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

Brianna M. Wright[1,2,3], Volker B. Deecke[4], Graeme M. Ellis[1], Andrew W. Trites[2,3], John K. B. Ford[1,2,3]

1. Pacific Biological Station, Fisheries and Oceans Canada, Nanaimo, British Columbia, Canada
2. Marine Mammal Research Unit, Institute for the Oceans and Fisheries, University of British Columbia, Vancouver, British Columbia, Canada
3. Department of Zoology, University of British Columbia, Vancouver, British Columbia, Canada
4. Centre for National Parks and Protected Areas, University of Cumbria, Ambleside, Cumbria, United Kingdom

Correspondence

Brianna M. Wright
Pacific Biological Station
3190 Hammond Bay Road, Nanaimo, British Columbia, V9T 6N7, Canada
Email Brianna.Wright@dfo-mpo.gc.ca

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

KEYWORDS

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

Introduction

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

Although captive studies have provided detailed information about the sonar capabilities of odontocetes, translating these findings into an understanding of how echolocation is used in the wild presents a considerable challenge. Biologging tags with sensors for detecting both sound and movement (e.g., digital acoustic recording tags or Dtags: Johnson & Tyack, 2003) have provided the first data directly linking movement behavior during foraging with echolocation signals produced by free-ranging odontocetes. For instance, click echoes rebounding from prey were first recorded in the wild using Dtags deployed on beaked whales (Johnson et al., 2004). Acoustic tags have also supplied the first verification that rapid bursts of clicking (known as buzzes) are used for fine-scale tracking during the final moments of prey pursuit (Madsen & Surlykke, 2013). Echo structures from buzzes by Blainville's beaked whales (*Mesoplodon densirostris*) showed that click rates within buzzes are correlated to prey range and allow whales to focus on individual targets during capture attempts (Johnson et al., 2008). This has been corroborated in other species by using tag data that relate the occurrence of buzzes to body movements consistent with close-range pursuit or prey captures. For example, beaked whale buzzes coincide with increased dynamic body acceleration (Johnson et al., 2004) or tight, circling swim paths (Johnson et al., 2008), buzzes of short-finned pilot whales (*Globicephala macrorhynchus*) occur immediately after directional high-speed sprints (Aguilar de Soto et al., 2008), and short-range sonar sounds of finless porpoises (*Neophocaena phocaenoides*) are associated with declines in speed indicative of tight turns made during prey pursuit (Akamatsu et al., 2010). Similarly, sperm whales (*Physeter macrocephalus*) produce rapid click sequences called creaks that have been associated with increased changes in body orientation during the bottom phases of dives, when prey captures are presumed to occur (Miller et al., 2004).

Schevill and Watkins (1966) were the first to describe echolocation clicks produced by the fish-eating resident killer whales (*Orcinus orca*) found in the eastern North Pacific, from acoustic recordings of a subadult male captured off Vancouver Island, Canada. This individual produced clicks series that appeared to function in echolocation, as he could only avoid a hydrophone placed in his path at night if he was emitting clicks (Schevill & Watkins, 1966). Since this initial captive study, the acoustic properties of echolocation clicks made by wild resident killer whales have been documented using hydrophone arrays (Au & Benoit-Bird, 2003; Au et al., 2004), confirming that click structure is consistent with the traits of an effective biosonar signal, namely broad bandwidth, brief duration and high amplitude (Au et al., 2004). Analysis of click properties has also shown that echolocating resident killer whales can detect prey at distances of 100 m or more, and are capable of fine target discrimination (Au et al., 2004). Click source levels are also strongly coupled with target distance, indicating that killer whales possess a type of time-varying gain control that can be used to discern relative target size (Au & Benoit-Bird, 2003). Furthermore, an experimental study of backscatter created by exposing live fish to simulated killer whale clicks found that echo structures reflected by Pacific salmon (*Oncorhynchus* spp.) differed depending on species (Au et al., 2010). Resident killer whales may therefore use echolocation to identify the size and species of fish they encounter (Au et al., 2010). This ability is particularly important given their preference for consuming mature (4-5 year old) Chinook salmon (*O. tshawytscha*; Ford et al., 1998; Ford & Ellis, 2006).

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

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

Methods

Dtag deployments and focal follows

We recorded the echolocation and diving behavior of foraging northern resident killer whales from August to September of 2009-2012, in the coastal waters off northeastern Vancouver Island, British Columbia, Canada. We deployed digital acoustic recording tags (Dtags; Johnson & Tyack, 2003) on individual whales that allowed us to compute their three-dimensional body orientation at high resolution using data from the tag's pressure sensor, triaxial accelerometers and magnetometers. In addition to animal orientation data, the tags continuously recorded underwater sounds using two hydrophones. When encountered, individual northern resident killer whales were visually identified by their natural markings using a photo-identification catalog (Ellis et al., 2011), following the technique developed by Bigg (1982). A whale was then selected and approached in a 9.3 m command-bridge diesel-powered vessel (*MV* Roller Bay), and a Dtag was deployed from the bow using a hand-held, 7 m carbon fiber pole. Tagging was opportunistic in that if an animal other than the individual we originally selected presented us with a good opportunity to deploy a tag, we would do so. Ideally, the tag was attached just below the base of the dorsal fin via its four suction-cups, so that it cleared the water when the whale surfaced to facilitate tracking of the animal using the tag's VHF transmitter. Only adults and larger juvenile killer whales (≥3 years of age) were approached for tagging, and repeat deployments on the same individuals were avoided. The sampling rate for the pressure sensor, accelerometers, and magnetometer was 50 Hz for Dtag-2 deployments (2009-2011) and 250 Hz for Dtag-3 deployments (2012). Acoustic data were recorded with 16-bit resolution at sampling rates of 96, 192 or 240 kHz, depending on the tag model and deployment year (Table 1). Prior to analysis, hydrophone recordings with 240 kHz sampling rates were down-sampled to 192 kHz to allow real-time audio playback in Adobe Audition CS5.5 (Adobe Inc., San Jose, CA, USA).

We conducted a focal follow (Altmann, 1974) of each tagged whale and noted surface observations of its foraging behavior using a digital voice recorder that was time-synchronized with the Dtag sensors. The research vessel (*MV* Roller Bay, used for both Dtag deployments and focal follows) operated using Arneson drive propulsion (surface-piercing propellers), a propulsion type that has been shown to produce lower underwater sound levels compared to traditional propellers in controlled experiments (Wladichuk et al., 2019). This minimized the chance that noise disturbance from the research vessel would affect the whales' behavior during focal follows. The need for concurrent surface observations limited the deployments to daylight hours. Following the methodology of Ford and Ellis (2006), we identified the times and locations of successful prey captures by collecting fish scales and tissue fragments using a fine-meshed dip net when tagged whales surfaced from successful feeding dives. We examined the surfacing locations of tagged individuals for evidence of prey remains whenever they exhibited behavioral cues indicative of foraging (e.g., changes in swim speed and direction, long dive durations, and milling by nearby conspecifics; Ford & Ellis, 2006). Since resident killer whales spread out to forage independently or in small subgroups, and typically surface with prey in their mouths prior to consuming it or carrying it towards other whales for sharing (Ford & Ellis, 2006; Wright et al., 2016), we could attribute fish remains to the individual that made the capture with high confidence. Our analyses included only those foraging dives for which fish remains could be attributed to the tagged whale, and for which no other individuals participated in the prey capture. Fish scale and tissue samples were used to identify the species and age of the captured fish. Age was determined using schlerochronology (MacLellan, 2004), and species was determined using scale morphology or genetic analysis (Withler et al., 2004).

Dtag calibration, dive identification and pseudotrack construction

We calibrated the Dtag sensor data to correct for the orientation of the tag relative to the body axes of the whale using a custom calibration routine run in Matlab version 7.8.0/R2009a (The MathWorks Inc., Natick, MA, USA). Dtag calibration methodology is described in more detail by Johnson & Tyack (2003). Calibration converted the raw sensor measurements of pressure into depth, and accelerometer and magnetometer data into the three rotational measures of pitch, roll, and heading. The resulting estimates of each whale's body position over time were automatically down-sampled from the raw sensor sampling rates to 5 Hz during this process. For some deployments, changes in the position of the Dtag on the animal due to tag slippage required performing new calibrations for every new orientation of the tag. We identified individual dives within the calibrated data using an automated filter that defined a dive as any submersion with depth ≥1 m, bounded by surfacing events of <1 m depth. This filter calculated the start and end times (in seconds since tag activation) and the maximum depth for each identified dive. We also visualized the time series of whale body orientations for each deployment using the software TrackPlot 2.3 (Ware et al., 2006), which combined the calibrated pitch, roll, heading and depth values to create a three-dimensional representation (dead-reckoned pseudotrack) of tagged whale movements (see inset, Figure 1).

