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1 Behavioral context of echolocation and prey-handling sounds produced by killer whales (*Orcinus*
2 *orca*) during pursuit and capture of Pacific salmon (*Oncorhynchus* spp.)

3

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20 Availability of preferred salmonid prey and a sufficiently quiet acoustic environment in which to
21 forage are critical to the survival of resident killer whales (*Orcinus orca*) in the northeastern Pacific.
22 Although piscivorous killer whales rely on echolocation to locate and track prey, the relationship
23 between echolocation, movement, and prey capture during foraging by wild individuals is poorly
24 understood. We used acoustic biologging tags to relate echolocation behavior to prey pursuit and
25 capture during successful feeding dives by fish-eating killer whales in coastal British Columbia,
26 Canada. The significantly higher incidence and rate of echolocation prior to fish captures compared
27 to afterward confirms its importance in prey detection and tracking. Extremely rapid click sequences
28 (buzzes) were produced before or concurrent with captures of salmon at depths typically exceeding
29 50 m, and were likely used by killer whales for close-range prey targeting, as in other odontocetes.
30 Distinctive crunching and tearing sounds indicative of prey handling behavior occurred at relatively
31 shallow depths following fish captures, matching concurrent observations that whales surfaced with
32 fish prior to consumption and often shared prey. Buzzes and prey-handling sounds are potentially
33 useful acoustic signals for estimating foraging efficiency and determining if resident killer whales
34 are meeting their energetic requirements.

35

36 **KEYWORDS**

37 echolocation, foraging behavior, prey handling, biologging tag, killer whale, *Orcinus orca*, salmon
38 predation

39

40 *Introduction*

41 Early scientific work established that toothed whales produce pulses of clicks that function
42 as sophisticated echolocation signals (Kellogg et al., 1953; Kellogg, 1958) to facilitate prey detection
43 and tracking. Since the discovery of cetacean sonar, studies of captive individuals (whose behaviors
44 can be readily observed and manipulated) have revealed much about the echolocation capabilities
45 of odontocetes. Captive studies have shown that dolphins can find and distinguish a large variety of
46 targets with great accuracy using sonar clicks, even when their vision is restricted (e.g., Nachtigall,
47 1980; Norris et al., 1961; Verfuß et al., 2009). Experiments using trained dolphins or porpoises
48 presented with target detection tasks (e.g., Au, et al., 1982; Evans & Powell, 1967; Johnson, 1967;
49 Morozov et al., 1972; Wisniewska et al., 2012) also revealed that odontocete click intervals are
50 equivalent to the two-way transit time of a click to a target, plus a lag time for signal processing,
51 which means that click repetition rates are correlated with target range (Au, 1993).

52 Although captive studies have provided detailed information about the sonar capabilities of
53 odontocetes, translating these findings into an understanding of how echolocation is used in the wild
54 presents a considerable challenge. Biologging tags with sensors for detecting both sound and
55 movement (e.g., digital acoustic recording tags or Dtags: Johnson & Tyack, 2003) have provided
56 the first data directly linking movement behavior during foraging with echolocation signals
57 produced by free-ranging odontocetes. For instance, click echoes rebounding from prey were first
58 recorded in the wild using Dtags deployed on beaked whales (Johnson et al., 2004). Acoustic tags
59 have also supplied the first verification that rapid bursts of clicking (known as buzzes) are used for
60 fine-scale tracking during the final moments of prey pursuit (Madsen & Surlykke, 2013). Echo
61 structures from buzzes by Blainville's beaked whales (*Mesoplodon densirostris*) showed that click
62 rates within buzzes are correlated to prey range and allow whales to focus on individual targets
63 during capture attempts (Johnson et al., 2008). This has been corroborated in other species by using

64 tag data that relate the occurrence of buzzes to body movements consistent with close-range pursuit
65 or prey captures. For example, beaked whale buzzes coincide with increased dynamic body
66 acceleration (Johnson et al., 2004) or tight, circling swim paths (Johnson et al., 2008), buzzes of
67 short-finned pilot whales (*Globicephala macrorhynchus*) occur immediately after directional high-
68 speed sprints (Aguilar de Soto et al., 2008), and short-range sonar sounds of finless porpoises
69 (*Neophocaena phocaenoides*) are associated with declines in speed indicative of tight turns made
70 during prey pursuit (Akamatsu et al., 2010). Similarly, sperm whales (*Physeter macrocephalus*)
71 produce rapid click sequences called creaks that have been associated with increased changes in
72 body orientation during the bottom phases of dives, when prey captures are presumed to occur
73 (Miller et al., 2004).

74 Schevill and Watkins (1966) were the first to describe echolocation clicks produced by the
75 fish-eating resident killer whales (*Orcinus orca*) found in the eastern North Pacific, from acoustic
76 recordings of a subadult male captured off Vancouver Island, Canada. This individual produced
77 clicks series that appeared to function in echolocation, as he could only avoid a hydrophone placed
78 in his path at night if he was emitting clicks (Schevill & Watkins, 1966). Since this initial captive
79 study, the acoustic properties of echolocation clicks made by wild resident killer whales have been
80 documented using hydrophone arrays (Au & Benoit-Bird, 2003; Au et al., 2004), confirming that
81 click structure is consistent with the traits of an effective biosonar signal, namely broad bandwidth,
82 brief duration and high amplitude (Au et al., 2004). Analysis of click properties has also shown that
83 echolocating resident killer whales can detect prey at distances of 100 m or more, and are capable
84 of fine target discrimination (Au et al., 2004). Click source levels are also strongly coupled with
85 target distance, indicating that killer whales possess a type of time-varying gain control that can be
86 used to discern relative target size (Au & Benoit-Bird, 2003). Furthermore, an experimental study
87 of backscatter created by exposing live fish to simulated killer whale clicks found that echo

88 structures reflected by Pacific salmon (*Oncorhynchus* spp.) differed depending on species (Au et al.,
89 2010). Resident killer whales may therefore use echolocation to identify the size and species of fish
90 they encounter (Au et al., 2010). This ability is particularly important given their preference for
91 consuming mature (4-5 year old) Chinook salmon (*O. tshawytscha*; Ford et al., 1998; Ford & Ellis,
92 2006).

93 The link between echolocation and foraging behavior in resident killer whales was first
94 described using passive acoustic methods in combination with observations of group behavior at the
95 surface (e.g., Barrett-Lennard et al., 1996; Ford, 1989; Holt et al., 2013). Barrett-Lennard et al.
96 (1996) determined that resident killer whales produced comparatively louder and more variable
97 echolocation clicks than individuals of the transient/Bigg's (marine-mammal hunting) killer whale
98 ecotype, and also used echolocation significantly more often while feeding than during all other
99 activity states combined. Similarly, Holt et al. (2013) found that echolocation by southern resident
100 killer whales increased during group activities that were consistent with foraging. Like other
101 odontocetes, killer whales have also been recorded producing buzzes (Awbrey et al., 1982; Ford,
102 1989; Holt et al., 2013), and these sounds have more recently been linked to prey captures using
103 high-resolution movement and acoustic tags deployed on southern resident killer whales (Holt et al.,
104 2019; Tennessen et al., 2019). Holt et al. (2019) also used tag data to provide the first link between
105 increasing dive depths (consistent with foraging) and more rapid echolocation rates for resident
106 killer whales. Resident killer whales require sufficient prey availability for population growth and
107 recovery, and given the role of echolocation in obtaining this prey, access to sufficiently quiet
108 habitats is an important component of foraging success (Fisheries and Oceans Canada, 2018). A
109 better understanding of the relationship between echolocation, diving behaviour, and foraging
110 success is needed for effective conservation planning to minimize acoustic disturbance that will
111 negatively impact resident killer whale populations.

112 In this study, we recorded the echolocation patterns of individual northern resident killer
113 whales during salmon pursuit and capture using high-resolution acoustic recording tags. Foraging
114 success was validated using surface-based observations and prey fragment sampling. For successful
115 salmon foraging events, we were able to investigate patterns of echolocation in detail and examined
116 the relationships between echolocation behavior, dive depth, and salmon species relative to the
117 timing of fish captures. We also analyzed the relationship between buzz production and prey-capture
118 times to confirm whether these sounds function in close-proximity targeting at the end of chases, as
119 has been demonstrated in other studies. Crunching and tearing sounds that likely resulted from prey
120 handling and prey sharing were also identified, and provide a potential acoustic metric for
121 identifying foraging success. Our study advances the understanding of how individual killer whales
122 use echolocation during the pursuit and capture of salmon prey.

123 *Methods*

124 *Dtag deployments and focal follows*

125 We recorded the echolocation and diving behavior of foraging northern resident killer
126 whales from August to September of 2009-2012, in the coastal waters off northeastern Vancouver
127 Island, British Columbia, Canada. We deployed digital acoustic recording tags (Dtags; Johnson &
128 Tyack, 2003) on individual whales that allowed us to compute their three-dimensional body
129 orientation at high resolution using data from the tag's pressure sensor, triaxial accelerometers and
130 magnetometers. In addition to animal orientation data, the tags continuously recorded underwater
131 sounds using two hydrophones. When encountered, individual northern resident killer whales were
132 visually identified by their natural markings using a photo-identification catalog (Ellis et al.,
133 2011), following the technique developed by Bigg (1982). A whale was then selected and
134 approached in a 9.3 m command-bridge diesel-powered vessel (*MV* Roller Bay), and a Dtag was

135 deployed from the bow using a hand-held, 7 m carbon fiber pole. Tagging was opportunistic in
136 that if an animal other than the individual we originally selected presented us with a good
137 opportunity to deploy a tag, we would do so. Ideally, the tag was attached just below the base of
138 the dorsal fin via its four suction-cups, so that it cleared the water when the whale surfaced to
139 facilitate tracking of the animal using the tag's VHF transmitter. Only adults and larger juvenile
140 killer whales (≥ 3 years of age) were approached for tagging, and repeat deployments on the same
141 individuals were avoided. The sampling rate for the pressure sensor, accelerometers, and
142 magnetometer was 50 Hz for Dtag-2 deployments (2009-2011) and 250 Hz for Dtag-3
143 deployments (2012). Acoustic data were recorded with 16-bit resolution at sampling rates of 96,
144 192 or 240 kHz, depending on the tag model and deployment year (Table 1). Prior to analysis,
145 hydrophone recordings with 240 kHz sampling rates were down-sampled to 192 kHz to allow real-
146 time audio playback in Adobe Audition CS5.5 (Adobe Inc., San Jose, CA, USA).

147 We conducted a focal follow (Altmann, 1974) of each tagged whale and noted surface
148 observations of its foraging behavior using a digital voice recorder that was time-synchronized with
149 the Dtag sensors. The research vessel (*MV* Roller Bay, used for both Dtag deployments and focal
150 follows) operated using Arneson drive propulsion (surface-piercing propellers), a propulsion type
151 that has been shown to produce lower underwater sound levels compared to traditional propellers in
152 controlled experiments (Wladichuk et al., 2019). This minimized the chance that noise disturbance
153 from the research vessel would affect the whales' behavior during focal follows. The need for
154 concurrent surface observations limited the deployments to daylight hours. Following the
155 methodology of Ford and Ellis (2006), we identified the times and locations of successful prey
156 captures by collecting fish scales and tissue fragments using a fine-meshed dip net when tagged
157 whales surfaced from successful feeding dives. We examined the surfacing locations of tagged
158 individuals for evidence of prey remains whenever they exhibited behavioral cues indicative of

159 foraging (e.g., changes in swim speed and direction, long dive durations, and milling by nearby
160 conspecifics; Ford & Ellis, 2006). Since resident killer whales spread out to forage independently
161 or in small subgroups, and typically surface with prey in their mouths prior to consuming it or
162 carrying it towards other whales for sharing (Ford & Ellis, 2006; Wright et al., 2016), we could
163 attribute fish remains to the individual that made the capture with high confidence. Our analyses
164 included only those foraging dives for which fish remains could be attributed to the tagged whale,
165 and for which no other individuals participated in the prey capture. Fish scale and tissue samples
166 were used to identify the species and age of the captured fish. Age was determined using
167 schlerochronology (MacLellan, 2004), and species was determined using scale morphology or
168 genetic analysis (Withler et al., 2004).

169 *Dtag calibration, dive identification and pseudotrack construction*

170 We calibrated the Dtag sensor data to correct for the orientation of the tag relative to the
171 body axes of the whale using a custom calibration routine run in Matlab version 7.8.0/R2009a (The
172 MathWorks Inc., Natick, MA, USA). Dtag calibration methodology is described in more detail by
173 Johnson & Tyack (2003). Calibration converted the raw sensor measurements of pressure into depth,
174 and accelerometer and magnetometer data into the three rotational measures of pitch, roll, and
175 heading. The resulting estimates of each whale's body position over time were automatically down-
176 sampled from the raw sensor sampling rates to 5 Hz during this process. For some deployments,
177 changes in the position of the Dtag on the animal due to tag slippage required performing new
178 calibrations for every new orientation of the tag. We identified individual dives within the calibrated
179 data using an automated filter that defined a dive as any submersion with depth ≥ 1 m, bounded by
180 surfacing events of < 1 m depth. This filter calculated the start and end times (in seconds since tag
181 activation) and the maximum depth for each identified dive. We also visualized the time series of

182 whale body orientations for each deployment using the software TrackPlot 2.3 (Ware et al., 2006),
183 which combined the calibrated pitch, roll, heading and depth values to create a three-dimensional
184 representation (dead-reckoned pseudotrack) of tagged whale movements (see inset, Figure 1).

