127.9±92.8 (99.5)	5.6±1.2 (5.2)	0–538	3.4–8.4	14845	2345	Pop-up date reached
^r 133398	Xtag	61	8/4/2014	8/13/2014	9	15	100	4.5±3.7 (4)	11.6±0.6 (11.5)	0–48	6–12.6	250		Premature release
133395	Xtag	63	8/4/2014	10/20/2014	77	15	80	20.3±19.6 (13.4)	9.6±2.3 (10.1)	0–161	3.5–12.8	545	980	Premature release
^r 142195	Xtag	67	12/18/2014	12/19/2014	0	15	100					0		Premature release
^r 129840	Xtag	79	12/17/2014	12/27/2014	9	15	100	46.2±39.6 (37.7)	6.2±0.3 (6)	0–172	5.7–6.6	130		Premature release
^r 142190	Xtag	59	8/4/2015	8/11/2015	6	15	100	13.8±24.5 (2)	8.9±1.8 (10)	0–194	3.4–10.6	63		Premature release
^r 142193	Xtag	68	8/4/2015	8/12/2015	7	15	99	6±13.6 (1.3)	9.8±1.2 (10.1)	0–118	4.2–10.9	111		Premature release
148493	HRXtag	57	8/4/2015	8/18/2015	14	2	93	5.3±6 (2.7)	10.3±0.4 (10.4)	0–38	7.4–10.9	154		Pop-up date reached
^r 142191	Xtag	66	8/6/2015	9/7/2015	32	15	80	12.4±16.8 (7.4)	9.9±1.8 (10.1)	0–204	4–13.5	127	168	Premature release
^r 142200	Xtag	64	11/21/2015	11/21/2015	0	15	92					28		Premature release
^r 142192	Xtag	68	11/20/2015	12/15/2015	25	15	5					110		Pop-up date reached
^r 142196	Xtag	70	11/20/2015	12/22/2015	31	15	93	74±54.7 (64.6)	5.7±0.4 (5.7)	0–301	4.5–6.6	145	267	Premature release
^r 142194	Xtag	89	11/22/2015	12/22/2015	30	15	89	44.1±28.4 (40.3)	6±0.3 (6)	0–172	4.5–6.8	152	265	Premature release
142189	Xtag	65	8/4/2015	11/01/2015	150	15	56	45.6±36.6 (48.4)	4.9±2.8 (3.5)	0–285	-0.6–10.6	256	2354	Pop-up date reached
^r 142199	Xtag	79	12/2/2015	1/20/2016	49	15	91	43.6±42.3 (32.3)	5.9±0.4 (6)	0–221	2.5–7	450	711	Premature release
^r 142197	Xtag	89	11/22/2015	1/21/2016	60	15	31	22.1±26.2 (6.7)	5.7±0.5 (5.8)	0–221	4–7	140	676	Premature release
^r 142198	Xtag	79	12/2/2015	1/22/2016	50	15	83	71.7±35.6 (67.2)	5.7±0.4 (5.7)	0–296	2.4–6.5	220	524	Premature release
^r 172919	MiniPAT	70	10/16/2017	10/21/2017	5	5	90	33.5±18.9 (30.5)	7.6±0.1 (7.6)	0–102	7.8–6.8	55		Premature release
^r 172903	MiniPAT	70	10/16/2017	10/25/2017	9	5	85	49.6±39.7 (42.5)	7.1±0.7 (7.3)	0–256	7.9–4.1	213		Premature release
^r 172918	MiniPAT	74	10/22/2017	11/2/2017	11	10	82	75.5±61.2 (85)	6.4±1.1 (6.8)	0–296	7.7–4	97		Premature release
^r 172911	MiniPAT	81	11/3/2017	11/16/2017	13	10	80	56.4±40.7 (57.5)	7.3±0.6 (7.3)	0–456	8.3–4	71		Premature release
^r 172920	MiniPAT	100	11/4/2017	11/30/2017	26	10	74	91.4±26.3 (89.5)	6.5±0.2 (6.6)	0–232	6.9–5.8	46		Premature release
172915	MiniPAT	77	11/3/2017	12/2/2017	29	10	84	64.7±29.9 (65)	6.6±0.3 (6.6)	0–208	7.4–4.3	28		Premature release