Reconstructing fish-capture events

We determined the beginning and end times of successful fish capture events by matching the times when prey samples (*N*=17) were collected to the corresponding kinematic behavior of tagged whales displayed in the Trackplot pseudotracks. The start of a fish capture event was defined as the beginning of the first dive prior to the time of prey sample collection (and all subsequent dives leading up to the sample collection) that contained movements indicative of searching or pursuit (i.e., convoluted, spiralling, and kinematically complex pseudotracks). Kinematic signatures that are characteristic of foraging dives by resident killer whales are described in more detail by Wright et al. (2017) and Tennessen et al. (2019). The precapture phase of the event included all kinematic and acoustic behavior from the first dive indicative of searching and/or pursuit until the time of prey capture. Often, this precapture phase was represented by the descent phase of a single, steep dive, but it could sometimes include multiple dives and/or chase behavior at the surface (see example in Figure 1). The capture itself was predicted to occur when kinematically complex pursuit behavior ceased abruptly and the whale began a directional, linear ascent (Figure 1). Dtag acoustic records were used to corroborate the kinematically-predicted capture times, as fluctuations in flow noise consistent with sudden acceleration changes often accompanied the kinematic transitions thought to represent fish captures (Wright et al., 2017). Estimated capture times typically coincided with the maximum depth of the dive immediately prior to the prey sample collection at the surface. Dives occurring after the whale surfaced with prey were also included in the fish capture event if the pseudotrack contained circling or milling behavior consistent with prey handling or sharing. We defined the end of the fish capture event as the time when the tagged whale resumed the shallow, directional swimming it had exhibited prior to the beginning of the hunting and chasing behavior (i.e., the postcapture phase was defined as all kinematic and acoustic behavior that occurred from the time of prey capture until directional swimming at the surface resumed). In this way, we ensured that each fish capture event included the entire process of the killer whale detecting, pursuing, catching and handling an individual salmon. After identifying the beginning and end times for each fish capture event, we extracted and analyzed the corresponding acoustic recordings from the Dtag hydrophones.

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

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

We distinguished between focal and nonfocal clicks by examining click spectrograms for the presence of a low frequency energy component (Jensen et al., 2011; Ward et al., 2008; Figure 2). Increased low frequency energy content (generally <10 kHz) results from the passage of sound through the tissues of the tagged whale prior to reaching the tag hydrophones, and is therefore evident in focal clicks but missing from nonfocal clicks (Zimmer et al., 2005). Once putative focal clicks had been identified, they were compared to an assessment of each echolocation click train using the angle of arrival (AoA) technique (Johnson et al., 2006; Zimmer et al., 2005). Given the fixed position of the tag on the whale's body, echolocation clicks made by the focal individual should originate from a consistent angle relative to the tag over time. Nonfocal clicks, conversely, will display fluctuating AoA values as the position of a conspecific relative to the tagged whale changes. We assessed AoA consistency using a custom Matlab routine, described in more detail by Holt et al. (2019), that displayed corresponding plots of the tag-recorded spectrograms, waveforms, and the AoA calculations for each click train over time. A similar approach was also used by Arranz et al. (2016) to identify focal clicks of tagged Risso's dolphins (*Grampus griseus*). Any click train identified as focal based on a low frequency energy component, but which failed to coincide with any of the focal click trains identified using the more conservative AoA audit, was omitted from the analysis. Both the AoA audits and the visual identification of low frequency energy in focal clicks were conducted by the same analyst for all tags.

Following the methodology of Barrett-Lennard et al. (1996), consecutive focal echolocation clicks were assigned to the same click train if they were separated by ICIs of ≤2 s. To distinguish rapid buzz clicks (Figure 3) from regular echolocation clicks (Figure 2), we produced a histogram of natural log-transformed ICIs and used the break in its bimodal distribution at ~10 ms as the threshold for separating click train types (see Figure A1, Supplementary Information). We classified any echolocation train that contained at least one ICI below or equal to the 10 ms threshold as a buzz. The same threshold was previously used to differentiate regular echolocation from buzzes in Dtag recordings from the closely related southern resident killer whale population (Holt et al., 2013, Holt et al., 2019, Tennessen et al., 2019). Once click trains were classified by type (regular or buzz), we calculated the number of each type per prey-capture event, as well as the duration, click repetition rate, and mean ICI of each train. As most data were not normally distributed, we present most summary statistics as medians and interquartile ranges (IQR), unless otherwise stated.

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

Comparing echolocation patterns with concurrent kinematic behavior

We synchronized the acoustic recordings with the tag kinematic data to analyze the relationship between dive depth, echolocation, and the relative phase of the foraging dive (pre- or postcapture). By identifying the moment of capture for each successful foraging event (using both flow noise and kinematic cues, as previously described), we could compare the echolocation behavior of killer whales before and after a fish was caught. To accomplish this, we binned each foraging dive into 1 s time intervals and calculated both the presence/absence of clicking and the click repetition rate for each bin (see example of 1 s binned clicking rate data displayed in Figure 1). Click rates were then averaged across each dive's pre- and post-capture phases to examine differences in echolocation during active searching and chasing compared to during prey handling and consumption. The proportion of time spent echolocating within each dive phase (pre- and postcapture) was determined by summing the number of 1 s bins that contained clicks and dividing it by the total duration (s) of each phase. Differences in pre- and postcapture echolocation behavior were assessed using a Bayesian alternative to the paired-samples *t*-test (Kruschke, 2013) in R using the 'BayesianFirstAid' package (Bååth, 2014). The benefit of this Bayesian approach is that it assumes that the data follow a *t* distribution, which is more robust to outliers than the normal distribution typically assumed by frequentist approaches. Rather than testing whether the difference between two groups is zero, as a classical test would, the Bayesian analysis we use here asks how large the estimated difference is between the groups, and what the probability is that the true difference is larger than zero. Parameters were initialized using robust estimates of the mean (trimmed) and median absolute deviation with the goal of generating uniform priors and assisting with convergence of the Markov Chain Monte Carlo (MCMC) sampling, which had a burn-in of 500 samples and 3 chains with 10,000 samples per chain.

We calculated the dive depths of killer whales at the beginning of the first echolocation train for each prey-capture event, as well as the dive depths at the beginning of each buzz and examined these depths relative to the salmon species caught to further elucidate the prey species-specific differences in foraging tactics by northern resident killer whales previously identified by Wright et al. (2017). We also examined the timing and depths at which buzzes and prey-handling sounds occurred, relative to the moment of fish capture itself, to explore the behavioral context of these sounds and to investigate their utility as proxies for prey-capture attempts and successes, respectively. Comparisons of dive depths for initial echolocation trains, buzzes, and prey-handling sounds (grouped by salmon species or by capture phase) were also conducted using a Bayesian alternative to the two-sample *t*-test (Bååth, 2014).

Results

Dtag deployments and prey sampling

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

Patterns of echolocation during fish-capture events

A total of 19,773 focal echolocation clicks were identified from the 17 fish capture events. The majority of focal clicks consisted of single broadband pulses; however, clicks with doublet structures resembling those described by Awbrey et al. (1982) for Antarctic killer whales were occasionally recorded (surface reflection as the cause of these doublets could not be ruled out, however). Echolocation clicks were arranged into 175 separate trains, including 148 regular echolocation click trains and 27 buzzes (trains containing one or more ICI of ≤10 ms; Figure 3). Each fish capture event included a median of 8 regular click trains (IQR=5-12, range=0-18) with a 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 6.1 clicks s^{-1} (IQR=3.5-11.9 clicks s^{-1}). Fish capture events also included a median of 1 buzz each (although 5 of the 17 captures contained no buzzes; IQR=0-3, range=0-6). Median buzz duration 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} (IQR=25.5-96.7 clicks s^{-1}). The fish capture events for which no buzzes were detected included all three of the 2009 Dtag-2 captures, as well as a single capture from both 2010 and 2011. Regular click trains and buzzes were produced by tagged whales at median depths of 48.7 m (IQR=5.5-112.1 m) and 122.9 m (IQR=70.5-148.2 m), respectively.

We examined the depth at which whales emitted their first click train during the precapture phase of a fish capture event and found that echolocation was initiated at depths <40 m for most salmon captures (82.3%, *n*=14, Table 2). Whales that initially pursued fish at the surface produced their first echolocation trains at a much shallower median depth (0.7 m, IQR=0.6-1.8 m, *n*=5) than those that did not locate prey at the surface but dove prior to initiating chase behavior (25.9 m, IQR=12.2-50.2 m, *n*=12). The initial click train produced during a capture event commenced at a greater median depth for captures involving Chinook salmon (20.0 m, IQR=5.2-32.7 m, *n*=9), 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). When mean initial echolocation depths for Chinook captures were compared to all other salmon species combined using the Bayesian alternative to a *t*-test, the estimated difference was 16 m deeper for Chinook captures and the probability that the difference between the means was greater than zero was 0.791. However, the 95% credible interval for the difference between these means (-28 to 74 m) also included zero and the possibility that no difference exists can therefore not be ruled out entirely. The greatest depth at which a whale first began echolocating during a fish capture was 196.5 m, which was equivalent to 96% of its maximum dive depth (204.5 m) for that particular fish capture event (deployment oo11_246a, Table 2, Figure 5). Buzz trains also began at a greater median depth for Chinook captures (162.5 m, IQR=84.0-186.0 m, *n*=13) compared to chum captures (119.5 m, IQR=59.7-127.3 m, *n*=14), while no buzzes were emitted by whales that pursued coho salmon (*n*=2, Figure 5). Like initial echolocation trains, the difference in mean depths of buzzes during Chinook versus chum captures was also deeper for Chinook buzzes (by about 38 m), and the probability that the difference between the means was greater than zero was high (0.915). However, the 95% credible interval of the difference in means (-19 to 92 m) also included zero, and it is therefore possible (although unlikely) that no true difference in buzz depth between salmon species exists.