185 *Reconstructing fish-capture events*

186 We determined the beginning and end times of successful fish capture events by matching
187 the times when prey samples ($N=17$) were collected to the corresponding kinematic behavior of
188 tagged whales displayed in the Trackplot pseudotracks. The start of a fish capture event was defined
189 as the beginning of the first dive prior to the time of prey sample collection (and all subsequent dives
190 leading up to the sample collection) that contained movements indicative of searching or pursuit
191 (i.e., convoluted, spiralling, and kinematically complex pseudotracks). Kinematic signatures that are
192 characteristic of foraging dives by resident killer whales are described in more detail by Wright et
193 al. (2017) and Tennessen et al. (2019). The precapture phase of the event included all kinematic and
194 acoustic behavior from the first dive indicative of searching and/or pursuit until the time of prey
195 capture. Often, this precapture phase was represented by the descent phase of a single, steep dive,
196 but it could sometimes include multiple dives and/or chase behavior at the surface (see example in
197 Figure 1). The capture itself was predicted to occur when kinematically complex pursuit behavior
198 ceased abruptly and the whale began a directional, linear ascent (Figure 1). Dtag acoustic records
199 were used to corroborate the kinematically-predicted capture times, as fluctuations in flow noise
200 consistent with sudden acceleration changes often accompanied the kinematic transitions thought to
201 represent fish captures (Wright et al., 2017). Estimated capture times typically coincided with the
202 maximum depth of the dive immediately prior to the prey sample collection at the surface. Dives
203 occurring after the whale surfaced with prey were also included in the fish capture event if the
204 pseudotrack contained circling or milling behavior consistent with prey handling or sharing. We

205 defined the end of the fish capture event as the time when the tagged whale resumed the shallow,
206 directional swimming it had exhibited prior to the beginning of the hunting and chasing behavior
207 (i.e., the postcapture phase was defined as all kinematic and acoustic behavior that occurred from
208 the time of prey capture until directional swimming at the surface resumed). In this way, we ensured
209 that each fish capture event included the entire process of the killer whale detecting, pursuing,
210 catching and handling an individual salmon. After identifying the beginning and end times for each
211 fish capture event, we extracted and analyzed the corresponding acoustic recordings from the Dtag
212 hydrophones.

213 *Defining focal clicks, click trains, buzzes and prey-handling sounds*

214 We amplified the Dtag audio recordings by 10 dB on both channels to improve detectability
215 of quiet sounds in the spectrograms. We then examined 10 s scrolling displays of spectrograms and
216 waveforms both visually and aurally using Adobe Audition CS5.5 to identify echolocation clicks
217 potentially made by the tagged whale. All spectrogram images presented here were generated in R
218 4.0.4 (R Core Team, 2021) using the sound analysis package ‘seewave’ (Sueur et al., 2008). We
219 noted the time of peak amplitude for every echolocation click emitted by the tagged animal (relative
220 to the start of each fish capture event) by examining the click’s waveform. Inter-click intervals (ICI,
221 s) were calculated as the difference between peak amplitude times for each pair of successive focal
222 echolocation clicks. Nonfocal clicks were omitted from the analysis.

223 We distinguished between focal and nonfocal clicks by examining click spectrograms for
224 the presence of a low frequency energy component (Jensen et al., 2011; Ward et al., 2008; Figure
225 2). Increased low frequency energy content (generally <10 kHz) results from the passage of sound
226 through the tissues of the tagged whale prior to reaching the tag hydrophones, and is therefore
227 evident in focal clicks but missing from nonfocal clicks (Zimmer et al., 2005). Once putative focal

228 clicks had been identified, they were compared to an assessment of each echolocation click train
229 using the angle of arrival (AoA) technique (Johnson et al., 2006; Zimmer et al., 2005). Given the
230 fixed position of the tag on the whale's body, echolocation clicks made by the focal individual
231 should originate from a consistent angle relative to the tag over time. Nonfocal clicks, conversely,
232 will display fluctuating AoA values as the position of a conspecific relative to the tagged whale
233 changes. We assessed AoA consistency using a custom Matlab routine, described in more detail by
234 Holt et al. (2019), that displayed corresponding plots of the tag-recorded spectrograms, waveforms,
235 and the AoA calculations for each click train over time. A similar approach was also used by Arranz
236 et al. (2016) to identify focal clicks of tagged Risso's dolphins (*Grampus griseus*). Any click train
237 identified as focal based on a low frequency energy component, but which failed to coincide with
238 any of the focal click trains identified using the more conservative AoA audit, was omitted from the
239 analysis. Both the AoA audits and the visual identification of low frequency energy in focal clicks
240 were conducted by the same analyst for all tags.

241 Following the methodology of Barrett-Lennard et al. (1996), consecutive focal echolocation
242 clicks were assigned to the same click train if they were separated by ICIs of ≤ 2 s. To distinguish
243 rapid buzz clicks (Figure 3) from regular echolocation clicks (Figure 2), we produced a histogram
244 of natural log-transformed ICIs and used the break in its bimodal distribution at ~ 10 ms as the
245 threshold for separating click train types (see Figure A1, Supplementary Information). We classified
246 any echolocation train that contained at least one ICI below or equal to the 10 ms threshold as a
247 buzz. The same threshold was previously used to differentiate regular echolocation from buzzes in
248 Dtag recordings from the closely related southern resident killer whale population (Holt et al., 2013,
249 Holt et al., 2019, Tennessen et al., 2019). Once click trains were classified by type (regular or buzz),
250 we calculated the number of each type per prey-capture event, as well as the duration, click repetition

251 rate, and mean ICI of each train. As most data were not normally distributed, we present most
252 summary statistics as medians and interquartile ranges (IQR), unless otherwise stated.

253 Sounds associated with prey handling, prey sharing and consumption (Wright et al., 2017)
254 were also identified. These tearing and crunching noises were verified as prey-handling sounds by
255 comparing them to similar sounds we recorded on a pole-mounted underwater video camera and
256 hydrophone in 2005-2006, which documented northern resident killer whales handling and
257 consuming fish (Figure 4). Similar sounds have also been identified in the vicinity of individuals
258 from other populations of fish-eating killer whales engaged in foraging behavior (Holt et al., 2019,
259 Tennessen et al. 2019, D. Olsen, pers. comm.). We assumed that all prey-handling sounds recorded
260 by the Dtags originated from the focal animal, as these sounds were unlikely to be audible unless
261 they occurred close to the tag hydrophones. Once identified, prey-handling sounds were rated by the
262 same experienced analyst on their relative likelihood (certain, probable, or possible) of actually
263 representing prey-handling behavior. ‘Probable’ and ‘possible’ crunches had decreasing levels of
264 certainty because air bubbles and water flowing through or around the tag housing (particularly for
265 the Dtag-2) could not be ruled out as the sound source. We omitted all prey-handling sounds with
266 the lowest assigned certainty category (i.e., ‘possible’) from further analysis.

267 *Comparing echolocation patterns with concurrent kinematic behavior*

268 We synchronized the acoustic recordings with the tag kinematic data to analyze the
269 relationship between dive depth, echolocation, and the relative phase of the foraging dive (pre- or
270 postcapture). By identifying the moment of capture for each successful foraging event (using both
271 flow noise and kinematic cues, as previously described), we could compare the echolocation
272 behavior of killer whales before and after a fish was caught. To accomplish this, we binned each
273 foraging dive into 1 s time intervals and calculated both the presence/absence of clicking and the

274 click repetition rate for each bin (see example of 1 s binned clicking rate data displayed in Figure
275 1). Click rates were then averaged across each dive's pre- and post-capture phases to examine
276 differences in echolocation during active searching and chasing compared to during prey handling
277 and consumption. The proportion of time spent echolocating within each dive phase (pre- and
278 postcapture) was determined by summing the number of 1 s bins that contained clicks and dividing
279 it by the total duration (s) of each phase. Differences in pre- and postcapture echolocation behavior
280 were assessed using a Bayesian alternative to the paired-samples *t*-test (Kruschke, 2013) in R using
281 the 'BayesianFirstAid' package (Bååth, 2014). The benefit of this Bayesian approach is that it
282 assumes that the data follow a *t* distribution, which is more robust to outliers than the normal
283 distribution typically assumed by frequentist approaches. Rather than testing whether the difference
284 between two groups is zero, as a classical test would, the Bayesian analysis we use here asks how
285 large the estimated difference is between the groups, and what the probability is that the true
286 difference is larger than zero. Parameters were initialized using robust estimates of the mean
287 (trimmed) and median absolute deviation with the goal of generating uniform priors and assisting
288 with convergence of the Markov Chain Monte Carlo (MCMC) sampling, which had a burn-in of
289 500 samples and 3 chains with 10,000 samples per chain.

290 We calculated the dive depths of killer whales at the beginning of the first echolocation train
291 for each prey-capture event, as well as the dive depths at the beginning of each buzz and examined
292 these depths relative to the salmon species caught to further elucidate the prey species-specific
293 differences in foraging tactics by northern resident killer whales previously identified by Wright et
294 al. (2017). We also examined the timing and depths at which buzzes and prey-handling sounds
295 occurred, relative to the moment of fish capture itself, to explore the behavioral context of these
296 sounds and to investigate their utility as proxies for prey-capture attempts and successes,
297 respectively. Comparisons of dive depths for initial echolocation trains, buzzes, and prey-handling

298 sounds (grouped by salmon species or by capture phase) were also conducted using a Bayesian
299 alternative to the two-sample *t*-test (Bååth, 2014).

300 *Results*

301 *Dtag deployments and prey sampling*

302 Thirty-four Dtags were deployed on 32 individual northern resident killer whales in the late
303 summer and early autumn of 2009-2012. Prey fragments (fish scales and/or flesh) were collected at
304 the surface after 17 successful captures made by 7 of the tagged whales: three adult males, two adult
305 females, and two juveniles (<12 y; Table 1). Scale morphology and genetic analyses of prey
306 fragments revealed that 9 of the kills were Chinook salmon, 6 were chum (*O. keta*), and two were
307 coho (*O. kisutch*). Salmon caught by the tagged whales ranged in age from 2-5 years, with the
308 majority being 4-5 years old (65%, *n*=11).

309 *Patterns of echolocation during fish-capture events*

310 A total of 19,773 focal echolocation clicks were identified from the 17 fish capture events.
311 The majority of focal clicks consisted of single broadband pulses; however, clicks with doublet
312 structures resembling those described by Awbrey et al. (1982) for Antarctic killer whales were
313 occasionally recorded (surface reflection as the cause of these doublets could not be ruled out,
314 however). Echolocation clicks were arranged into 175 separate trains, including 148 regular
315 echolocation click trains and 27 buzzes (trains containing one or more ICI of ≤ 10 ms; Figure 3).
316 Each fish capture event included a median of 8 regular click trains (IQR=5-12, range=0-18) with a
317 median duration of 5.3 s (IQR=2.3-10.0 s, range=0.3-35.7 s) and a median click repetition rate of
318 6.1 clicks s^{-1} (IQR=3.5-11.9 clicks s^{-1}). Fish capture events also included a median of 1 buzz each
319 (although 5 of the 17 captures contained no buzzes; IQR=0-3, range=0-6). Median buzz duration
320 was 5.4 s (IQR=2.6-9.8 s, range=0.3-21.7 s) and median buzz click repetition rate was 47.4 clicks s^{-1} .

321 ¹ (IQR=25.5-96.7 clicks s⁻¹). The fish capture events for which no buzzes were detected included all
322 three of the 2009 Dtag-2 captures, as well as a single capture from both 2010 and 2011. Regular
323 click trains and buzzes were produced by tagged whales at median depths of 48.7 m (IQR=5.5-112.1
324 m) and 122.9 m (IQR=70.5-148.2 m), respectively.

325 We examined the depth at which whales emitted their first click train during the precapture
326 phase of a fish capture event and found that echolocation was initiated at depths <40 m for most
327 salmon captures (82.3%, $n=14$, Table 2). Whales that initially pursued fish at the surface produced
328 their first echolocation trains at a much shallower median depth (0.7 m, IQR=0.6-1.8 m, $n=5$) than
329 those that did not locate prey at the surface but dove prior to initiating chase behavior (25.9 m,
330 IQR=12.2-50.2 m, $n=12$). The initial click train produced during a capture event commenced at a
331 greater median depth for captures involving Chinook salmon (20.0 m, IQR=5.2-32.7 m, $n=9$),
332 compared to chum (9.3 m, IQR=2.6-32.8 m, $n=6$) or coho (7.4 m, IQR=5.7-9.1 m, $n=2$; Figure 5).
333 When mean initial echolocation depths for Chinook captures were compared to all other salmon
334 species combined using the Bayesian alternative to a t -test, the estimated difference was 16 m deeper
335 for Chinook captures and the probability that the difference between the means was greater than
336 zero was 0.791. However, the 95% credible interval for the difference between these means (-28 to
337 74 m) also included zero and the possibility that no difference exists can therefore not be ruled out
338 entirely. The greatest depth at which a whale first began echolocating during a fish capture was
339 196.5 m, which was equivalent to 96% of its maximum dive depth (204.5 m) for that particular fish
340 capture event (deployment oo11_246a, Table 2, Figure 5). Buzz trains also began at a greater median
341 depth for Chinook captures (162.5 m, IQR=84.0-186.0 m, $n=13$) compared to chum captures (119.5
342 m, IQR=59.7-127.3 m, $n=14$), while no buzzes were emitted by whales that pursued coho salmon
343 ($n=2$, Figure 5). Like initial echolocation trains, the difference in mean depths of buzzes during
344 Chinook versus chum captures was also deeper for Chinook buzzes (by about 38 m), and the

345 probability that the difference between the means was greater than zero was high (0.915). However,
346 the 95% credible interval of the difference in means (-19 to 92 m) also included zero, and it is
347 therefore possible (although unlikely) that no true difference in buzz depth between salmon species
348 exists.

