Basis of acoustic discrimination of chinook salmon from other salmons by echolocating *Orcinus orca*

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The "resident" ecotype of killer whales (*Orcinus orca*) in the waters of British Columbia and Washington State have a strong preference for Chinook salmon even in months when Chinook comprise less than about 10% of the salmon population. The foraging behavior of killer whales suggests that they depend on echolocation to detect and recognize their prey. In order to determine possible cues in echoes from salmon species, a series of backscatter measurements were made at the Applied Physics Laboratory (Univ. of Wash.) Facility on Lake Union, on three different salmon species using simulated killer whale echolocation signals. The fish were attached to a monofilament net panel and rotated while echoes were collected, digitized and stored on a laptop computer. Three transducer depths were used; same depth, 22° and 45° above the horizontal plane of the fish. Echoes were collected from five Chinook, three coho and one sockeye salmon. Radiograph images of all specimens were obtained to examine the swimbladder shape and orientation. The results show that echo structure from similar length but different species of salmon were different and probably recognizable by foraging killer whales.

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I. INTRODUCTION

The "resident" ecotype of killer whales (*Orcinus orca*) that frequent the waters of British Columbia and Washington State have a strong preference for Chinook or King salmon (*Oncorhynchus tshawytscha*). Ford *et al.* (1998) and Ford and Ellis (2006) have found that even in months when Chinook may constitute less than 10% of the salmon population, the whales still forage mainly for Chinook salmon. From about mid-September through October, when the density of Chinook is very low, the whales will switch to chum salmon (Ford and Ellis, 2006). Visual observations of the behavior of foraging killer whales strongly suggest that they depend on echolocation to detect and recognize their prey. They are often observed swimming close to the surface seemingly searching for prey. Then they would submerge and come up approximately 50 to 100 m away with a Chinook salmon in their mouths, suggesting that at the time of submersion, a prey was detected and recognized. After observing this behavior time and time again over several years involving many different individuals, the use of echolocation seems unequivocal. The only other rational possibility is that Chinook salmon produces some kind of sound that is distinctive from sounds produced by other salmon species that can be detected at distances greater than about 50 m, a very unlikely possibility.

Echolocating killer whales probably use a variety of cues in discriminating and recognizing their prey. One such cue may be the swimming behavior of the salmon such as speed and movement pattern, another may be the depth at which Chinook salmon prefer to transit deep water bodies on the way to their spawning grounds. Beacham (1986) analyzing the troll depth at which four different species of salmon were caught found that Chinook salmons preferred deeper depths than coho (*Oncorhynchus kisutch)*, pink (*O. gorbuscha*) and sockeye salmon (*O. nerka*) and that 77% of Chinooks caught were at depths between 27 and 55 m. However, the other salmon species were caught in this same depth range although not as often, and some Chinooks were caught at shallower depth. Chinook salmon is the largest of the salmon species so that the intensity of the echoes for Chinook salmon will on the average be higher than echoes from other salmon species. However, the data of Ford and Ellis (2006) indicate that killer whales often caught Chinooks that were within the size range of other salmons and that only one out of 191 observed catches consisted of a Chinook salmon with a fork length greater than 42.5 cm. Another cue from echolocation may be the temporal and spectral structure of the acoustic backscatter that may be specific to different salmon species.

Our hypothesis is that the echo structure of backscatter from Chinook salmon is uniquely distinctive from the other salmon species because of differences in the volume, shape and tilt angle of the swimbladder. Swimbladders have been identified as the primary cause of acoustic backscattering in several species (Harden-Jones and Pearce, 1950; Foote, 1980; Clay and Horne, 1994), accounting for as much as 90%–95% of the echo energy. Some studies have found that the scattering field for the entire fish can be reconstructed mainly from the properties of the swimbladder (Foote, 1980; Foote and Ona, 1985; Clay and Horne, 1994). Furthermore, the temporal resolution property of the broadband echolocation signals used by killer whales should be sufficient to resolve differences in echo structure for different salmon species. Au and Benoit-Bird (2003) examined the echo structure from 7 species of deep dwelling snappers using simulated dolphin echolocation signals and found the echoes from the different species to be different. X-ray images showed differences in the morphology of the swimbladders and they attributed differences in the echo structure to these morphological differences.