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

Prey-handling sounds

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

Discussion

Patterns of echolocation during successful fish captures

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

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

We found that resident killer whales used echolocation even in situations where visibility was likely to be relatively good, with click trains generally beginning at relatively shallow depths (<40 m) during the precapture phases of fish capture events (Figure 5). Resident killer whales also produced clicks when chasing fish along the surface (Table 2). This implies that vision and echolocation are probably acting in concert during detection and tracking of prey, and that echolocation may be critical to successful prey capture even when vision is unrestricted. This conclusion is supported by Barrett-Lennard et al. (1996), who found no correlation between water clarity and the frequency of echolocation use by resident killer whales. In other words, whales did not increase their reliance on echolocation under conditions of reduced visibility, or vice versa. The interchange between the use of echolocation and vision by foraging cetaceans is not well understood; however, Torres (2017) suggests that there is considerable overlap in the spatial scales (i.e., distances from prey) over which dolphins use these two sensory modalities, and as such, vision and echolocation likely provide simultaneous sensory information on prey locations and movements. More specifically, underwater visual acuity in killer whales has been shown to be sensitive enough that it undoubtedly plays a role in guiding their behavior (White et al., 1971). In addition, we also determined that echolocation was not continuous throughout any of the Dtag-recorded fish capture events. Even during the search and pursuit (precapture) phase, whales typically echolocated less than 50% of the time (median=34.1%, IQR=26.1%-38.0%, Table 2, Figure 8). These results are supported by previous observations that resident killer whales emit only periodic (rather than continuous) echolocation trains while pursuing and capturing salmon (Ford, 1989). Whales are therefore likely using other sensory cues, in addition to echolocation, to track prey at depths with limited light availability where visual tracking is not possible. These cues could include passive listening for swimming sounds or other noises potentially produced by salmon (Barrett-Lennard et al., 1996; Murchy et al., 2018; Torres, 2017), or passive electroreception of bioelectric fields generated by prey, as has been shown in another odontocete species, the Guiana dolphin (*Sotalia guianensis*, Czech-Damal et al. 2012).

Although the precapture phase of most fish capture events began with killer whales echolocating closer to the surface, occasionally individuals descended silently and only produced their first click train after attaining a greater depth. Generally, whales that did not initially encounter and chase fish at the surface delayed echolocation until they had reached a median depth of 25.9 m (IQR=12.2-50.2 m). Resident killer whales preferentially feed on Chinook salmon (Ford et al., 1998; Ford & Ellis, 2006; Ford et al., 2009), which have a significantly deeper average vertical distribution than other Pacific salmon species (Wright et al., 2017). We found that whales targeting Chinook often descended silently until they reached the typical depth range occupied by this species (>30 m, see Wright et al. 2017) before emitting echolocation clicks (median depth of first click train = 20.0 m, IQR=5.2-32.7 m, Figure 5). Holt et al. (2019) similarly found that southern resident killer whales that dove to depths corresponding to Chinook habitat (≥30 m) also delayed their first click train until a mean depth of 27.3 m. Conversely, whales pursuing more surface-oriented salmon species, such as chum and coho (Wright et al., 2017), initiated their first precapture click trains at shallower median depths (9.3 m and 7.4 m, respectively, Figure 5, Table 2). This suggests that killer whales alter their echolocation behavior depending on the species of salmon they are targeting, and previous research has indicated that killer whales are likely able to differentiate between salmon species based on echolocation backscatter patterns (Au et al., 2010).

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

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

Echolocation behavior of foraging northern resident killer whales changed significantly once a fish had been caught, implying that echolocation may fulfil different functions during different stages of prey capture. For example, during active searching or pursuit of fish (precapture phase), killer whales spent a significantly greater proportion of their dive time echolocating (median=34.1%) than they did after catching a fish (postcapture phase: median=3.7%; mean paired difference=21.0%; >0.999 probability that the difference between means is >0). Greater echolocation effort prior to captures was expected, since foraging whales are assumed to use echolocation to locate, track and acoustically identify prey. Pursuing highly mobile prey (like salmon) requires killer whales to respond to evasive behaviors by the prey, which they likely accomplish by using echolocation to obtain information about prey movements. The higher mean clicking rate (mean paired difference = 4.8 clicks s^{-1}; >0.999 probability that the difference between means is >0) displayed by resident killer whales during the precapture compared to the postcapture phase (Figure 6) was also expected, since click repetition rates are directly related to target range. Continuous reductions in target distance during prey pursuit permit shorter intervals between clicks because the echoes return and can be processed by the whale at increasingly faster rates (Madsen & Surlykke, 2013). Closer proximity also leads to more rapid changes in the attack angle between predator and prey (Au et al., 2004), requiring the whale to increase its clicking rate to receive updates on increasingly evasive fish movements and prevent an escape. Similar increases in clicking effort and shortened inter-click intervals were observed for finless porpoises performing body movements consistent with prey searching and pursuit (Akamatsu et al., 2010). Higher echolocation effort by northern resident killer whales prior to prey captures (both in time spent echolocating and click repetition rates) suggests that echolocation is pivotal to foraging success.

After capturing a fish, tagged killer whales slowed their median echolocation rate from 4.0 to 0.1 clicks s^{-1} and spent a median of only 3.7% of their time engaged in echolocation behavior (Table 2, Figures 6 & 8). Postcapture clicking may aid in navigation back to the surface, or could assist during prey handling to track pieces of prey as it is being torn apart. Both tasks are unlikely to require frequent or rapid sensory updates, hence the reduction in both echolocation rate and time spent echolocating following a capture. Foraging whales may also use postcapture echolocation to find conspecifics, typically offspring, with which they frequently share their prey (Wright et al., 2016). However, only one of the tagged whales (G31, deployment oo11_246a, Table 2) exhibited confirmed prey sharing behavior, and she did not echolocate at all during the postcapture phase of any of her dives (*n*=5). This may be because this whale was engaged in very steep, vertical dives with limited horizontal displacement, which would cause her to surface close to her juvenile offspring without having to search for them. It could also mean that provisioned individuals in this case moved towards G31, rather than her having to locate and carry the fish to them; both active and passive types of sharing behavior have been reported during prey sharing by resident killer whales (Ford & Ellis, 2006). Further investigation using a larger sample size of shared kills by multiple individuals is required to determine the relative importance and use of echolocation by resident killer whales during prey sharing behavior. Because some tagged whales were completely silent after capturing a fish, echolocation is likely not critical for postcapture navigation, prey handling or sharing, and implies that these tasks can sometimes be accomplished using other sensory inputs, such as visual cues or passive listening.

Buzzes and prey-handling sounds

Many odontocete species use buzzes for close-range prey targeting (Aguilar Soto et al., 2008; DeRuiter et al., 2009; Holt et al., 2019; Johnson et al., 2004; Johnson et al., 2008; Tennessen et al. 2019; Wisniewska et al., 2014). These sounds consist of echolocation clicks emitted at increasingly higher rates as the target distance (and thus the time required to receive an echo) decreases (Cahlander et al., 1964). While regular echolocation clicks are thought to function in the detection and identification of more distant targets, buzzes are produced during extremely close approaches, when rapid updates on prey movements become possible and necessary (Johnson et al., 2006). Most buzzes (85.2%, n=23) produced by tagged northern resident killer whales occurred at depths >50 m (Figure 9), with a median starting depth of 122.9 m (IQR=70.5-148.2 m), which was very similar to buzz depths reported for foraging southern residents (median=118.3 m) by Holt et al. (2019). Buzz depths reflect the greater depths at which prey were eventually caught, and it is not an unexpected finding given the tendency of Chinook, coho, and chum salmon to descend in response to predator pursuit (Wright et al., 2017). With the exception of two prey-capture events, buzzes were always preceded by trains of regular echolocation clicks that were probably used to locate and track prey during the initial part of a foraging dive. The two buzzes with no preceding regular echolocation clicks were the first echolocation trains of two dives made by G31 (deployment oo11_246a, Table 2) at depths of 101.5 and 196.5 m, respectively. In these cases, G31 may have already located prey either using near-surface echolocation conducted prior to diving, or during a preceding successful capture, and thus would not need to employ slower echolocation trains prior to buzzing.

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

Buzzes were not a completely reliable acoustic estimator of prey-capture attempts because they were absent from five of the successful fish captures, including all three captures recorded on the 2009 tags. Given the lower apparent source levels of these sounds (DeRuiter et al., 2009; Johnson et al., 2006; Madsen et al., 2005; Miller et al., 1995; Wisniewska et al., 2012; Wisniewska et al., 2014), buzzes may have been present but were acoustically masked due to poor signal-to-noise ratios caused by high flow noise, particularly on the 2009 recordings. It is also possible that no buzzes were actually produced during these captures, as Tennessen et al. (2019) similarly detected foraging dives by southern resident killer whales that contained prey-handling sounds but not buzzes, and Holt et al. (2019) detected buzz trains in only nine of 15 foraging dives by southern residents that were confirmed successful by prey sample collection at the surface. Furthermore, buzzes should not be interpreted as a 1:1 indicator of capture attempts because northern resident killer whales often produced multiple buzzes (1 buzz per capture: n=6; 2-6 buzzes per capture: n=6) while pursuing and capturing a single fish (see example with three buzzes in Figure 1). Therefore, some buzzes are likely to represent close approaches to prey targets that resulted in misses rather than captures. Other odontocetes, such as beaked whales, are similarly known to produce multiple buzzes in series while tracking the same prey target (Johnson et al., 2008; Madsen et al., 2013).