172902	MiniPAT	69	11/3/2017	12/5/2017	32	10	58	97.2±33.3 (96.5)	6.4±0.3 (6.4)	0–256	6.9–4.3	50	226	Premature release
^r 172916	MiniPAT	65	10/23/2017	12/11/2017	50	10	50	57.5±36.6 (53)	7.5±0.4 (7.5)	0–272	8.4–4.6	145	375	Premature release
^r 172907	MiniPAT	82	10/22/2017	12/28/2017	67	5	74	77.2±51.9 (68)	6.3±0.7 (6.3)	0–360	7.7–4	121	862	Premature release
^r 172913	MiniPAT	80	10/31/2017	1/6/2018	68	10	43	72.1±50.4 (67)	5.9±0.8 (6.2)	0–312	7.2–4	310	714	Premature release
^r 172905	MiniPAT	76	10/16/2017	1/8/2018	85	7.5	43	37.7±30.6 (32)	6.9±0.8 (7.1)	0–140	8.4–5	180	725	Premature release
^r 172917	MiniPAT	71	11/3/2017	1/26/2018	84	10	47	63.7±28.9 (71.5)	6.7±0.9 (6.8)	0–132	8.6–4.1	290	957	Premature release
^r 172908	MiniPAT	80	10/10/2017	2/17/2018	130	10	79	19.5±19.8 (11.5)	4.4±1.9 (4.1)	0–256	8.1–1.2	350	2518	Premature release
172910	MiniPAT	76	10/27/2017	2/23/2018	120	10	49	68.4±47.6 (61.5)	6.4±0.7 (6.5)	0–272	7.7–2.6	1690	2123	Premature release
^r 172901	MiniPAT	83	11/3/2017	3/26/2018	143	10	41	68.4±31.1 (72)	5.4±0.8 (5.4)	0–196	6.9–3.8	460	1314	Premature release
^r 172912	MiniPAT	82	11/3/2017	4/8/2018	156	10	60	93.1±69.1 (91)	5.2±0.9 (4.9)	0–352	7.2–3.5	134	1227	Premature release
172904	MiniPAT	77	11/2/2017	5/2/2018	181	10	89	82.7±52.9 (93.5)	5.1±0.8 (5.1)	0–320	7.3–3.5	1425	2937	Pop-up date reached
172906	MiniPAT	70	11/3/2017	7/20/2018	260	10	71	50±45.9 (30)	5.5±1.6 (5.1)	0–352	10.7–3.3	230	2581	Premature release
172909	MiniPAT	73	10/22/2017											Missing
172914	MiniPAT	63	10/19/2017				0							Premature release
129839	Xtag	59	8/2/2014											Missing
129841	Xtag	72	8/3/2014											Missing
129842	Xtag	62	8/3/2014											Missing
129844	Xtag	60	8/5/2014											Missing
133396	Xtag	62	8/3/2014											Missing
133397	Xtag	59	8/5/2015											Missing

a) Data days to the time period PSATs were attached to a live fish

b) Depth and temperature are reported as mean ± standard deviation, with median values in parentheses

c) For Pop-up reason, “Pop-up date reached” refers to tags released from fish on its programmed date. “Premature release” refers to tags which triggered a fail-safe mechanism by remaining at a constant pressure (±2.5 m) for a period of 2–7 days. “Missing” refers to tags which failed to transmit to satellites and were unaccounted for.

p) Denotes fish which tag records indicated that the tagged fish was ingested by a predator

u) Denotes fish in which tag records indicated that the tagged fish experienced unknown mortality

r) Denotes fish which appeared to have died immediately after release