A prior acoustic backscatter measurement was conducted by Dahl and Mathisen (1983) with two salmonid species *Salmo gairdneri* (rainbow trout) and *Salmo clarki* (cutttroat trout) at a frequency of 420 kHz and a pulse length of 400 μs. The subjects were anesthetized and attached to two lines extended from a rotor to a harness attached to the fish by suture. The polar plots of target strength exhibited considerable amount of fluctuation in magnitude resulting in plots that had lots of lobes. Burwen and Fleischman (1998) have also measured the side-aspect target strength of tethered and free-swimming Chinook and sockeye salmon using a narrow band split beam sonar. More recently, Burwen *et al.* (2007) have used a high-frequency imaging sonar (DIDSON) operating at 1.8 MHz to count Chinook salmon swimming up the Kenai river in Alaska. Our backscatter measurements are not related to these prior studies on two important points. We used a broadband simulated killer whale echolocation signal at much lower frequencies; the others used a narrow band tone-burst signal and the salmonid species used by Dahl and Mathisen are not known to be prey of fish eating killer whales. The objective of this study is to examine the backscatter from different salmon species using simulated killer whale biosonar signals and determine if differences in the echo structure could be a cue for killer whales to discriminate Chinook salmon from other salmon species.

II. PROCEDURE

A. Experimental geometry

Backscatter measurements were performed on the R/V J. E. Henderson that was tied to the Applied Physics Laboratory (APL), U. of Washington's pier in Lake Union. The Henderson is a 70-ft steel-hulled catamaran with a large interior laboratory space and a wet well between the hulls. It is equipped with full instrumentation for calibration of underwater acoustic equipment. The laboratory deck has a series of 1×3 m panels that could be removed to provide direct access to the lake. The measurement geometry is depicted in Fig. 1(a) showing a rotor with a pvc pipe supporting a monofilament net. Fish subjects were constrained in a monofilament bag that was attached to the center of the monofilament net which was attached to a rotor. A subject could be clipped to the net in the two different aspects so that they could be rotated in either the lateral or dorsal planes as depicted in Fig. 1(b). A bi-static system was used with two custom-made transducers consisting of 1–3 piezo-ceramic circular disks. The active element in the projector had a diameter of 10.2 cm with a thickness of 1.3 cm and the hydrophone element had a diameter of 6.4 cm and a thickness of 0.64 cm. They were mounted side by side on an aluminum plate attached to an aluminum pole and the plate could be pivoted to be flush with the pole and at angles of 22.5° and 45° from the pole axis. For the 0° and 22.5° elevation angles, the transducers were placed 3.1 m from the specimens its depth varied appropriately to direct the beam toward the specimens which were always at a depth of 1.5 m. For the 45° elevation angle, the transducer was placed at a horizontal distance 1.3 m from the salmon.