The prey-handling sounds we detected could be useful indicators of prey capture success that would provide information for estimating the foraging efficiency of resident killer whales. Like buzzes, multiple prey-handling sounds (median=3, IQR=1-6, see example in Figure 1) were usually produced during the capture and handling of one fish, and care should therefore be taken when interpreting these acoustic cues. Holt et al. (2019) similarly found that prey-handling sounds made during prey captures by southern resident killer whales occurred in bouts, rather than as single incidents. Most prey-handling sounds by northern residents occurred after the estimated time of fish capture (93.5%, n=58, Figure 10), as expected, since these sounds most likely arise from whales tearing a fish into pieces for consumption or sharing with other individuals. Postcapture prey-handling sounds were also produced at relatively shallow depths (median=11.3 m, IQR=8.5-18.5 m; Figure 10), which supports previous observations that resident killer whales routinely bring prey to the surface prior to handling and consumption (Ford & Ellis, 2006). Holt et al. (2019) found a slightly deeper but comparable median depth of 21.4 m for prey-handling sounds produced by the southern resident killer whale population. We detected two prey-handling sounds that happened concurrently with the estimated time (±3 s) of a single prey capture by G31 (deployment oo11_246a) and took place at much greater depths (~131 m; Figure 10) than any of the post-capture prey handling sounds. For this reason, we believe that these sounds resulted from the whale initially grabbing the fish with its jaws as it was captured. Both our study and Holt et al. (2019) failed to detect prey-handling sounds for three of 17 and nine of 15 foraging dives, respectively, that were known to be successful because they resulted in collection of prey samples. Prey-handling sounds are therefore not a completely reliable indicator of foraging success as they are sometimes not picked up by the tag hydrophones. Flow noise and tag placement may both have some bearing on the detectability of these sounds.

Unexpectedly, a further two prey handling sounds (also from a single capture, but by G64, deployment oo10_256a) occurred approximately 18 and 231 s prior to the estimated capture time for this foraging dive (Figure 9). Although this could suggest the capture of multiple prey during a single dive, with only the final fish being brought to the surface, the dive pseudotrack showed continuous chasing of a single fish (i.e., breaks in the kinematic pursuit behavior that might imply multiple chases and prey captures were not observed). Since most salmon caught by killer whales are relatively large (Ford & Ellis, 2006) with high caloric densities (O'Neill, Ylitalo, & West, 2014), pursuing them is likely energetically demanding but also highly rewarding if successful. The physiological drive for a killer whale to replenish its oxygen stores and offload carbon dioxide after a successful capture probably takes precedence over the benefits of remaining submerged and pursuing additional prey, especially considering that capturing one salmon may require several minutes or more of active chasing (see precapture durations in Table 2). Thus, killer whales likely adopt the strategy of returning to the surface immediately after catching a fish, as is suggested by our kinematic Dtag data. Furthermore, at sea, adult Pacific salmon typically travel singly or in small groups of 2-4 individuals, rather than in dense schools (Nero & Huster, 1996), which would make it more difficult for killer whales to capture multiple salmon in quick succession during the same dive. Rather than indicating the capture of multiple prey in a single dive, it is possible that precapture prey-handling sounds could instead represent instances of the same fish being grabbed by the whale but escaping before eventually being recaptured. During our long-term field observations of resident killer whale hunting behavior, we have encountered fish with killer whale teeth rake marks indicating that an escape occurred. The whale in question, G64, was a juvenile female (10 years old), and thus perhaps was more likely to engage in multiple capture attempts of the same fish as compared to an older, more experienced adult. This is supported by Holt et al. (2019), who found that prey-handling sounds in general were more likely to be detected during dives by juvenile whales than those by adults, which suggests that juveniles may require longer handling times to process and consume prey. It is also possible that these two precapture prey-handling noises could be misidentified sounds arising from other sources, such as air bubbles or water turbulence around the tag housing, and may not actually represent true instances of prey handling.

Buzzes and prey-handling sounds can provide valuable information about the foraging efficiency of individuals, but only when considered in combination with prey sampling efforts and/or kinematic signatures of predation success (e.g., dive depth and jerk peak, see Holt et al., 2019 and Tennessen et al., 2019), given the difficulties associated with imperfect detection and interpretation of these two acoustic signals. Since prey availability and acoustic disturbance have both been recognized as key threats to the recovery of resident killer whales (Fisheries and Oceans Canada, 2018), it is important to determine whether individuals are meeting their daily energy requirements under current habitat conditions (both in terms of acoustic conditions and salmon abundance). Analyzing foraging dives for the presence of buzzes and prey-handling sounds could be useful in this respect, as the frequency of these events could indicate prey encounter rates (Johnson et al., 2009) and potential energetic gain (i.e., number of fish consumed). The amount of energy expended to successfully capture fish could also be estimated from Dtag data using fluking stroke rate (Johnson et al., 2009) or a measure of total body acceleration (Wilson et al., 2006). Combining these kinematic indicators of effort with acoustic indicators of capture success and additional information about the energy density of prey (e.g., O'Neill et al., 2014) could allow for the calculation of catch per unit effort (CPUE) for foraging resident killer whales. Comparing CPUE values to estimates of daily energetic requirements (e.g., Noren, 2011) would help verify whether nutritional stress is impacting the health and survival of resident killer whales.

Conclusions

We used biologging acoustic tags to provide a direct link between echolocation patterns, diving behavior and verified prey captures by individual northern resident killer whales feeding on Pacific salmon. We confirmed that patterns of echolocation produced by foraging resident killer whales are consistent with its function in prey detection and tracking, as click repetition rate and time invested in echolocation both varied greatly with the phase (pre- versus postcapture) of a fish capture event. Echolocation behavior during foraging dives also differed depending on the species of salmon that was targeted. We identified buzzes (capture attempts) and prey-handling sounds (capture successes) as potentially useful acoustic signals for estimating killer whale foraging efficiency. While this analysis provides a valuable addition to existing knowledge of the echolocation behavior of foraging resident killer whales, it is important to note that no Dtags were deployed during nighttime hours during this study, and thus our results are only applicable to daytime foraging and echolocation behavior. It is possible that nighttime behaviors may differ considerably from the findings presented here. Our results are also useful for informing mitigation measures related to the acoustic disturbance of foraging killer whales during feeding and provide a baseline for behavioral comparison with similar studies on the highly endangered southern resident killer whale population (e.g., Holt et al., 2019), whose conservation status is much more precarious. In particular, population differences in the degree of interference with foraging success caused by vessel presence, vessel noise, and operation of vessel sonar equipment is of future interest.

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Figure Captions

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

Tables

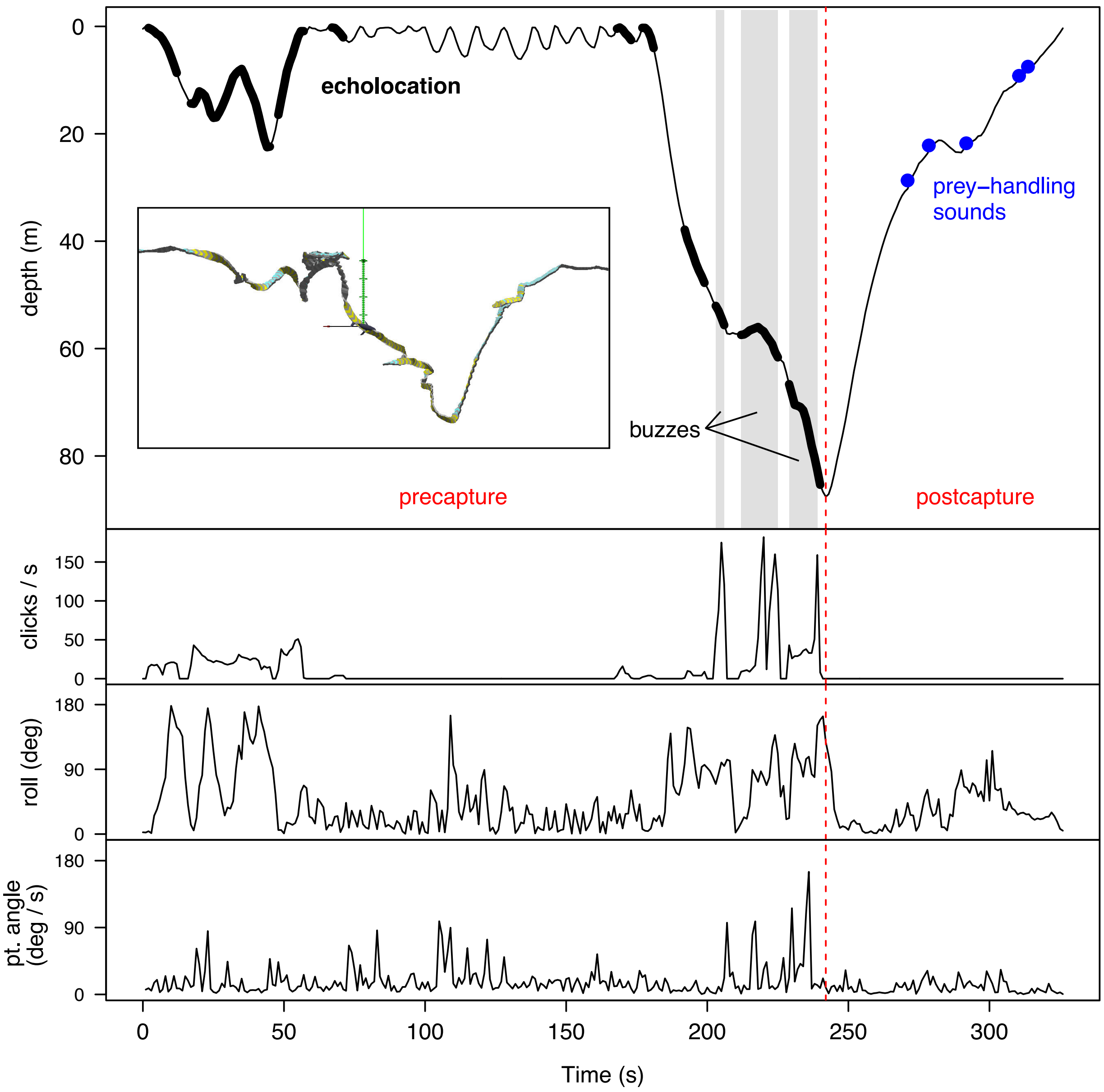
Table 1. Summary of Dtag deployments used to record echolocation and kinematic behavior by individual northern resident killer whales (N=7) during successful captures of Pacific salmon (N=17), 2009-2012. Deployment IDs reflect the species (oo = *Orcinus orca*), the year (e.g., 09=2009), Julian day (e.g.,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