349 Tagged killer whales produced echolocation clicks at higher repetition rates prior to
350 capturing a fish (clicking rates were averaged across all 1-second time bins occurring prior to capture
351 for each dive, and the median of these averages was 4.0 clicks s^{-1} , IQR=2.3-6.8 clicks s^{-1}) than
352 afterward (median=0.1 clicks s^{-1} , IQR=0-0.5 clicks s^{-1}), a difference that was statistically significant
353 (mean paired difference=4.8 clicks s^{-1} , 95% credible interval=2.5 to 7.1 clicks s^{-1} , probability that
354 mean difference is greater than zero: >0.999) (Table 2, Figures 6 and 7). They also spent a greater
355 percentage of time engaged in echolocation before capturing a fish (median=34.1%, IQR=26.1%-
356 38.0%) than they did afterward (median=3.7%, IQR=0%-20.7%; mean paired difference=21%, 95%
357 credible interval=13% to 30%, probability that mean difference is greater than zero: >0.999) (Table
358 2, Figure 8). In seven fish capture events, the tagged whale did not produce any echolocation clicks
359 after catching the fish (Table 2). Five of these captures came from a single tagged adult female, G31,
360 and the other two from a juvenile, I106. The five captures by G31 were the only prey that were
361 definitively shared with other individuals. The majority of buzzes occurred prior to the estimated
362 time of fish capture (92.6%, $n=25$), although two buzzes were detected 29 and 56 s after a fish was
363 presumably caught (Figure 9). These two postcapture buzzes were produced by a single tagged
364 whale (adult female G64) during the same capture of a chum salmon. The median depth of buzzes
365 that occurred before the fish capture (121.1 m, IQR=66.6-162.5 m, $n=25$) differed little from the
366 median depth of those occurring after the capture (128.4 m, IQR=125.6-131.1 m, $n=2$; estimated
367 difference of the means from the Bayesian alternative to the t -test = -2.9 m, Figure 9). Interestingly,
368 no buzzes were produced by whales simultaneous to the estimated moment of capture itself.

369 *Prey-handling sounds*

370 Prey-handling sounds, such as crunching or tearing noises ($N=62$, rated either ‘probable’ or
371 ‘certain’), were audible on the Dtag recordings for 14 of the 17 fish-capture events, with a median
372 of 3 crunches per capture (IQR=1-6). Prey-handling sounds resulted from a whale catching a fish in
373 its jaws or tearing apart the carcass following a capture. The source of the sounds was verified using
374 underwater video footage (recorded prior to this study in 2006) that documented northern resident
375 killer whales handling and consuming fish (Figure 4). These video recordings contained sounds that
376 matched the crunch spectrograms (both visually and aurally) recorded by the Dtags, and occurred
377 as whales were seen biting fish and tearing them into smaller pieces on the video. The majority of
378 prey-handling sounds recorded by the Dtags occurred after the estimated time of capture (94%,
379 $n=58$), while two occurred around the same time (± 3 s) as the capture (Figure 10). Unexpectedly, an
380 additional two prey-handling sounds from a single chum capture event by G64 (deployment
381 oo10_256a) were audible prior to the estimated fish capture time (Figure 10). Prey-handling sounds
382 occurring after fish captures happened at a shallower median depth (11.3 m, IQR=8.5-18.5 m, $n=58$)
383 than those occurring either prior to or around the same time as captures (131.0 m, IQR=130.9-133.5
384 m, $n=4$; estimated difference of the means = 120 m, 95% credible interval = 111-133 m, probability
385 that difference of the means is greater than zero >0.999 ; Figure 10).

386 *Discussion*

387 *Patterns of echolocation during successful fish captures*

388 The median click repetition rate of 6.1 clicks s^{-1} (regular click trains) that we recorded for
389 tagged northern residents performing successful salmon captures was comparable to click repetition
390 rates previously reported for this ecotype. Schevill and Watkins (1966) reported click repetition rates
391 of 6-18 clicks s^{-1} , Ford (1989) found that click repetition rates generally fell between 2 and 50 clicks

392 s^{-1} and Barrett-Lennard et al. (1996) calculated a median click rate of 7.1 clicks s^{-1} for resident killer
393 whales. The median duration of 5.3 s (IQR=2.3-10.0 s) for regular click trains produced by tagged
394 killer whales in our study was also similar to the mean click train duration of 7.2 s reported by
395 Barrett-Lennard et al. (1996). The median depth of 48.7 m (IQR=5.5-112.1 m) for all regular click
396 trains (ICI > 10 ms) in our study was slightly shallower than the median depth of 73.6 m calculated
397 by Holt et al. (2019) for fast click trains ($10 \text{ ms} < \text{ICI} \leq 100 \text{ ms}$) produced by southern resident killer
398 whales. This difference is likely due to the inclusion of slow click trains (ICI > 100 ms) in our
399 calculation, which are more likely to occur at shallower dive depths (Holt et al., 2019).

400 We found that resident killer whales used echolocation even in situations where visibility
401 was likely to be relatively good, with click trains generally beginning at relatively shallow depths
402 (<40 m) during the precapture phases of fish capture events (Figure 5). Resident killer whales also
403 produced clicks when chasing fish along the surface (Table 2). This implies that vision and
404 echolocation are probably acting in concert during detection and tracking of prey, and that
405 echolocation may be critical to successful prey capture even when vision is unrestricted. This
406 conclusion is supported by Barrett-Lennard et al. (1996), who found no correlation between water
407 clarity and the frequency of echolocation use by resident killer whales. In other words, whales did
408 not increase their reliance on echolocation under conditions of reduced visibility, or vice versa. The
409 interchange between the use of echolocation and vision by foraging cetaceans is not well understood;
410 however, Torres (2017) suggests that there is considerable overlap in the spatial scales (i.e.,
411 distances from prey) over which dolphins use these two sensory modalities, and as such, vision and
412 echolocation likely provide simultaneous sensory information on prey locations and movements.
413 More specifically, underwater visual acuity in killer whales has been shown to be sensitive enough
414 that it undoubtedly plays a role in guiding their behavior (White et al., 1971). In addition, we also
415 determined that echolocation was not continuous throughout any of the Dtag-recorded fish capture

416 events. Even during the search and pursuit (precapture) phase, whales typically echolocated less
417 than 50% of the time (median=34.1%, IQR=26.1%-38.0%, Table 2, Figure 8). These results are
418 supported by previous observations that resident killer whales emit only periodic (rather than
419 continuous) echolocation trains while pursuing and capturing salmon (Ford, 1989). Whales are
420 therefore likely using other sensory cues, in addition to echolocation, to track prey at depths with
421 limited light availability where visual tracking is not possible. These cues could include passive
422 listening for swimming sounds or other noises potentially produced by salmon (Barrett-Lennard et
423 al., 1996; Murchy et al., 2018; Torres, 2017), or passive electroreception of bioelectric fields
424 generated by prey, as has been shown in another odontocete species, the Guiana dolphin (*Sotalia*
425 *guianensis*, Czech-Damal et al. 2012).

426 Although the precapture phase of most fish capture events began with killer whales
427 echolocating closer to the surface, occasionally individuals descended silently and only produced
428 their first click train after attaining a greater depth. Generally, whales that did not initially encounter
429 and chase fish at the surface delayed echolocation until they had reached a median depth of 25.9 m
430 (IQR=12.2-50.2 m). Resident killer whales preferentially feed on Chinook salmon (Ford et al., 1998;
431 Ford & Ellis, 2006; Ford et al., 2009), which have a significantly deeper average vertical distribution
432 than other Pacific salmon species (Wright et al., 2017). We found that whales targeting Chinook
433 often descended silently until they reached the typical depth range occupied by this species (>30 m,
434 see Wright et al. 2017) before emitting echolocation clicks (median depth of first click train = 20.0
435 m, IQR=5.2-32.7 m, Figure 5). Holt et al. (2019) similarly found that southern resident killer whales
436 that dove to depths corresponding to Chinook habitat (≥ 30 m) also delayed their first click train until
437 a mean depth of 27.3 m. Conversely, whales pursuing more surface-oriented salmon species, such
438 as chum and coho (Wright et al., 2017), initiated their first precapture click trains at shallower
439 median depths (9.3 m and 7.4 m, respectively, Figure 5, Table 2). This suggests that killer whales

440 alter their echolocation behavior depending on the species of salmon they are targeting, and previous
441 research has indicated that killer whales are likely able to differentiate between salmon species based
442 on echolocation backscatter patterns (Au et al., 2010).

443 Although little work has been conducted on the auditory capabilities of adult Pacific salmon,
444 auditory threshold tests on juvenile Chinook (Halvorsen et al., 2009), juvenile Atlantic salmon
445 (*Salmo salar*; Hawkins & Johnstone, 1978; Knudsen et al., 1992) and 2 year-old masu salmon (*O.*
446 *masou*; Kojima et al., 1992) suggest that these fish can only sense low frequency tones (up to several
447 hundred Hz) and thus are unlikely to hear killer whale echolocation clicks (which typically have
448 center frequencies between 45-80 kHz and bandwidths between 35-50 kHz; Au et al., 2004). It is
449 therefore doubtful that the delayed echolocation exhibited by killer whales conducting deeper
450 foraging dives for Chinook has arisen as a strategy to prevent detection by their prey. Evidence does
451 exist, however, that salmon can sense and react to the presence of killer whales, although how
452 sensitive this ability is and what type of stimulus the fish are reacting to is unknown. Historically,
453 Scheffer and Slipp (1948) reported that salmon responded to the presence of killer whales by either
454 moving to deeper water or hiding in the shallows close to shore, and that Chinook fishing was
455 negatively impacted for several days following the appearance of killer whales in an area. Our Dtag
456 data have indicated that Pacific salmon, especially Chinook, often dive steeply in response to killer
457 whale pursuit (Wright et al., 2017). During our field research, we have also frequently observed
458 chum and coho salmon using other escape strategies, such as hiding under boat hulls, floating kelp,
459 or logs. These behaviors may occur in response to very close approaches or pursuit, including failed
460 predation attempts (or successful predation of a nearby conspecific), or it is also possible that salmon
461 possess some means of passively sensing the approach of resident killer whales prior to an actual
462 chase or attack.

463 Killer whales conducting bouts of closely-spaced, consecutive foraging dives may not need
464 to echolocate at the surface (before initiating a dive) if they have prior knowledge of prey locations.
465 For instance, G31 (deployment oo11_246a) successfully captured 5 fish within 2 hr, and began
466 echolocating in comparatively shallow water for most of these captures, all of which consisted of
467 fairly steep, single dives that descended to ~130-260 m (Table 2). However, for the fourth capture,
468 G31 did not echolocate at all until reaching almost 200 m in depth. She was probably able to forgo
469 echolocation near the surface because she had located a group of fish during the preceding capture,
470 which had ended only 4 min earlier and was in the same general location (prey samples for the third
471 and fourth capture were collected ~700 m apart). G31 resumed shallow initiation of echolocation
472 clicks (at 32.7 m depth) on her fifth and final prey-capture event (during which she descended to
473 180.7 m, see Table 2). Echolocation was probably necessary again because this dive was farther
474 from the preceding capture (~1,400 m) and more time had elapsed (11 min), requiring the whale to
475 either relocate salmon or to find new prey. It is also possible that northern resident killer whales
476 sometimes dove deeper before echolocating to avoid noisy conditions at the surface (e.g., vessel
477 noise, rainfall) that can mask returning echoes from prey or reduce target detection distances (Au et
478 al., 2004).