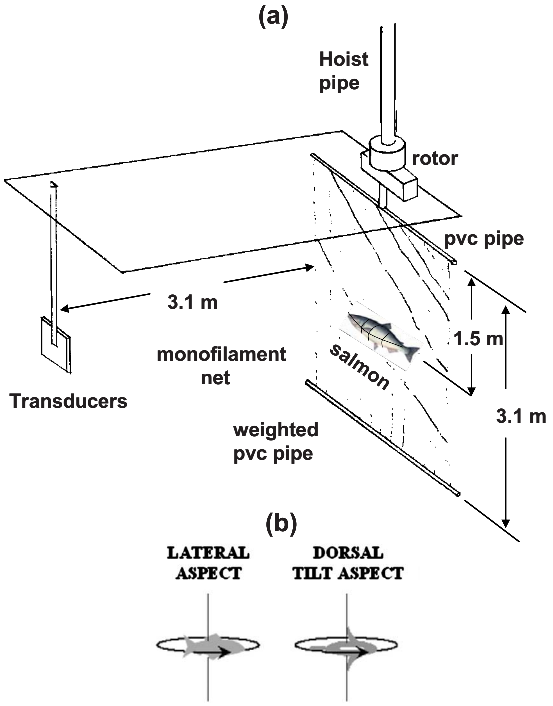

FIG. 1. (Color online) (a) A schematic of the experimental geometry with a salmon in a net bag that is attached to a monofilament net curtain. A weighted pvc pipe is shown on the bottom of the net and the pvc pipe supporting the top of the net was kept above the water. The rotary assembly was attached to a pipe on a hoist that was used to lower and raise the net assembly. (b) orientations of the salmon as they were rotated.

A Data Translation DT-9832 data acquisition module controlled by a laptop computer via a USB link was used to produce the orca-like incident signal and digitize the resulting echoes from the target. The output of the DT-9832 was directed to a Hafler Transnova power amplifier to drive the projector. Reference measurements were conducted prior to the backscatter measurements by having the projector transmit a simulated orca-echolocation signal directly at the receiving hydrophone, temporarily located at the position of the salmon. The waveform and frequency spectra of the incident signal are shown in Fig. 2. The transmitted signal was a replica of a previously measured echolocation signal of free ranging killer whales (Au *et al.*, 2004) that had a peak

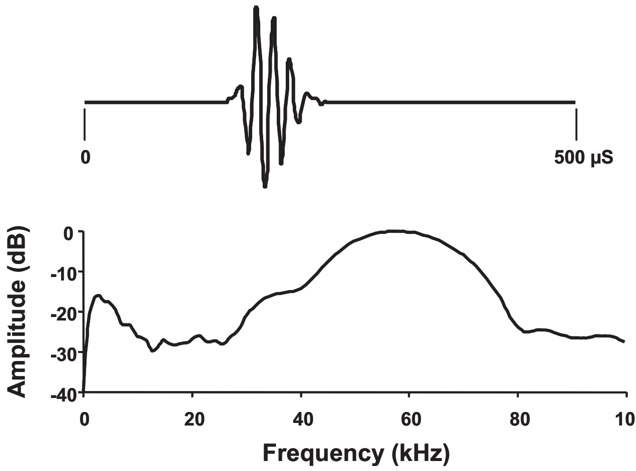

FIG. 2. The waveform and frequency spectrum of a simulated killer whale echolocation signal.

frequency of 55 kHz and a duration of approximately 105 μs. Measurements were also performed on a reference 3.81 cm diameter solid tungsten carbide sphere having a target strength of −41 dB at a frequency of 55 kHz (Foote, 1990). The calibrated target was placed 3.1 m from the transducers. All backscatter measurements were conducted with the echoes time-gated and bandpassed filtered at 10 and 150 kHz before being digitized at a sample rate of 1 MHz. A total of 2048 points were digitized per echo and stored to disk.

B. Salmon Specimens

Six Chinook, four coho and one sockeye salmon were obtained from the Issaquah Salmon Hatchery in Issaquah, Washington and transported by truck to the R/V Henderson. Backscatter data was not obtained with all the specimens. The lengths of three Chinook salmon from which useful backscatter data were obtained varied between 43 and 49 cm (standard length), and a fourth was 88 cm long. The standard length of the three coho salmon varied between 51 and 56 cm and the standard length of the one sockeye was 55 cm. Each fish was anesthetized with 60 mg per liter of water of Tricaine Methanesulfonate (MS-222). Once anesthetized, the fish was enclosed in a fitted monofilament net sock that restrained swimming movements but allowed gill pumping and movement of the caudal peduncle. Echoes from the fish were collected as a function of azimuth. The rotor incremented approximately 2.2° after each transmission and reception cycle until the fish was rotated through 360°. Most of the measurements were done with the fish in the lateral aspect having its dorsal surface pointed upwards and the ventral surface pointing downwards. Measurements were done with some of the fish in the dorsal aspect (side of fish aligned with the horizontal plane) as depicted in Fig. 1(b). All backscatter measurements started with the head of the fish facing the transducers.