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

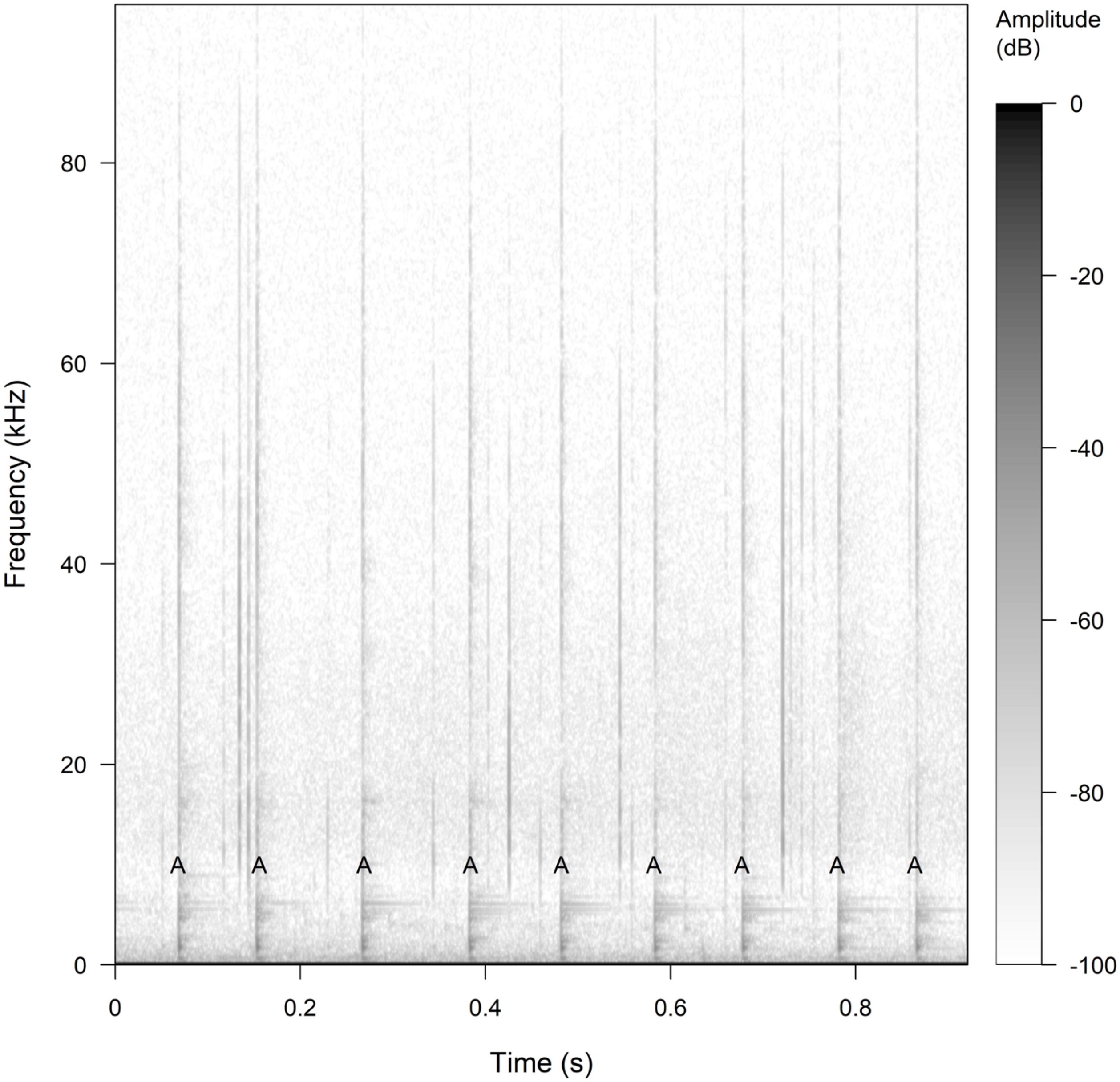
Deployment	Depth of 1st click train (m)	Initial surface pursuit?	Capture depth (m)	Prey species	Shared?	Capture phase duration (s)		Mean click rate (clicks s^{-1})		% time spent clicking	
						precapture	postcapture	precapture	postcapture	precapture	postcapture
oo09_234a	20.0	no	101.6	Chinook	no	241	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)

Figure 1



0
20
40
60
80
depth (m)
echolocation
buzzes
prey−handling sounds
precapture
postcapture
150
100
50
0
clicks / s
180
90
0
roll (deg)
180
90
0
pt. angle (deg / s)
0
50
100
150
200
250
300
Time (s)

Figure 2


Amplitude (dB)
0
-20
-40
-60
-80
-100
Frequency (kHz)
0
20
40
60
80
Time (s)
0
0.2
0.4
0.6
0.8
A
A
A
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A
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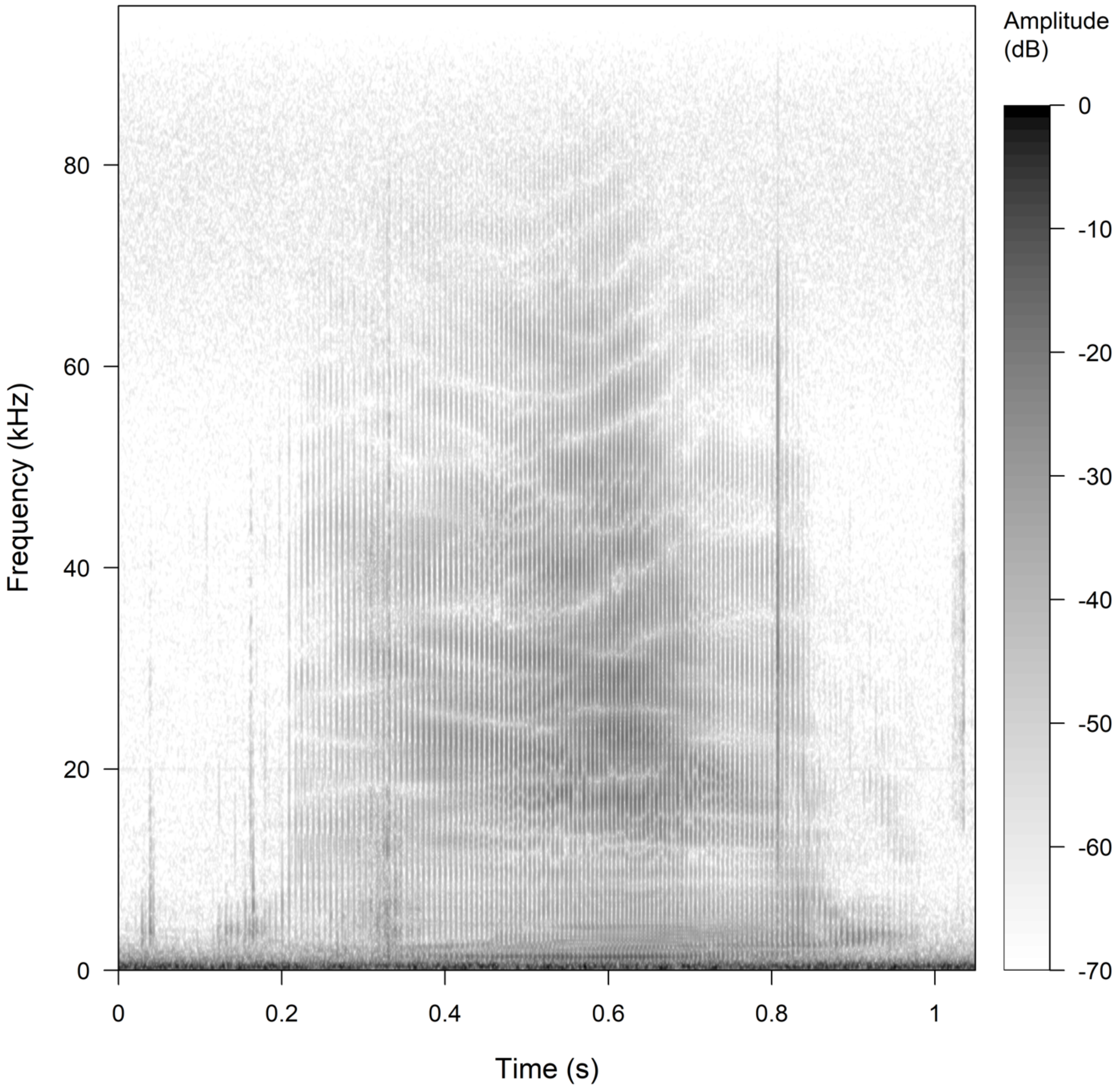
A