479 Echolocation behavior of foraging northern resident killer whales changed significantly once
480 a fish had been caught, implying that echolocation may fulfil different functions during different
481 stages of prey capture. For example, during active searching or pursuit of fish (precapture phase),
482 killer whales spent a significantly greater proportion of their dive time echolocating
483 (median=34.1%) than they did after catching a fish (postcapture phase: median=3.7%; mean paired
484 difference=21.0%; >0.999 probability that the difference between means is >0). Greater
485 echolocation effort prior to captures was expected, since foraging whales are assumed to use
486 echolocation to locate, track and acoustically identify prey. Pursuing highly mobile prey (like

487 salmon) requires killer whales to respond to evasive behaviors by the prey, which they likely
488 accomplish by using echolocation to obtain information about prey movements. The higher mean
489 clicking rate (mean paired difference = 4.8 clicks s^{-1} ; >0.999 probability that the difference between
490 means is >0) displayed by resident killer whales during the precapture compared to the postcapture
491 phase (Figure 6) was also expected, since click repetition rates are directly related to target range.
492 Continuous reductions in target distance during prey pursuit permit shorter intervals between clicks
493 because the echoes return and can be processed by the whale at increasingly faster rates (Madsen &
494 Surlykke, 2013). Closer proximity also leads to more rapid changes in the attack angle between
495 predator and prey (Au et al., 2004), requiring the whale to increase its clicking rate to receive updates
496 on increasingly evasive fish movements and prevent an escape. Similar increases in clicking effort
497 and shortened inter-click intervals were observed for finless porpoises performing body movements
498 consistent with prey searching and pursuit (Akamatsu et al., 2010). Higher echolocation effort by
499 northern resident killer whales prior to prey captures (both in time spent echolocating and click
500 repetition rates) suggests that echolocation is pivotal to foraging success.

501 After capturing a fish, tagged killer whales slowed their median echolocation rate from 4.0
502 to 0.1 clicks s^{-1} and spent a median of only 3.7% of their time engaged in echolocation behavior
503 (Table 2, Figures 6 & 8). Postcapture clicking may aid in navigation back to the surface, or could
504 assist during prey handling to track pieces of prey as it is being torn apart. Both tasks are unlikely
505 to require frequent or rapid sensory updates, hence the reduction in both echolocation rate and time
506 spent echolocating following a capture. Foraging whales may also use postcapture echolocation to
507 find conspecifics, typically offspring, with which they frequently share their prey (Wright et al.,
508 2016). However, only one of the tagged whales (G31, deployment oo11_246a, Table 2) exhibited
509 confirmed prey sharing behavior, and she did not echolocate at all during the postcapture phase of
510 any of her dives ($n=5$). This may be because this whale was engaged in very steep, vertical dives

511 with limited horizontal displacement, which would cause her to surface close to her juvenile
512 offspring without having to search for them. It could also mean that provisioned individuals in this
513 case moved towards G31, rather than her having to locate and carry the fish to them; both active and
514 passive types of sharing behavior have been reported during prey sharing by resident killer whales
515 (Ford & Ellis, 2006). Further investigation using a larger sample size of shared kills by multiple
516 individuals is required to determine the relative importance and use of echolocation by resident killer
517 whales during prey sharing behavior. Because some tagged whales were completely silent after
518 capturing a fish, echolocation is likely not critical for postcapture navigation, prey handling or
519 sharing, and implies that these tasks can sometimes be accomplished using other sensory inputs,
520 such as visual cues or passive listening.

521 *Buzzes and prey-handling sounds*

522 Many odontocete species use buzzes for close-range prey targeting (Aguilar Soto et al., 2008;
523 DeRuiter et al., 2009; Holt et al., 2019; Johnson et al., 2004; Johnson et al., 2008; Tennessen et al.
524 2019; Wisniewska et al., 2014). These sounds consist of echolocation clicks emitted at increasingly
525 higher rates as the target distance (and thus the time required to receive an echo) decreases
526 (Cahlander et al., 1964). While regular echolocation clicks are thought to function in the detection
527 and identification of more distant targets, buzzes are produced during extremely close approaches,
528 when rapid updates on prey movements become possible and necessary (Johnson et al., 2006). Most
529 buzzes (85.2%, $n=23$) produced by tagged northern resident killer whales occurred at depths >50 m
530 (Figure 9), with a median starting depth of 122.9 m (IQR=70.5-148.2 m), which was very similar to
531 buzz depths reported for foraging southern residents (median=118.3 m) by Holt et al. (2019). Buzz
532 depths reflect the greater depths at which prey were eventually caught, and it is not an unexpected
533 finding given the tendency of Chinook, coho, and chum salmon to descend in response to predator

534 pursuit (Wright et al., 2017). With the exception of two prey-capture events, buzzes were always
535 preceded by trains of regular echolocation clicks that were probably used to locate and track prey
536 during the initial part of a foraging dive. The two buzzes with no preceding regular echolocation
537 clicks were the first echolocation trains of two dives made by G31 (deployment oo11_246a, Table
538 2) at depths of 101.5 and 196.5 m, respectively. In these cases, G31 may have already located prey
539 either using near-surface echolocation conducted prior to diving, or during a preceding successful
540 capture, and thus would not need to employ slower echolocation trains prior to buzzing.

541 Buzzes could have other functions in addition to close-range prey targeting, as two of these
542 sounds made by a single tagged killer whale (G64, oo10_256a) during one of its foraging dives
543 occurred postcapture (Figure 9). DeRuiter et al. (2009) found that captive harbor porpoises
544 (*Phocoena phocoena*) continued buzzing after catching a fish, and concluded that buzzes might help
545 to re-detect escaped prey or locate additional prey following a kill. Buzzes produced >5 s after a fish
546 capture were thought to assist porpoises in navigating back to their trainer (DeRuiter et al., 2009).
547 Northern resident killer whales could use postcapture buzzes in a similar way, either to navigate
548 back to the surface, or to locate nearby whales for prey sharing. Killer whales could also use buzzes
549 during prey handling, as we have often observed them biting fish in half at the surface and then
550 circling back for the sinking portion. Buzzes could assist whales to relocate these portions of their
551 prey, especially in instances where fish are not shared. The postcapture buzzes we detected could
552 also be nonfocal, however, this is less likely given our conservative two-level methodology (low
553 frequency energy component and consistent AoAs) for identifying focal clicks.

554 Buzzes were not a completely reliable acoustic estimator of prey-capture attempts because
555 they were absent from five of the successful fish captures, including all three captures recorded on
556 the 2009 tags. Given the lower apparent source levels of these sounds (DeRuiter et al., 2009; Johnson
557 et al., 2006; Madsen et al., 2005; Miller et al., 1995; Wisniewska et al., 2012; Wisniewska et al.,

558 2014), buzzes may have been present but were acoustically masked due to poor signal-to-noise ratios
559 caused by high flow noise, particularly on the 2009 recordings. It is also possible that no buzzes
560 were actually produced during these captures, as Tennessen et al. (2019) similarly detected foraging
561 dives by southern resident killer whales that contained prey-handling sounds but not buzzes, and
562 Holt et al. (2019) detected buzz trains in only nine of 15 foraging dives by southern residents that
563 were confirmed successful by prey sample collection at the surface. Furthermore, buzzes should not
564 be interpreted as a 1:1 indicator of capture attempts because northern resident killer whales often
565 produced multiple buzzes (1 buzz per capture: $n=6$; 2-6 buzzes per capture: $n=6$) while pursuing and
566 capturing a single fish (see example with three buzzes in Figure 1). Therefore, some buzzes are
567 likely to represent close approaches to prey targets that resulted in misses rather than captures. Other
568 odontocetes, such as beaked whales, are similarly known to produce multiple buzzes in series while
569 tracking the same prey target (Johnson et al., 2008; Madsen et al., 2013).

570 The prey-handling sounds we detected could be useful indicators of prey capture success
571 that would provide information for estimating the foraging efficiency of resident killer whales. Like
572 buzzes, multiple prey-handling sounds (median=3, IQR=1-6, see example in Figure 1) were usually
573 produced during the capture and handling of one fish, and care should therefore be taken when
574 interpreting these acoustic cues. Holt et al. (2019) similarly found that prey-handling sounds made
575 during prey captures by southern resident killer whales occurred in bouts, rather than as single
576 incidents. Most prey-handling sounds by northern residents occurred after the estimated time of fish
577 capture (93.5%, $n=58$, Figure 10), as expected, since these sounds most likely arise from whales
578 tearing a fish into pieces for consumption or sharing with other individuals. Postcapture prey-
579 handling sounds were also produced at relatively shallow depths (median=11.3 m, IQR=8.5-18.5 m;
580 Figure 10), which supports previous observations that resident killer whales routinely bring prey to
581 the surface prior to handling and consumption (Ford & Ellis, 2006). Holt et al. (2019) found a

582 slightly deeper but comparable median depth of 21.4 m for prey-handling sounds produced by the
583 southern resident killer whale population. We detected two prey-handling sounds that happened
584 concurrently with the estimated time (± 3 s) of a single prey capture by G31 (deployment oo11_246a)
585 and took place at much greater depths (~ 131 m; Figure 10) than any of the post-capture prey
586 handling sounds. For this reason, we believe that these sounds resulted from the whale initially
587 grabbing the fish with its jaws as it was captured. Both our study and Holt et al. (2019) failed to
588 detect prey-handling sounds for three of 17 and nine of 15 foraging dives, respectively, that were
589 known to be successful because they resulted in collection of prey samples. Prey-handling sounds
590 are therefore not a completely reliable indicator of foraging success as they are sometimes not picked
591 up by the tag hydrophones. Flow noise and tag placement may both have some bearing on the
592 detectability of these sounds.

593 Unexpectedly, a further two prey handling sounds (also from a single capture, but by G64,
594 deployment oo10_256a) occurred approximately 18 and 231 s prior to the estimated capture time
595 for this foraging dive (Figure 9). Although this could suggest the capture of multiple prey during a
596 single dive, with only the final fish being brought to the surface, the dive pseudotrack showed
597 continuous chasing of a single fish (i.e., breaks in the kinematic pursuit behavior that might imply
598 multiple chases and prey captures were not observed). Since most salmon caught by killer whales
599 are relatively large (Ford & Ellis, 2006) with high caloric densities (O'Neill, Ylitalo, & West, 2014),
600 pursuing them is likely energetically demanding but also highly rewarding if successful. The
601 physiological drive for a killer whale to replenish its oxygen stores and offload carbon dioxide after
602 a successful capture probably takes precedence over the benefits of remaining submerged and
603 pursuing additional prey, especially considering that capturing one salmon may require several
604 minutes or more of active chasing (see precapture durations in Table 2). Thus, killer whales likely
605 adopt the strategy of returning to the surface immediately after catching a fish, as is suggested by

606 our kinematic Dtag data. Furthermore, at sea, adult Pacific salmon typically travel singly or in small
607 groups of 2-4 individuals, rather than in dense schools (Nero & Huster, 1996), which would make
608 it more difficult for killer whales to capture multiple salmon in quick succession during the same
609 dive. Rather than indicating the capture of multiple prey in a single dive, it is possible that precapture
610 prey-handling sounds could instead represent instances of the same fish being grabbed by the whale
611 but escaping before eventually being recaptured. During our long-term field observations of resident
612 killer whale hunting behavior, we have encountered fish with killer whale teeth rake marks
613 indicating that an escape occurred. The whale in question, G64, was a juvenile female (10 years
614 old), and thus perhaps was more likely to engage in multiple capture attempts of the same fish as
615 compared to an older, more experienced adult. This is supported by Holt et al. (2019), who found
616 that prey-handling sounds in general were more likely to be detected during dives by juvenile whales
617 than those by adults, which suggests that juveniles may require longer handling times to process and
618 consume prey. It is also possible that these two precapture prey-handling noises could be
619 misidentified sounds arising from other sources, such as air bubbles or water turbulence around the
620 tag housing, and may not actually represent true instances of prey handling.

621 Buzzes and prey-handling sounds can provide valuable information about the foraging
622 efficiency of individuals, but only when considered in combination with prey sampling efforts
623 and/or kinematic signatures of predation success (e.g., dive depth and jerk peak, see Holt et al., 2019
624 and Tennessen et al., 2019), given the difficulties associated with imperfect detection and
625 interpretation of these two acoustic signals. Since prey availability and acoustic disturbance have
626 both been recognized as key threats to the recovery of resident killer whales (Fisheries and Oceans
627 Canada, 2018), it is important to determine whether individuals are meeting their daily energy
628 requirements under current habitat conditions (both in terms of acoustic conditions and salmon
629 abundance). Analyzing foraging dives for the presence of buzzes and prey-handling sounds could

630 be useful in this respect, as the frequency of these events could indicate prey encounter rates
631 (Johnson et al., 2009) and potential energetic gain (i.e., number of fish consumed). The amount of
632 energy expended to successfully capture fish could also be estimated from Dtag data using fluking
633 stroke rate (Johnson et al., 2009) or a measure of total body acceleration (Wilson et al., 2006).
634 Combining these kinematic indicators of effort with acoustic indicators of capture success and
635 additional information about the energy density of prey (e.g., O'Neill et al., 2014) could allow for
636 the calculation of catch per unit effort (CPUE) for foraging resident killer whales. Comparing CPUE
637 values to estimates of daily energetic requirements (e.g., Noren, 2011) would help verify whether
638 nutritional stress is impacting the health and survival of resident killer whales.