Upon completion of a backscatter measurement, each salmon was radiographed using a portable x-ray imaging system (SAIC ARS2 with an "Xtec Laseray 90P"). Radiographs were obtained in both lateral and dorsal planes. For radiographs in the lateral aspect, the salmons were laid on their side with the x-ray source pointing downward. For radiographs in the dorsal aspect, the fish had to be supported by bags filled with lead pellets that were used to prop the fish up. The aperture of the digital receiver was not large enough to image a whole fish in a single exposure so sections of each fish were sequentially radiographed in both planes. All radiograph images were stored on a computer hard drive. The specimens were then euthanized by MS-222 overdose, as per University of Washington animal care protocol.

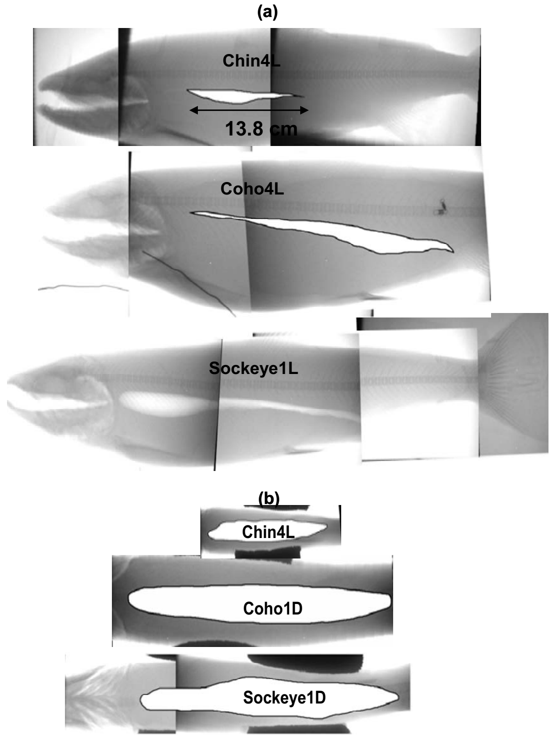

FIG. 3. Radiograph images of a Chinook, coho and sockeye salmon showing the swimbladder relative size, shape and tilt angle of the different species (a) in the lateral plane and (b) in the dorsal tilt plane. Some of the swimbladders were drawn from washed out images that allow discernment of the swimbladder boundaries but could not be reproduced.

III. RESULTS

Example radiograph images from the three species are shown in Fig. 3 for both the lateral and dorsal aspects. In some images, a white polygon was drawn over swimbladders to define boundaries that were not clear in the image. Distinct images of swimbladders in the dorsal plane are difficult to obtain as x-ray intensity diminishes as it travels through muscle and the spinal column. Images in Figs. 3 were formed by combining files from sequential radiographs. The images show differences in shape and volume among species, and that the sockeye salmon had the most elongated swimbladder, followed by the coho and then the Chinook. Swimbladders were tilted by approximately 4°–6° posterior with respect to the back bone (used as a proxy for the sagittal axis) of the specimens. Radiographic images are included here to illustrate that the swimbladders of different salmon species varied in shape and volume and not to provide detail morphometerics of swimbladder anatomy.