Figure 3



Amplitude (dB)
0
-10
-20
-30
-40
-50
-60
-70
Frequency (kHz)
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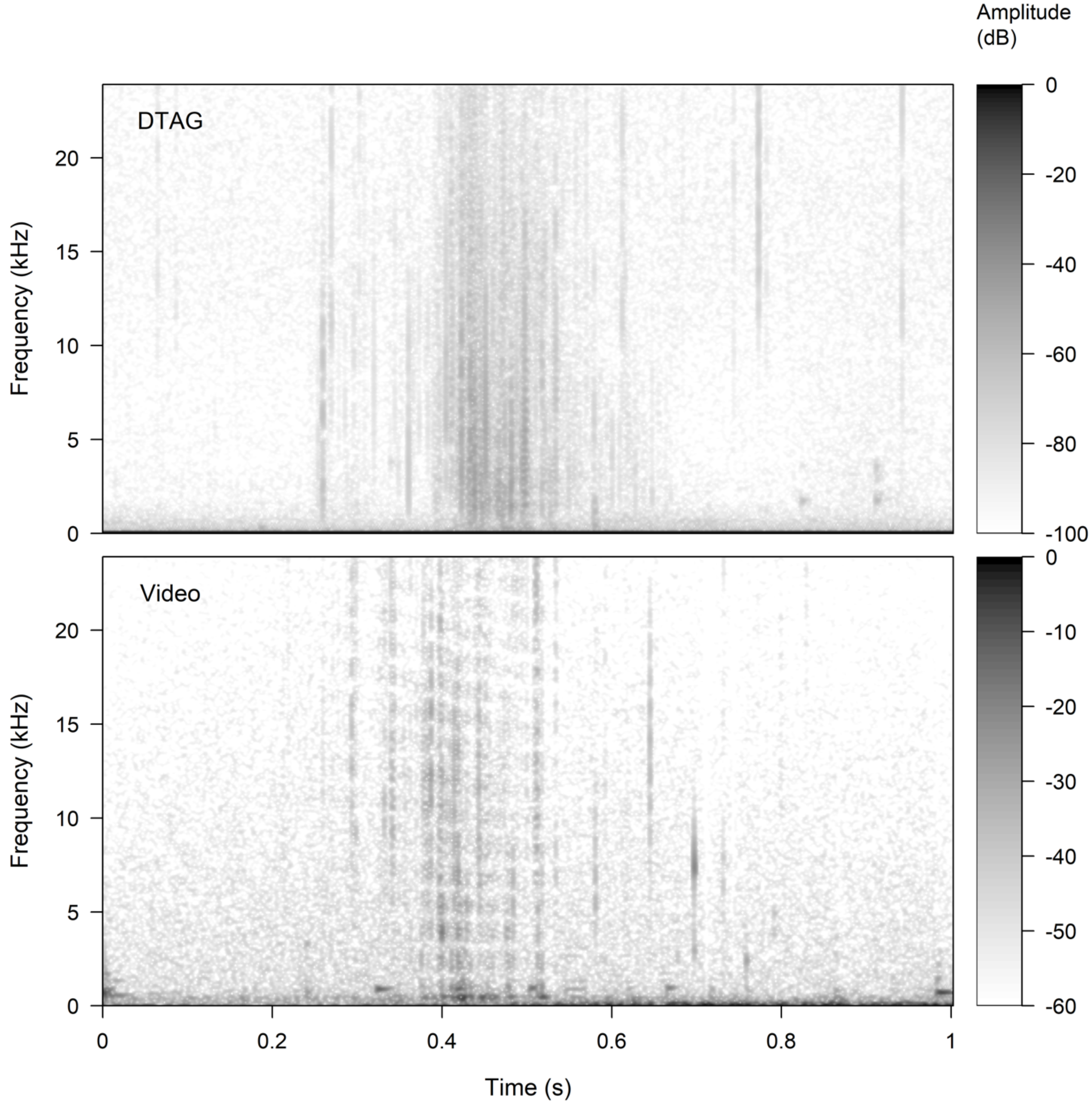
20
40
60
80
Time (s)
0
0.2
0.4
0.6
0.8
1

Figure 4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DTAG
Video
Frequency (kHz)
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10
15
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0
-20
-40
-60
-80
-100
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-10
-20
-30
-40
-50
-60
0
0.2
0.4
0.6
0.8
1
Time (s)

Figure 5

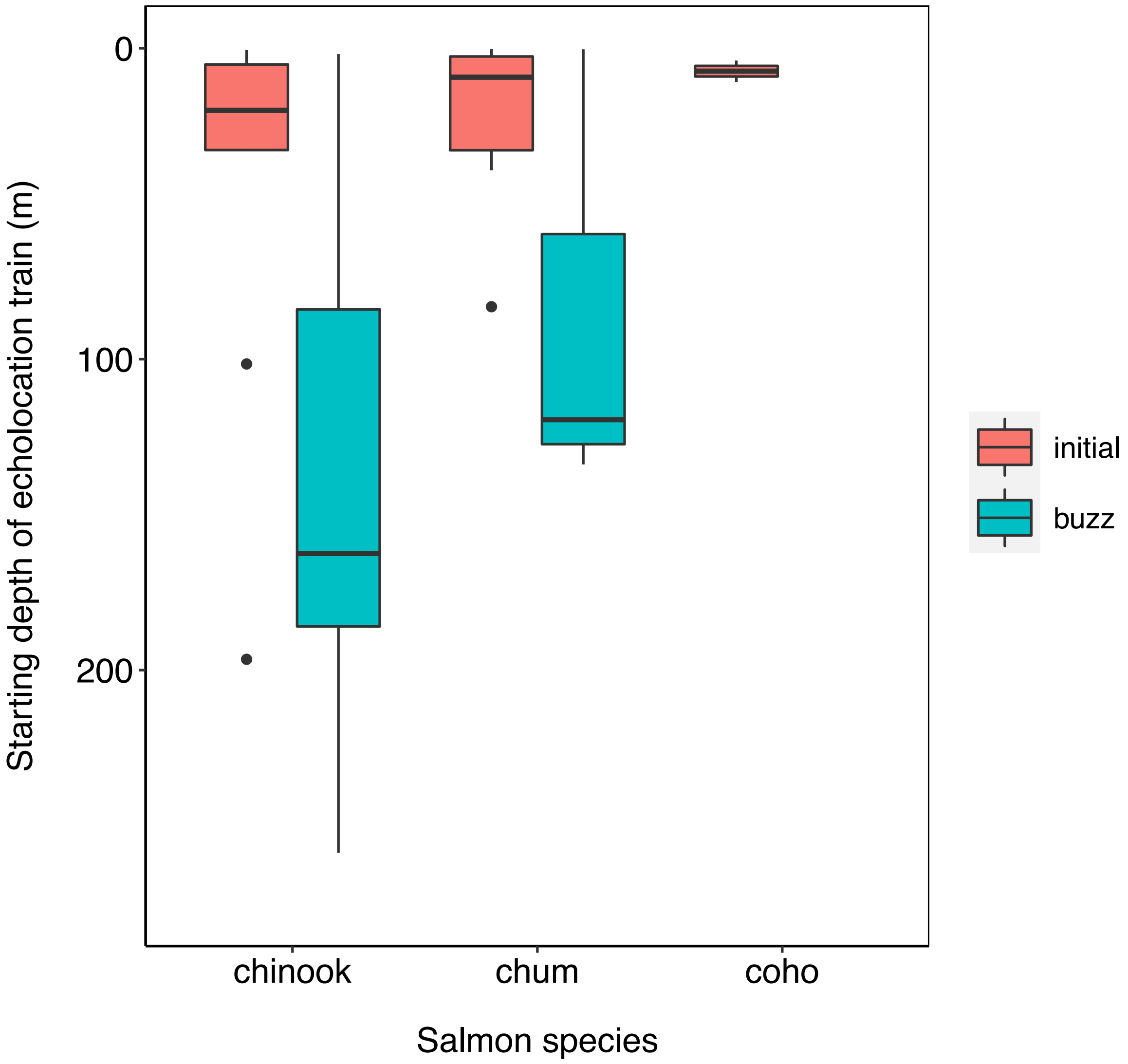

0
100
200
Starting depth of echolocation train (m)
chinook
chum
coho
Salmon species
initial
buzz