639 *Conclusions*

640 We used biologging acoustic tags to provide a direct link between echolocation patterns,
641 diving behavior and verified prey captures by individual northern resident killer whales feeding on
642 Pacific salmon. We confirmed that patterns of echolocation produced by foraging resident killer
643 whales are consistent with its function in prey detection and tracking, as click repetition rate and
644 time invested in echolocation both varied greatly with the phase (pre- versus postcapture) of a fish
645 capture event. Echolocation behavior during foraging dives also differed depending on the species
646 of salmon that was targeted. We identified buzzes (capture attempts) and prey-handling sounds
647 (capture successes) as potentially useful acoustic signals for estimating killer whale foraging
648 efficiency. While this analysis provides a valuable addition to existing knowledge of the
649 echolocation behavior of foraging resident killer whales, it is important to note that no Dtags were
650 deployed during nighttime hours during this study, and thus our results are only applicable to
651 daytime foraging and echolocation behavior. It is possible that nighttime behaviors may differ
652 considerably from the findings presented here. Our results are also useful for informing mitigation

653 measures related to the acoustic disturbance of foraging killer whales during feeding and provide a
654 baseline for behavioral comparison with similar studies on the highly endangered southern resident
655 killer whale population (e.g., Holt et al., 2019), whose conservation status is much more precarious.
656 In particular, population differences in the degree of interference with foraging success caused by
657 vessel presence, vessel noise, and operation of vessel sonar equipment is of future interest.

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899

900 *Figure Captions*

901 Figure 1. Chum salmon capture event by tagged northern resident killer whale I106 (8 year old
902 subadult, unknown sex), recorded over ~6 min on August 19, 2012 in Queen Charlotte Strait,
903 British Columbia, Canada. The top panel shows the time-depth profile of all the dives making up
904 the fish capture event, with bold lines indicating portions of the fish capture during which the
905 tagged whale was echolocating; buzz click trains are highlighted using gray shaded bands, and

906 prey-handling sounds are indicated by blue dots. The kinematically-estimated time of prey capture
907 is shown throughout the plots by the dashed red line (i.e., all data to the left of this line represents
908 the precapture phase, and everything to the right the postcapture phase). The 3-dimensional
909 pseudotrack representation of this prey capture event, as generated by TrackPlot software, is
910 shown in the inset of the top panel (yellow portions of the pseudotrack ribbon indicate body roll
911 >40 degrees in either direction). Lower panels show the echolocation click rate (clicks s^{-1}), the
912 absolute value of body roll (in degrees, with 180° indicating the whale is upside-down and 90°
913 indicating that it is oriented on its side in either direction), and the change in pointing angle
914 (degrees s^{-1} , a value that combines the measurements of heading and pitch, see Wright et al. 2017
915 for more details). All data were binned into 1 s intervals prior to visualization. A recording of the
916 sounds associated with this figure is available in the supplementary material for this study.

917
918 Figure 2. Spectrogram of focal echolocation clicks (marked with the letter “A”) made by a northern
919 resident killer whale tagged with an acoustic recording tag (Dtag) during a foraging dive, along with
920 simultaneous non-focal clicks (unmarked vertical lines) originating from conspecifics. The focal
921 clicks include low frequency energy content (≤ 10 kHz) that is absent in the non-focal clicks. The
922 spectrogram was generated using a Fast Fourier Transform (FFT) size of 1024 samples and 87.5%
923 overlap, resulting in a frequency resolution of 187.5 Hz and a temporal resolution of 1.3 ms. A
924 Hanning window was used for normalization. Amplitude displayed is relative (dB re 0).

925
926 Figure 3. Spectrogram of a focal buzz click train, a series of extremely rapid echolocation clicks
927 (containing at least one inter-click interval, or ICI, of ≤ 10 ms), produced by a northern resident killer
928 whale tagged with an acoustic recording tag (Dtag) during a foraging dive. The spectrogram was
929 generated using a Fast Fourier Transform (FFT) size of 1024 samples and 87.5% overlap, resulting

930 in a frequency resolution of 187.5 Hz and a temporal resolution of 1.3 ms. A Hanning window was
931 used for normalization. Amplitude displayed is relative (dB re 0). An audio recording of this buzz
932 has been included in the supplementary material for this study.

933
934 Figure 4. Spectrograms of two prey-handling sounds that occurred as whales tore fish into pieces and
935 consumed them. Top panel: this prey-handling sound was recorded by an acoustic recording tag
936 (Dtag) deployed on a foraging northern resident killer whale in August 2012. Bottom panel: this
937 prey-handling sound was recorded using a hydrophone in conjunction with a pole-mounted
938 underwater video camera that documented northern resident killer whales handling and consuming
939 fish in September 2006. The sound recorded by the acoustic tag was down-sampled from 240 kHz
940 to 48 kHz for comparison with the hydrophone-/video-recorded crunch (recorded at a sampling
941 frequency of 48 kHz). Both spectrograms were generated using a Fast Fourier Transform (FFT) size
942 of 512 samples and 87.5% overlap, resulting in a frequency resolution of 93.8 Hz and a temporal
943 resolution of 2.7 ms. A Hanning window was used for normalization. Amplitude displayed is relative
944 (dB re 0). An audio recording of the Dtag-recorded prey-handling sound has been included in the
945 supplementary material for this study.

946
947 Figure 5. Tukey boxplots showing the dive depths of tagged northern resident killer whales at the
948 start of the first echolocation train ('initial', orange fill, $N=17$) of each foraging event and the start
949 of all buzz trains ('buzz', blue fill, $N=27$), grouped by the species of salmon captured. No buzz
950 click trains were emitted by whales during captures of coho salmon. Boxplots indicate medians
951 (thick horizontal lines), first and third quartiles or the interquartile range, IQR (box extents),
952 minimums and maximums excluding outliers (vertical whiskers) and outliers, or values beyond
953 $IQR*1.5$ (dots).

954
955 Figure 6. Tukey boxplots showing mean echolocation click rates (clicks s^{-1}), averaged across the
956 precapture and postcapture phases of each fish-capture event ($N=17$), by tagged northern resident
957 killer whales. Clicking rate was calculated for each second of binned time during a capture event
958 and then averaged across each phase (pre- or postcapture), which were delineated using estimated
959 capture times based on kinematic and flow noise cues recorded on the Dtags. Boxplots indicate
960 medians (thick horizontal lines), first and third quartiles or the interquartile range, IQR (box extents),
961 minimums and maximums excluding outliers (vertical whiskers) and outliers, or values beyond
962 $IQR*1.5$ (dots). The summed duration of analysed 1-second time bins shown in this figure was 3779
963 s for all precapture phases (mean precapture duration = 222 ± 88.3 s), and 1898 s for all postcapture
964 phases (mean postcapture duration = 112 ± 67.1 s).

965
966 Figure 7. Echolocation click repetition rates (clicks s^{-1} , plotted on a logarithmic scale) relative to the
967 time that each salmon was captured (dashed vertical line at time = 0 s) for 17 prey-capture events
968 by northern resident killer whales tagged with acoustic recording tags. Negative time values (to the
969 left of the dashed line) indicate clicking rates prior to salmon captures, while positive values indicate
970 clicking rates after a fish was caught. Capture times were determined based on kinematic and flow
971 noise cues recorded on the Dtags. The thicker black line indicates mean clicks s^{-1} , averaged across
972 5 s intervals of binned time for all 17 prey captures. Shaded bands represent the 1-99% (light gray)
973 and 25-75% (dark gray) percentiles of the click rate data, also binned into 5 s intervals.

974
975 Figure 8. Tukey boxplots showing the proportion of time northern resident killer whales tagged with
976 acoustic recording tags spent emitting echolocation clicks before versus after catching a salmon
977 ($n=17$). Proportions were calculated by determining the number of 1-second time bins that contained

978 echolocation clicks for each phase of each capture event, and dividing this by the total duration of
979 the phase (pre- or postcapture). Capture phases were delineated using estimated capture times based
980 on kinematic and flow noise cues recorded on the Dtags. Boxplots indicate medians (thick horizontal
981 lines), first and third quartiles or the interquartile range, IQR (box extents), minimums and
982 maximums excluding outliers (vertical whiskers) and outliers, or values beyond $IQR \times 1.5$ (dots). The
983 summed duration of analyzed 1-second time bins shown in this figure was 3779 s for all precapture
984 phases (mean precapture duration = 222 ± 88.3 s), and 1898 s for all postcapture phases (mean
985 postcapture duration = 112 ± 67.1 s).

986
987 Figure 9. Scatter plot showing the occurrence of buzzes ($N=27$) made by tagged northern resident
988 killer whales relative to dive depth (m) and the time (s) of fish capture. The moment of capture is
989 indicated by the dashed vertical line at $x=0$ and was determined based on kinematic and flow noise
990 cues recorded on the Dtags; precapture buzzes are shown as orange dots and postcapture buzzes as
991 blue dots. Plotted for 12 of 17 successful foraging dives for which prey fragment samples (fish scales
992 and/or tissue) were collected at the surface. No buzzes were detected on the Dtag hydrophone
993 recordings for 5 of the successful fish-capture events (all of the prey captures from 2009 tag
994 deployments and one capture each in 2010 and 2011). Mean number of buzzes per fish-capture event
995 was 1.6 ± 1.7 .

996
997 Figure 10. Scatter plot showing the occurrence of prey-handling sounds ($N=62$) made by northern
998 resident killer whales tagged with acoustic recording tags (Dtags) relative to dive depth (m) and the
999 time (s) of fish capture. The moment of capture is indicated by the dashed vertical line at $x=0$ and
1000 was determined based on kinematic and flow noise cues recorded on the Dtags; precapture prey-
1001 handling sounds are shown as orange dots and postcapture prey-handling sounds as blue dots.

1002 Plotted for 14 of 17 successful foraging dives for which prey fragment samples (fish scales and/or
1003 tissue) were collected at the surface. No prey-handling sounds were detected on the Dtag
1004 hydrophone recordings for 3 of the 17 successful fish-capture events. Postcapture prey-handling
1005 sounds were made at shallower depths (14.6 ± 11.3 m) than those made prior to or simultaneously
1006 with the fish capture (133.4 ± 4.9 m). Mean number of prey-handling sounds per fish-capture event
1007 was 3.6 ± 3.2 .

1008
1009 Supplementary Information, Figure S1. Histogram of probability densities for log-transformed
1010 inter-click intervals (ICI, seconds) of echolocation clicks produced by tagged northern resident
1011 killer whales during successful foraging dives. Solid red curve shows the probability density
1012 function and the red vertical dashed line indicates the threshold at 10 ms that was used to
1013 distinguish buzzes from regular click trains. Any echolocation train that contained at least one ICI
1014 below or equal to the 10 ms threshold was classified as a buzz.

1015 *Tables*

1016 Table 1. Summary of Dtag deployments used to record echolocation and kinematic behavior by individual northern resident killer
1017 whales ($N=7$) during successful captures of Pacific salmon ($N=17$), 2009-2012. Deployment IDs reflect the species (oo = *Orcinus orca*),
1018 the year (e.g., 09=2009), Julian day (e.g., 231) and sequence (e.g., 'a') of tag deployment. Whale IDs and ages were established using a
1019 published photographic identification catalogue of northern resident killer whales (Ellis et al., 2011).

Deployment	Whale ID	Sex	Age (years)	Audio sampling rate (kHz)	Tag model	Recording time (hr)	# prey captures
oo09_234a	A46	M	27	96	Dtag-2	3.9	1
oo09_240a	A37	M	32	96	Dtag-2	3.6	2
oo10_256a	G64	F	10	192	Dtag-2	7.6	2
oo10_265a	G49	F	20	192	Dtag-2	2.9	2
oo11_246a	G31	F	30	192	Dtag-2	3.8	5
oo12_232a	I106	unknown	8	240	Dtag-3	5.8	2
oo12_235b	A66	M	16	240	Dtag-3	4.5	3

1020

1021

1022 Table 2. Details of prey capture events ($N=17$) and corresponding echolocation behavior by seven northern resident killer whales
1023 carrying acoustic recording tags between 2009-2012. Fish capture depths (m) were determined by examining three-dimensional
1024 reconstructions of dive tracks (pseudotracks) and estimating the time and depth at which pursuit behavior (i.e., convoluted, spiralling
1025 and kinematically complex dive paths) ceased abruptly, cues that were often concurrent with flow noise changes on the acoustic
1026 recordings. Estimated fish capture times typically corresponded to the maximum depth of the dive immediately prior to prey sample
1027 collection at the surface. The precapture phase included all kinematic behavior prior to the fish capture that was indicative of searching
1028 and pursuit, while the postcapture phase included all kinematic behavior immediately following each fish capture until the whale
1029 resumed shallow, directional swimming. The presence of chasing on the surface at the beginning of the event, the fish species caught
1030 and the occurrence of postcapture sharing with other whales is also noted.
1031