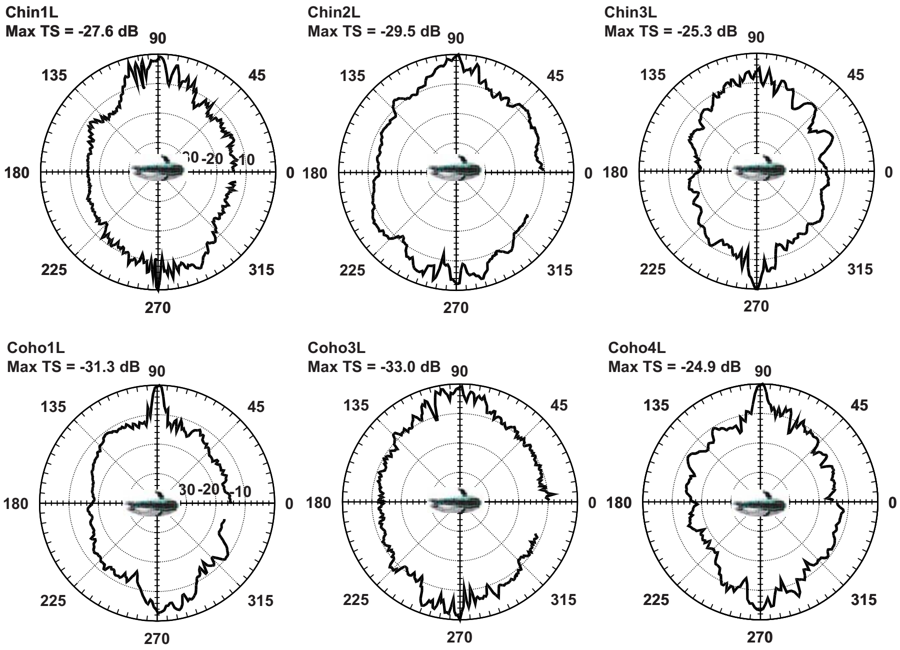

FIG. 4. (Color online) Polar plots of the target strength of Chinook and coho salmon species as each salmon was rotated in the lateral plane

Target strength was calculated in term of the energy flux density of the echoes and the incident signal as expressed in Eq. (1). E_r is the energy flux density of the echo reference to a distance one meter from the salmon and E_i is the energy flux density of the incident signal. Polar plots of the relative target strength in the lateral aspect for three Chinook and three coho salmon are shown in Fig. 4 for a 0° elevation angle (transducers and salmon at the same depth). Because energy flux density was used, the polar plots did not have sharp maxima and minima as those calculated using the peak-to-peak values of the sound pressure (Dahl and Mathisen, 1983; Benoit-Bird *et al.*, 2003; Au and Benoit-Bird 2003). The polar plots are normalized with the maximum value of the target strength indicated next to each plot. The maximum values typically occurred when the fish was broadside (90° and 270°) to the incident signal. The minimum values typically occurred when the tail and head pointed toward the transducers. The target strength at the tail (180°) and head (0°) aspects were between 14 and 20 dB below the values broadside. The actual target strength at any specific angle is the sum of the maximum value and the relative value shown in each polar plot. The general shape of the polar plots agreed with those of Dahl and Mathisen (1983) obtained with a 420 kHz signal, but without sharp maxima and minima. Unfortunately, the results for the sockeye salmon at the 0° elevation angle situation were inadvertently erased because of operator error in saving the data to disk. The polar plots of target strength are in general very similar in shape for all the specimens measured and probably would not provide much information on the salmon species producing the echoes.

$$TS_E = 10\log\left|\frac{E_r}{E_i}\right| \qquad (1)$$

Polar plots of the relative target strength of a Chinook, coho and sockeye salmon in the lateral plane measured at an elevation angle of 22.5° are shown in Fig. 5. This figure applies to a situation in which a killer whale is close to the surface echolocating on a distant salmon at depth in the water column. If a killer whale is at a depth of 1 m and a salmon at a depth of 40 m the direct path between the whale and the salmon will be 22.5° below the horizon for a horizontal distance of 94 m, well within the detection range for a Chinook salmon (Au *et al.*, 1974). The results shown in Fig. 5 are consistent with those in Fig. 4, showing minimal reflectivity when the incident signal was directed toward the tail and head of the salmons. The overall pattern of reflectivity was also similar in shape for the three species of salmon represented in the figure.