Figure 6

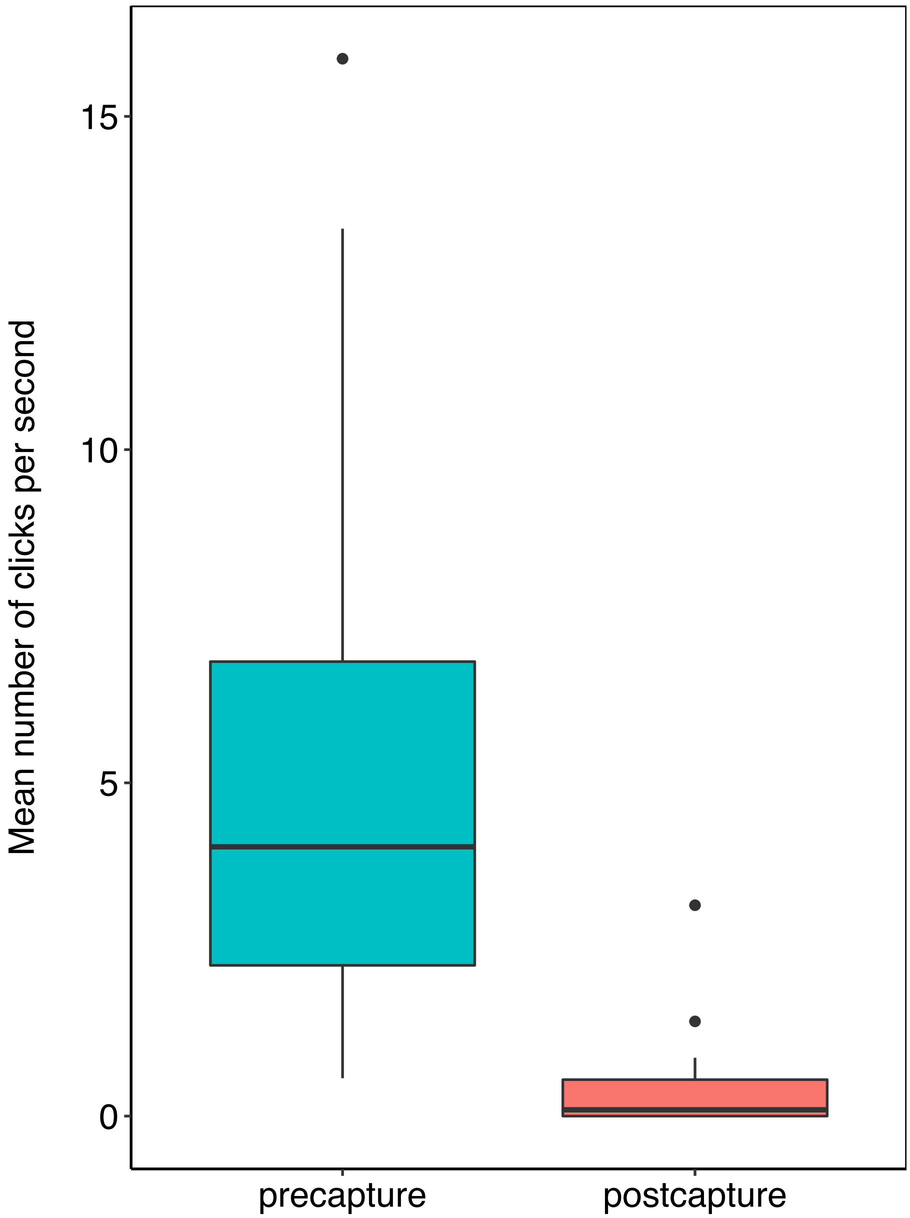

Mean number of clicks per second
15
10
5
0
precapture
postcapture

Figure 7

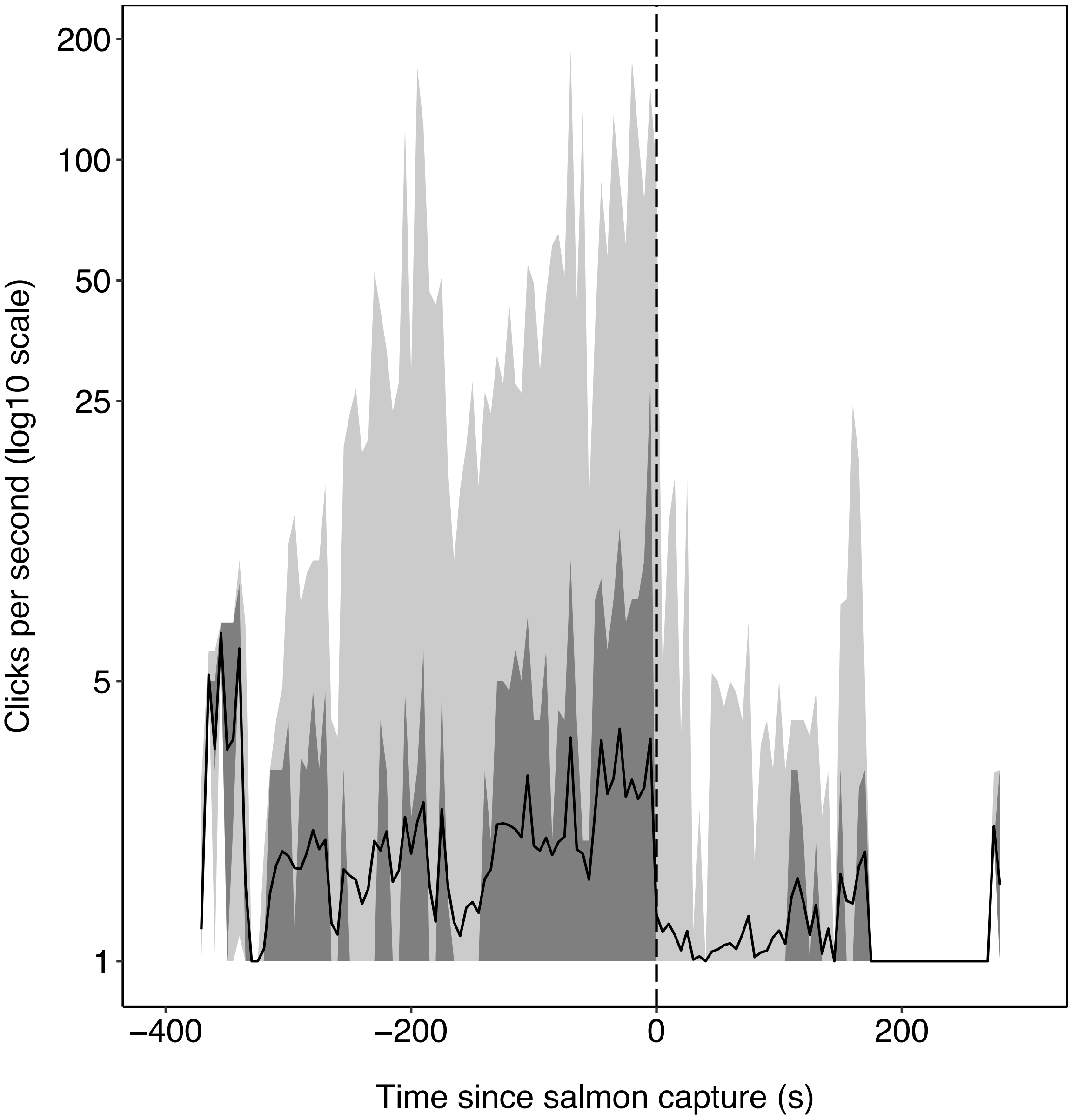
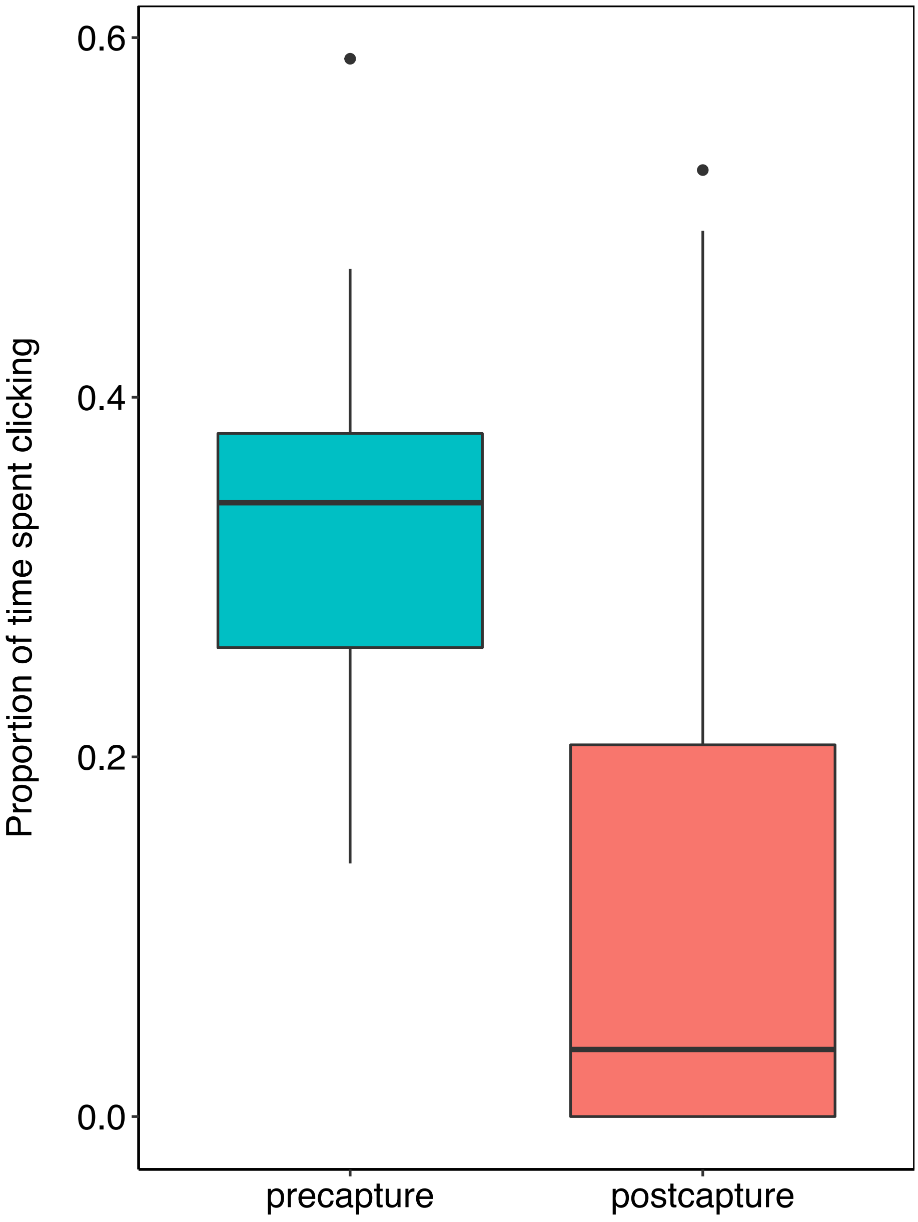