1032

Deployment	Depth of 1st click train (m)	Initial surface pursuit?	Capture depth (m)	Prey species	Shared?	Capture phase duration (s)		Mean click rate (clicks s ⁻¹)		% time spent clicking	
						precapture	postcapture	precapture	postcapture	precapture	postcapture
oo09_234a	20.0	no	101.6	Chinook	no	241	128	0.6	0.5	16.2	25.0
oo09_240a	4.0	yes	165.7	coho	no	349	170	1.5	0.4	41.3	14.7
oo09_240a	10.8	no	119.4	coho	no	167	179	0.8	0.4	34.1	20.7
oo10_256a	83.1	no	134.5	chum	no	298	285	3.5	0.1	21.5	5.3
oo10_256a	5.1	no	123.7	chum	no	372	152	4.0	0.1	26.1	2.0
oo10_265a	39.2	no	130.5	chum	possible	149	168	2.3	0.9	34.9	16.1
oo10_265a	13.5	no	133.7	chum	no	265	134	2.4	0.2	29.1	3.7
oo11_246a	101.5	no	201.9	Chinook	yes	219	87	5.9	0	36.5	0
oo11_246a	12.6	no	264.8	Chinook	yes	148	115	6.6	0	32.4	0
oo11_246a	31.7	no	131.1	Chinook	yes	277	57	6.8	0	37.9	0
oo11_246a	196.5	no	204.5	Chinook	yes	135	87	8.1	0	14.1	0
oo11_246a	32.7	no	180.7	Chinook	yes	129	95	6.5	0	38.0	0
oo12_232a	1.8	yes	0.7	chum	possible	282	15	2.6	0	23.4	0
oo12_232a	0.3	yes	87.6	chum	no	241	86	13.3	0	43.2	0
oo12_235b	5.2	no	102.7	Chinook	no	314	54	8.4	0.8	47.1	25.9
oo12_235b	0.6	yes	6.6	Chinook	no	119	19	15.9	1.4	58.8	52.6
oo12_235b	0.7	yes	0	Chinook	no	74	67	2.1	3.2	32.4	49.3
median						241	95	4.0	0.1	34.1	3.7
(IQR)						(148-282)	(67-152)	(2.3-6.8)	(0-0.5)	(26.1-38.0)	(0-20.7)

1033

Figure 1

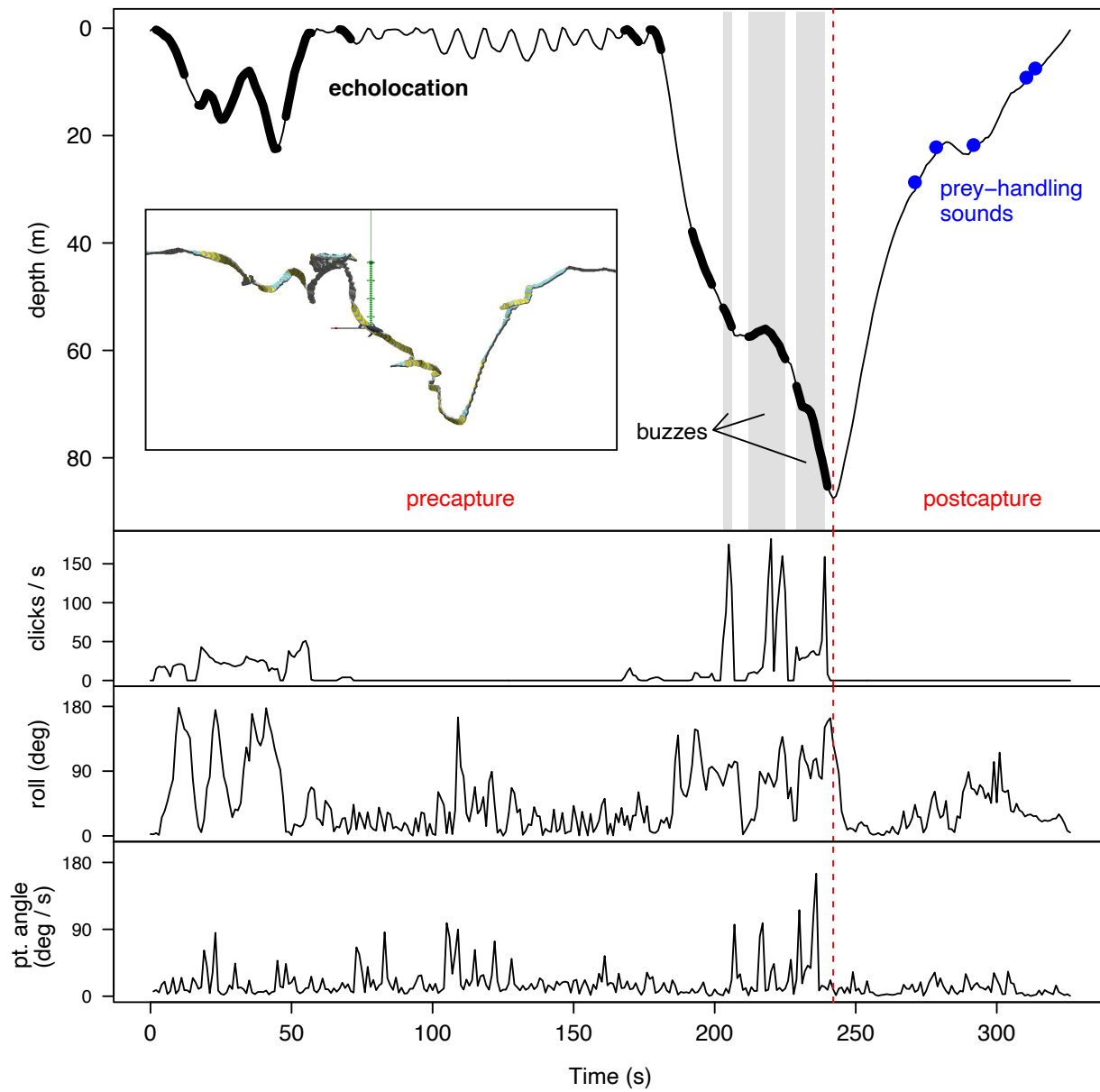


Figure 2

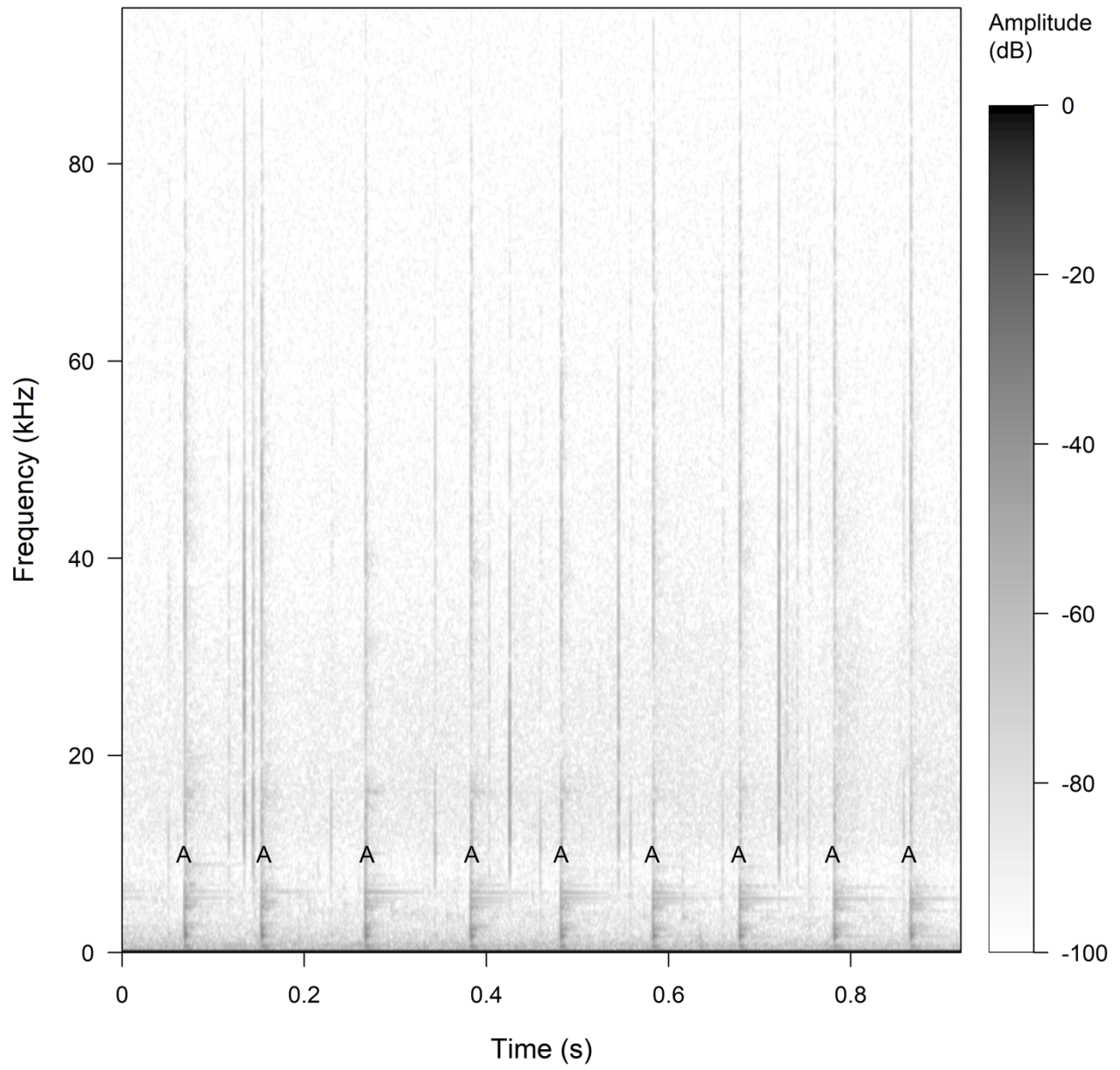


Figure 3

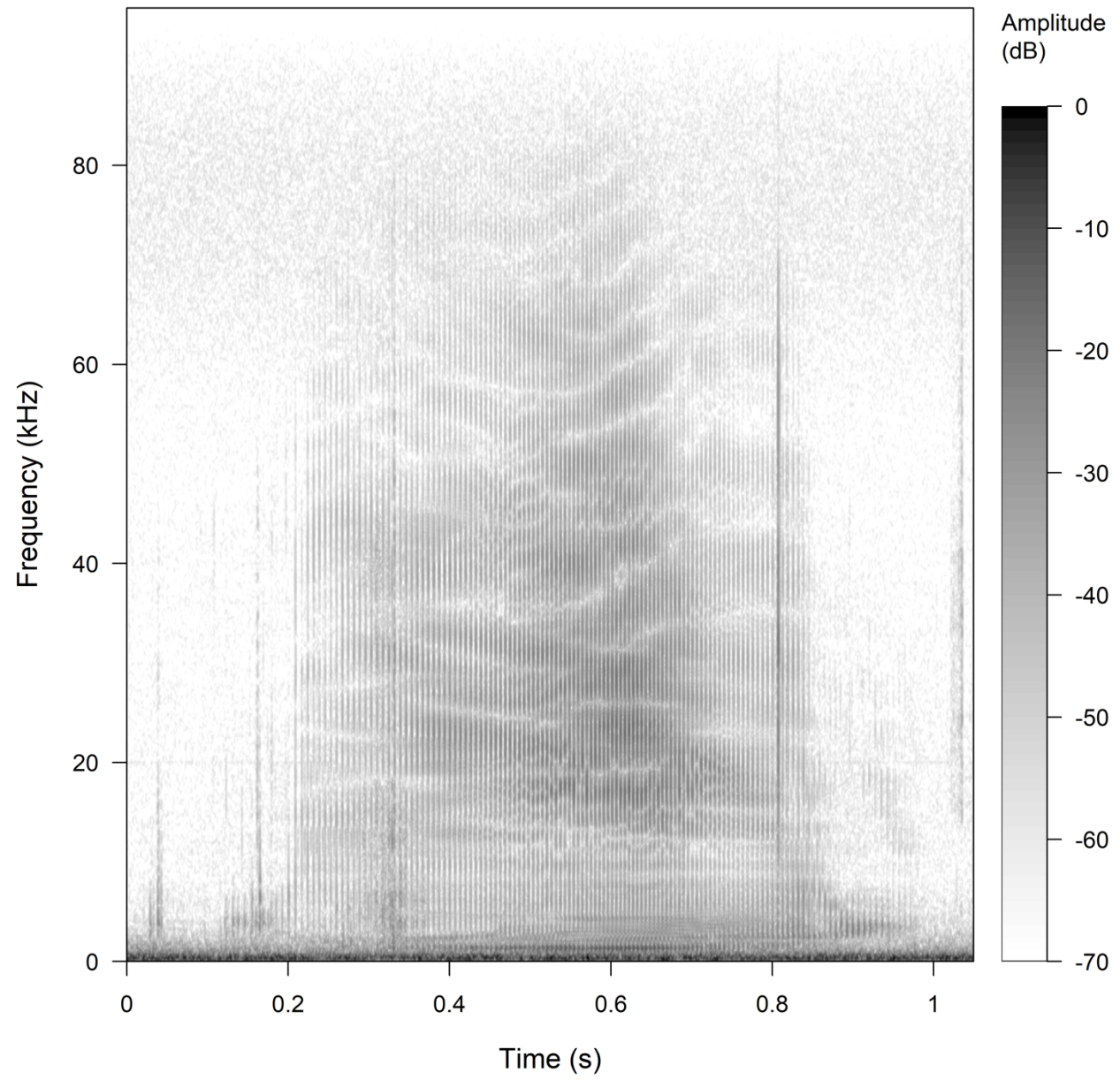


Figure 4

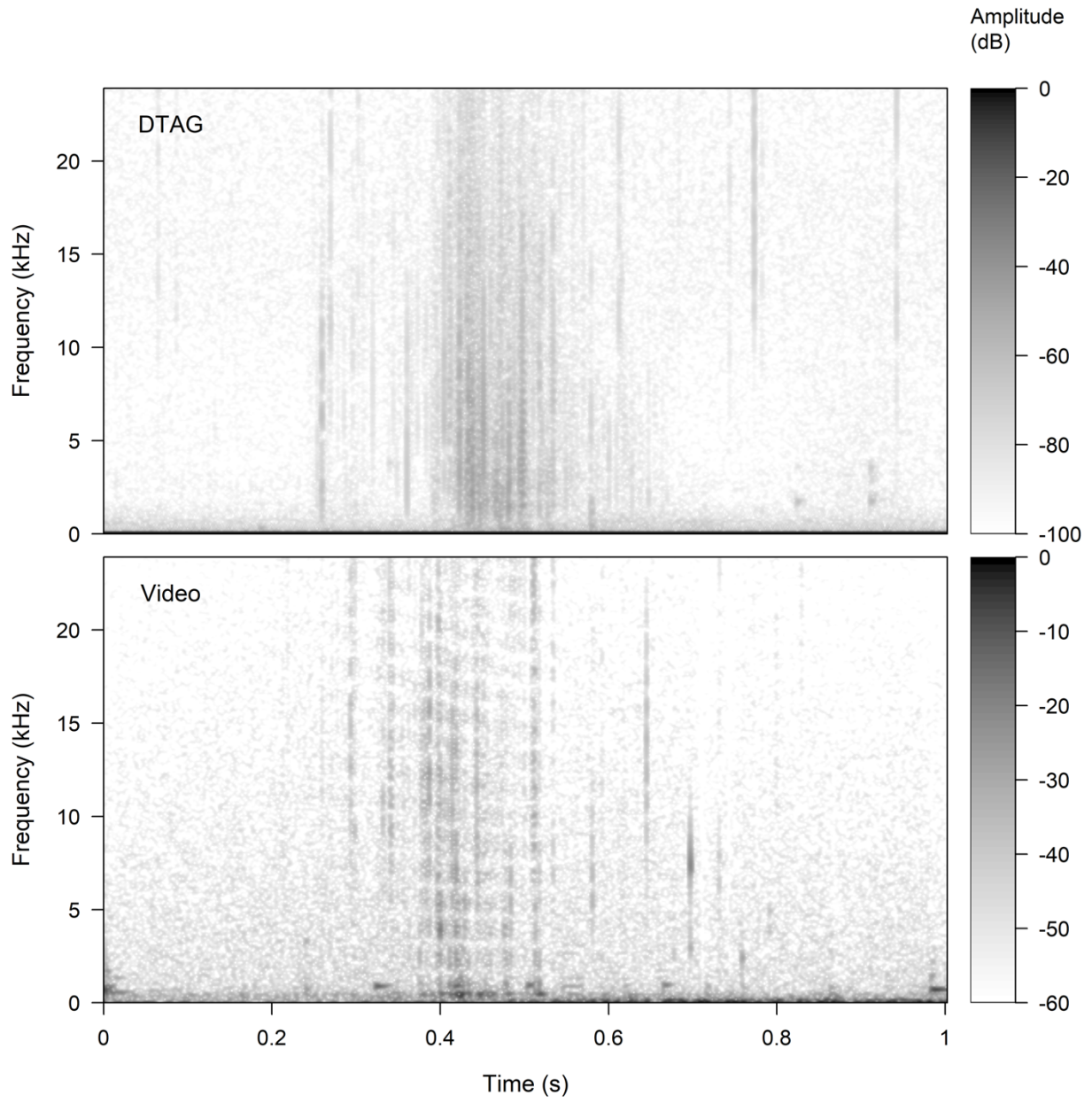


Figure 5

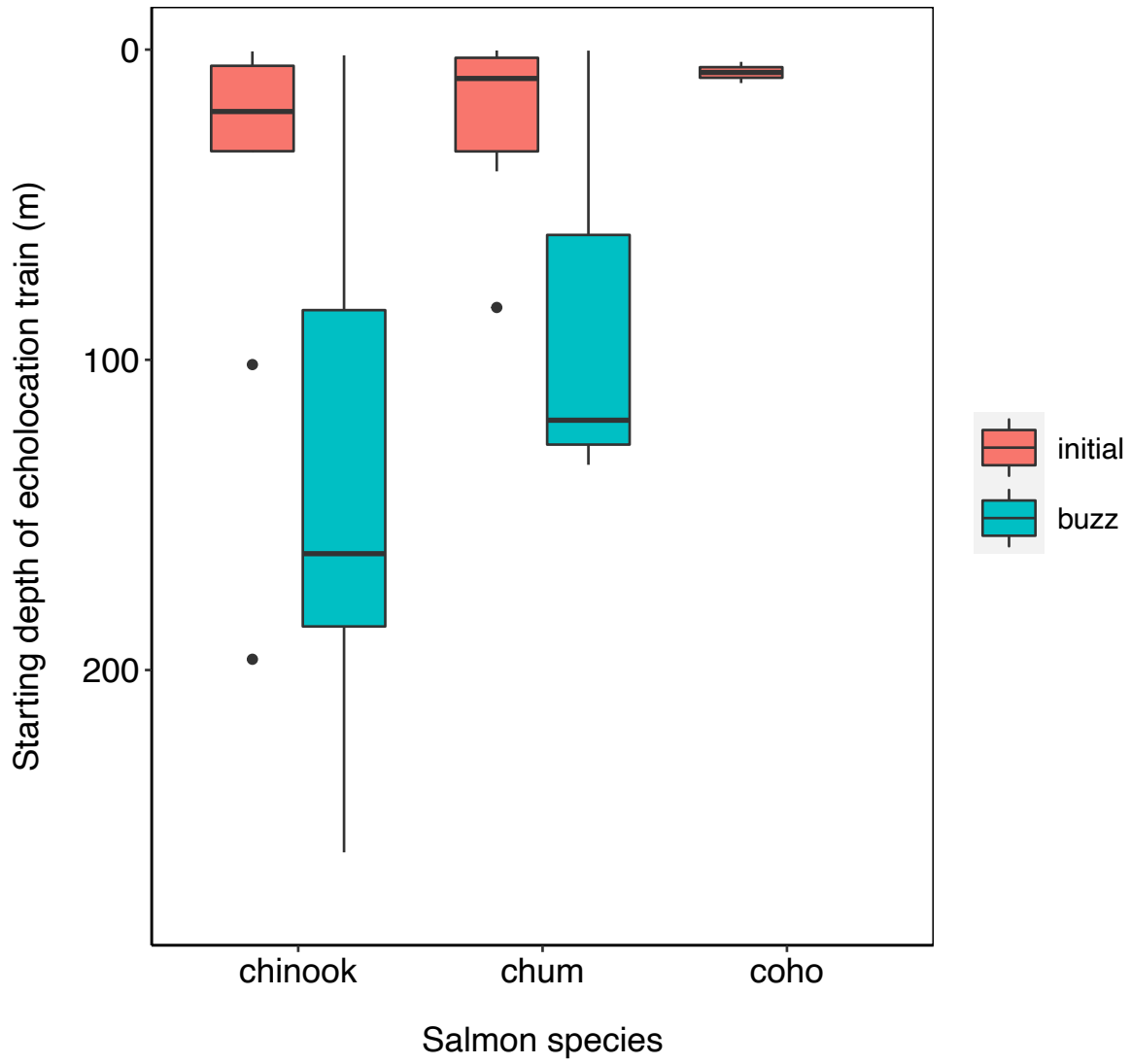


Figure 6

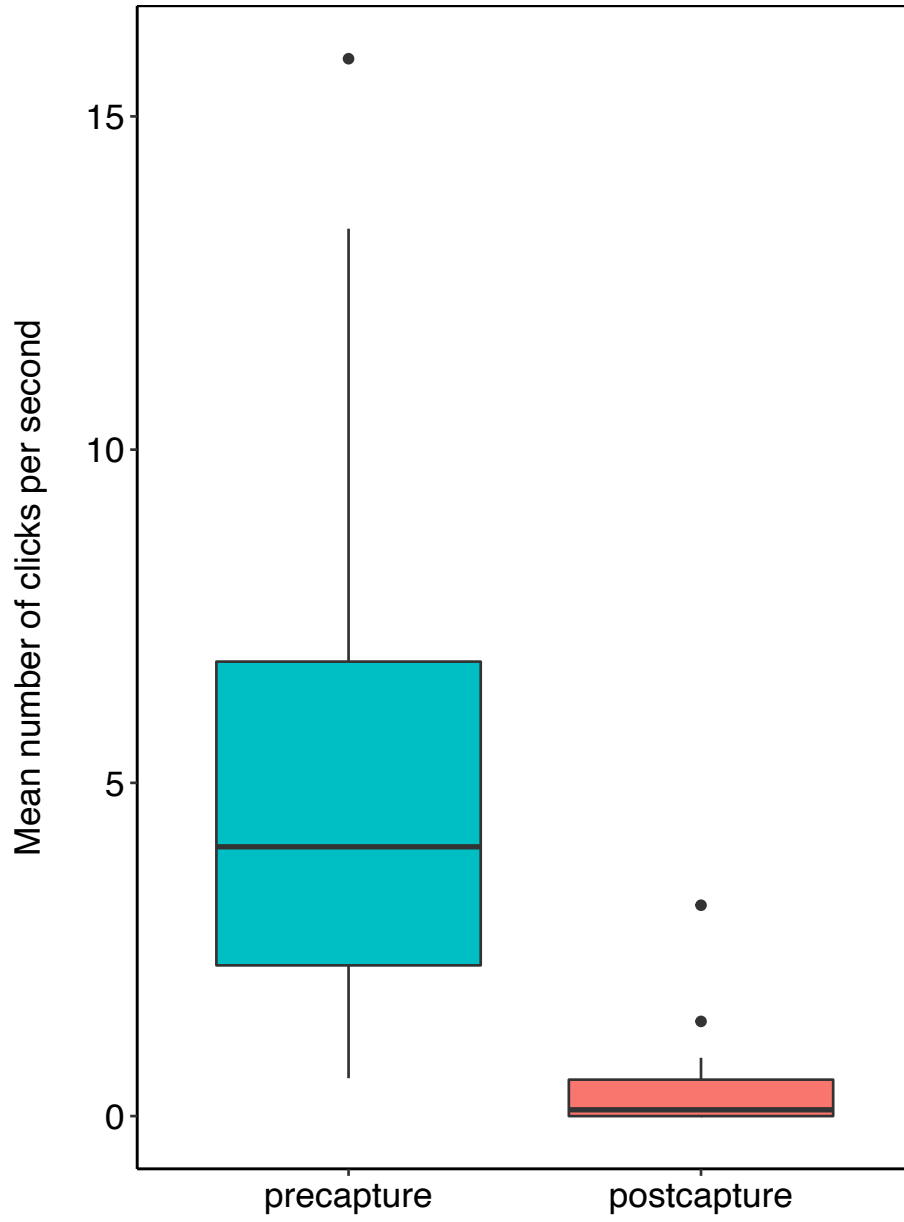


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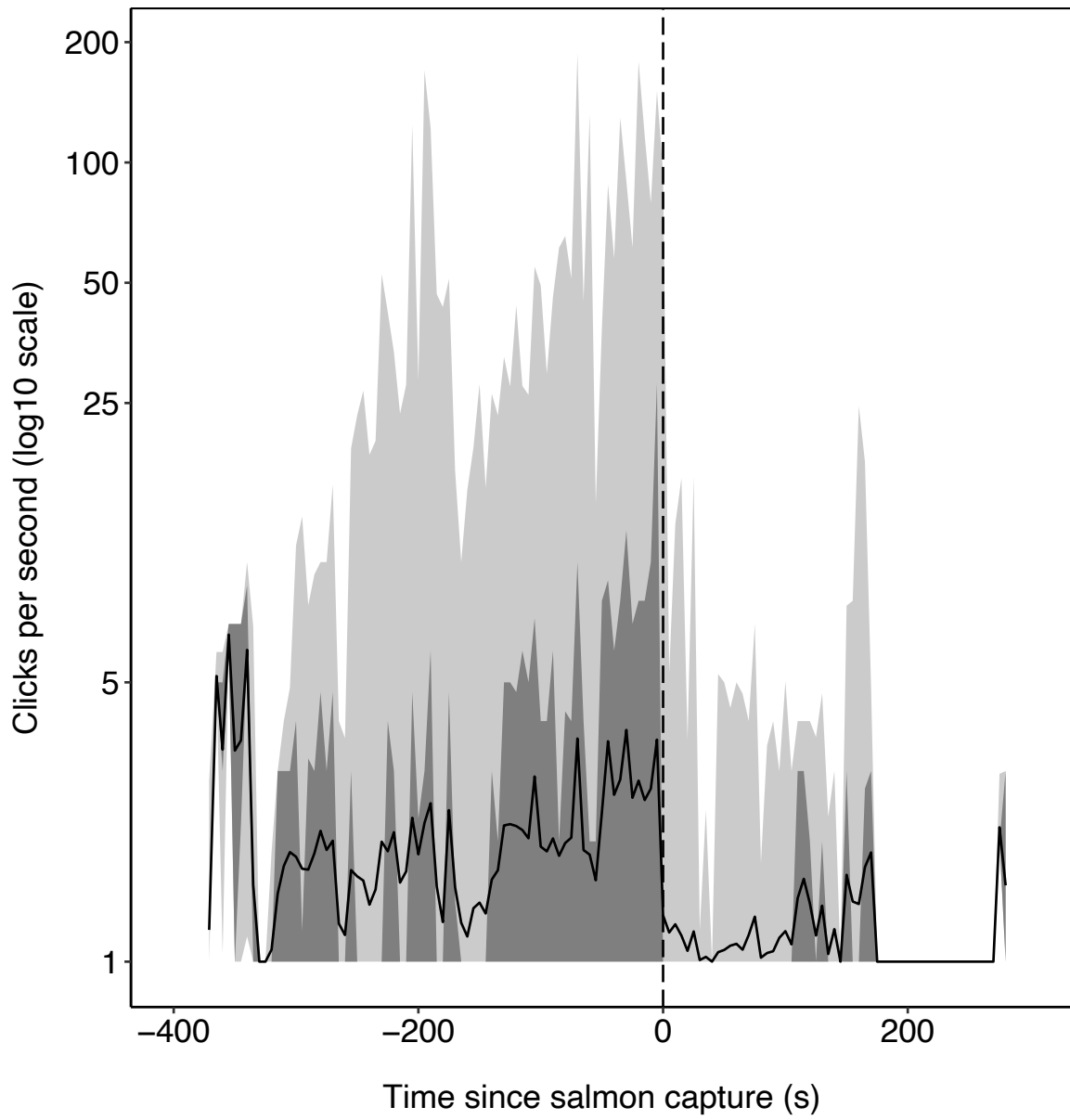