200
100
50
25
5
1
Clicks per second (log10 scale)
−400
−200
0
200
Time since salmon capture (s)

Figure 8



Proportion of time spent clicking
0.6
0.4
0.2
0.0
precapture
postcapture

Figure 9

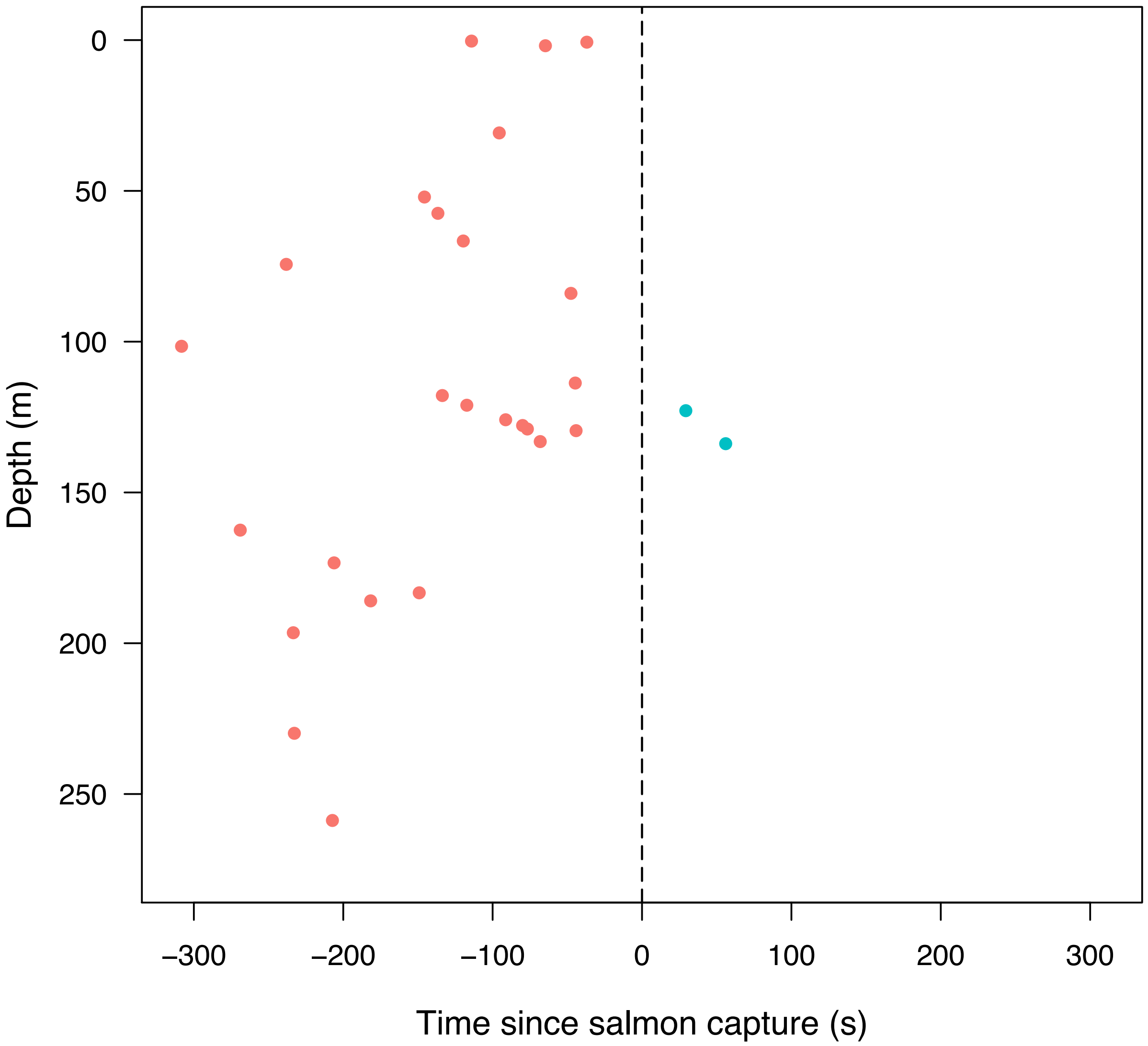
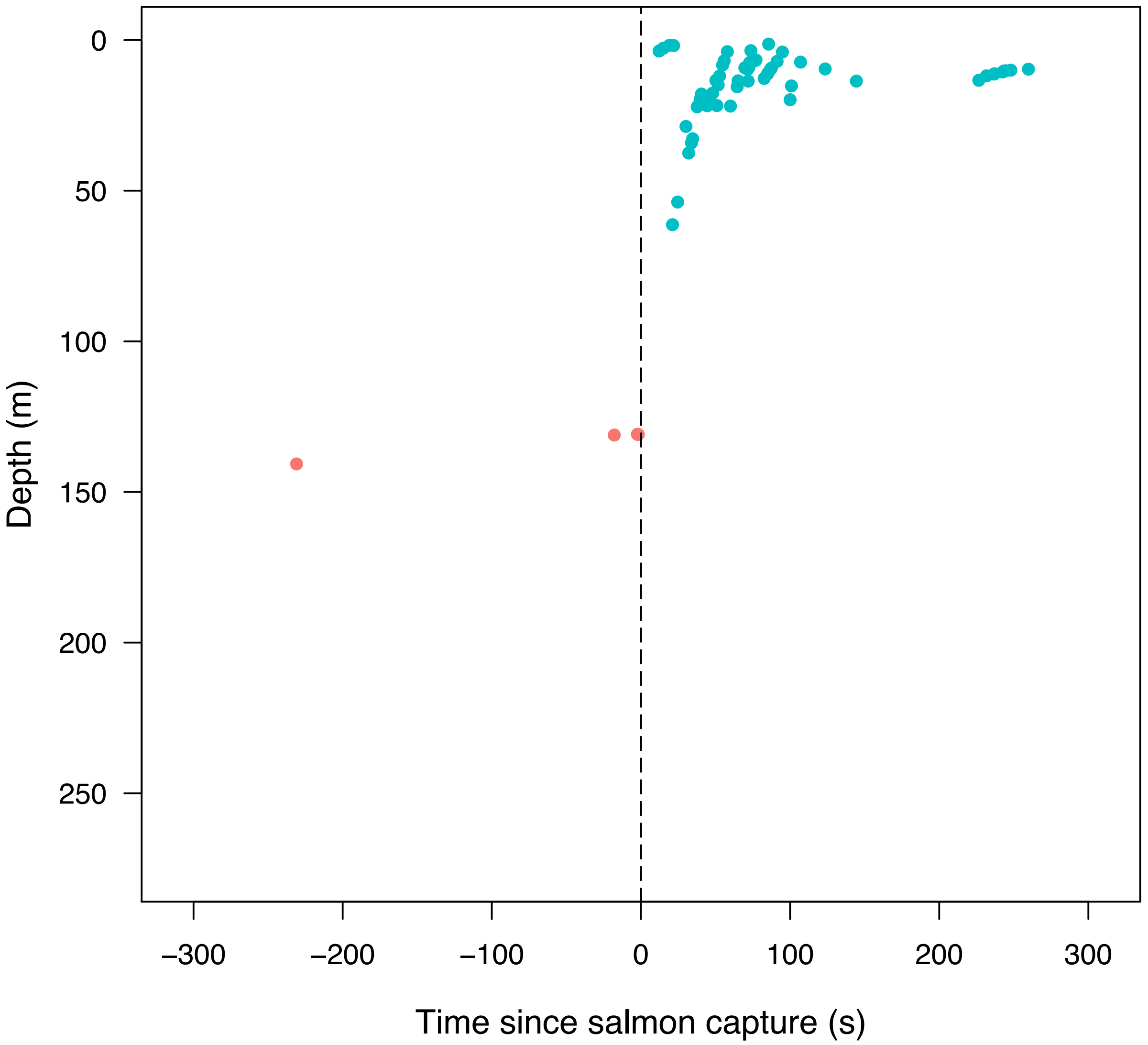

0
50
100
150
200
250
Depth (m)
−300
−200
−100
0
100
200
300
Time since salmon capture (s)

Figure 10



0
50
100
150
200
250
Depth (m)
−300
−200
−100
0
100
200
300
Time since salmon capture (s)

Supplementary Figure 1