Figure 8

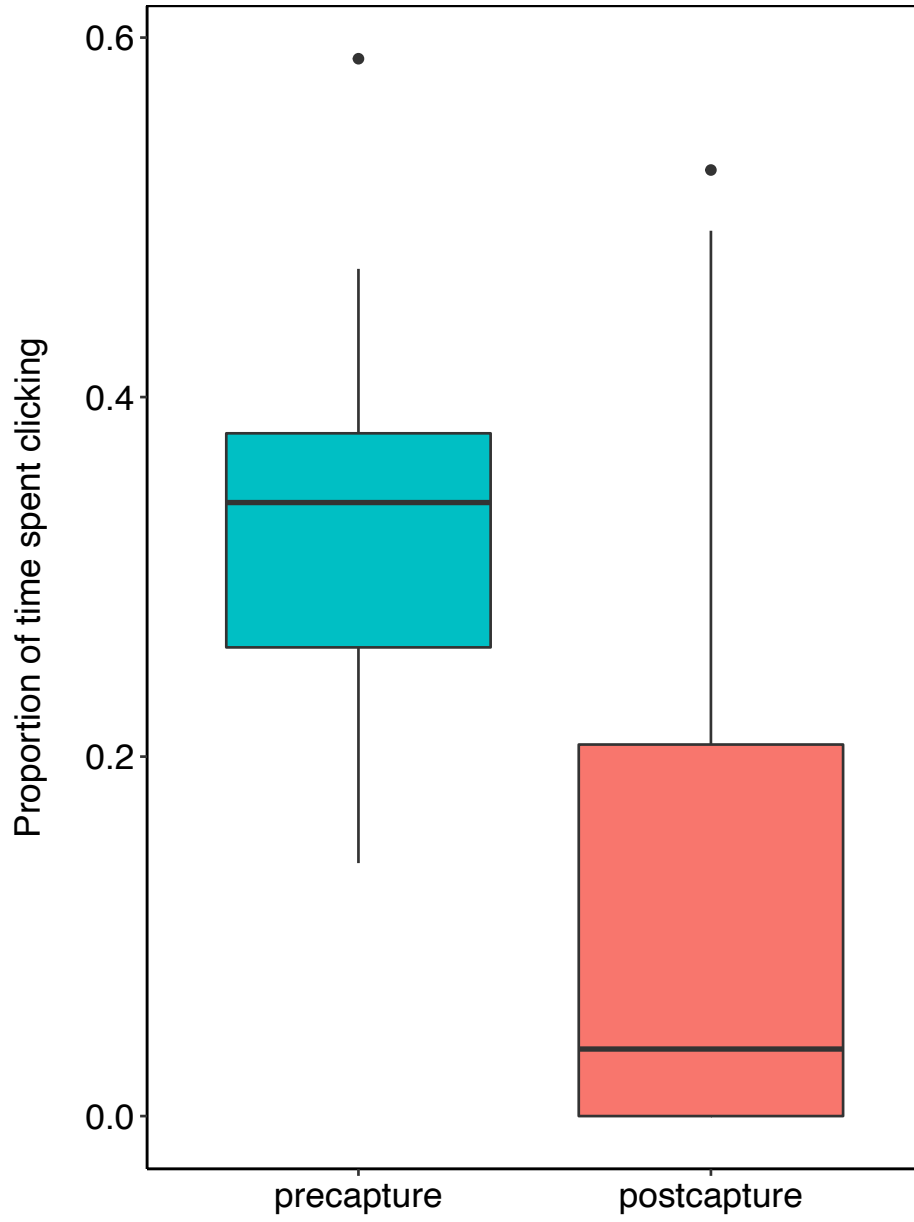


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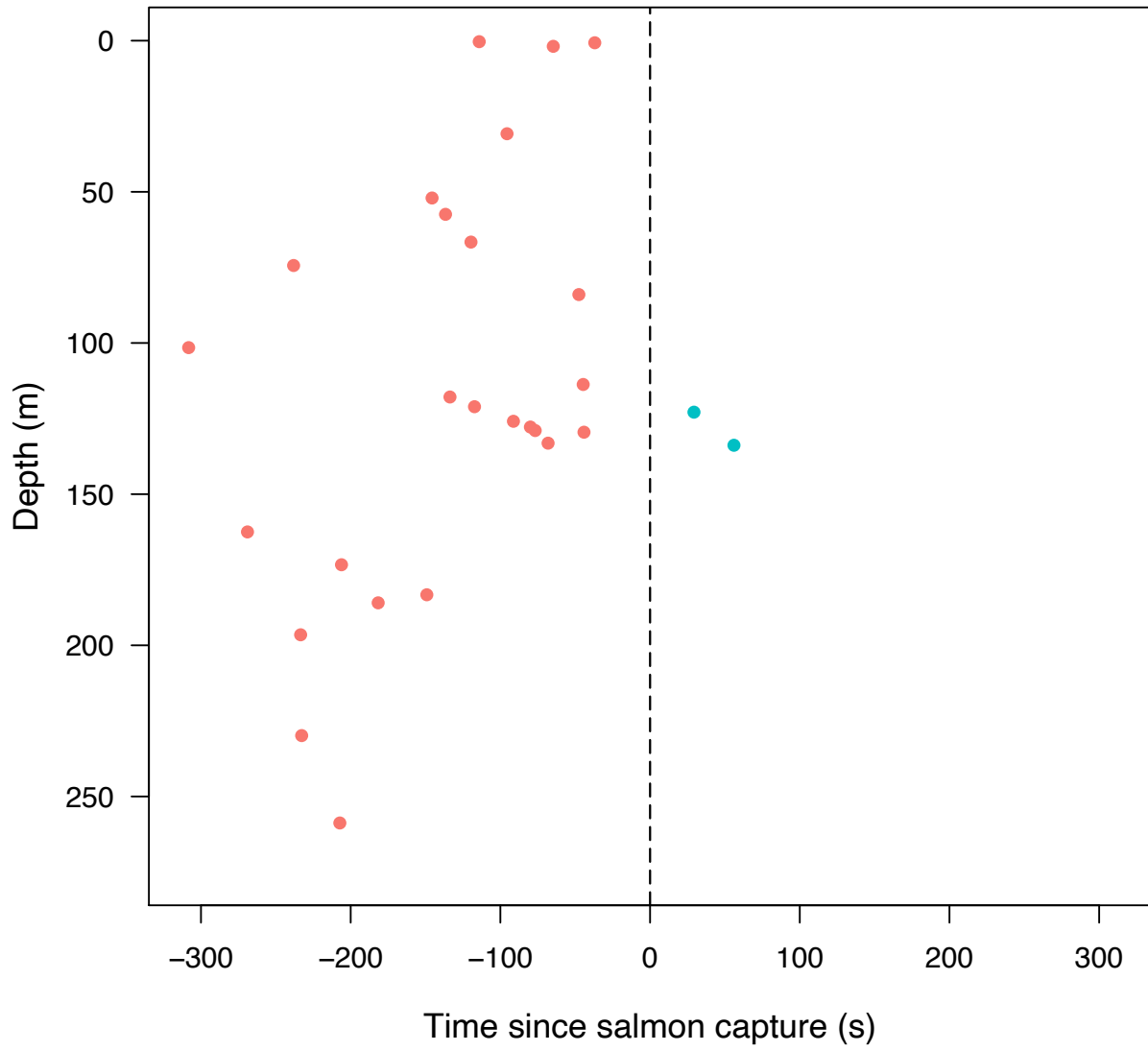
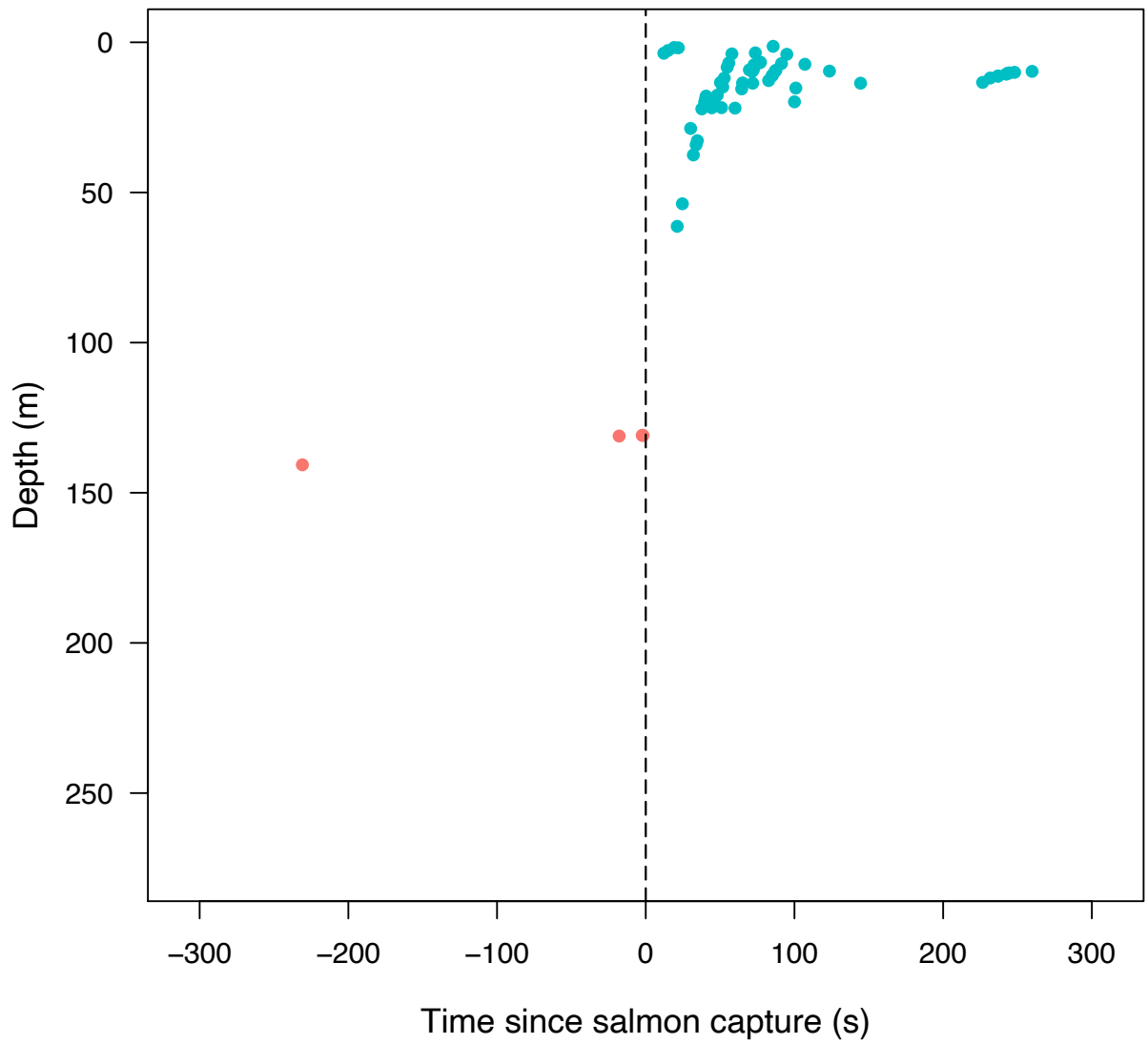


Figure 10



Supplementary Figure 1