Normalized echo waveforms for an elevation angle of 22.5° and different azimuth of the salmon are shown in Fig. 6. The waveform information was extracted from data used

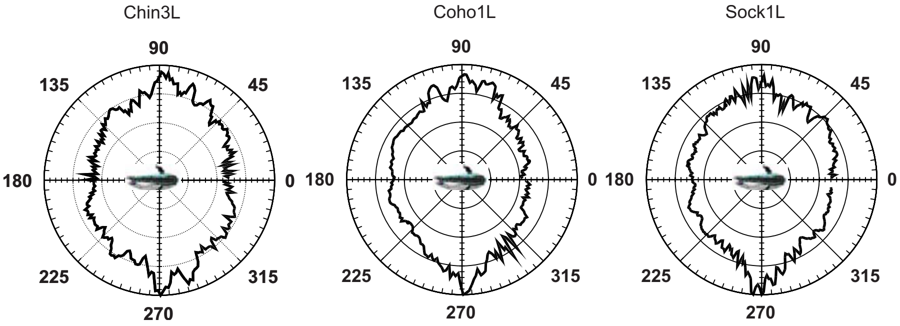

FIG. 5. (Color online) Polar plots of the target strength of a Chinook, coho and sockeye salmon as the salmons were rotated in the lateral plane for an elevation angle of 22.5°.

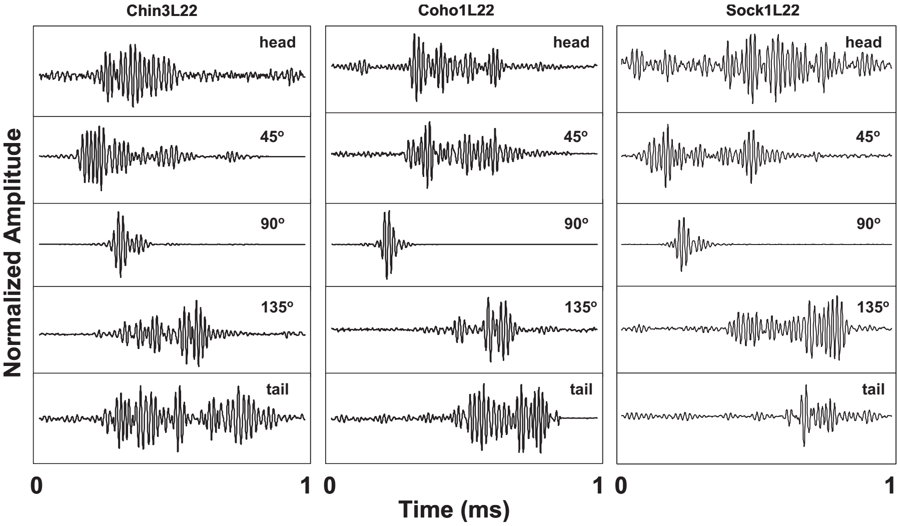

FIG. 6. The normalized echo waveforms for a 22.5° elevation angle and different aspect angles of the fish.

to calculate the target strength shown in the polar plots of Fig. 5. Differences in the echo structure for any specific aspect angle between the three species of salmon are present even for the broadside aspect. Echoes from the broadside aspect have the shortest time duration and echoes from the tail aspect have the longest duration. The differences in the echo duration from the head and tail aspects correspond relatively well with the differences in the length of the swimbladder. In Figs. 3 and 4, the images indicate that the sockeye salmon had the longest swimbladder, followed in turn by the coho and Chinook. The echoes in Fig. 6 for the head aspect were the longest in duration for the sockeye salmon, followed by the coho salmon. Differences in echo duration were less at the 45°, 90° and 135° aspect angles.

The effects of elevation angle on the echo waveform of a Chinook salmon from different aspect angles are shown in Fig. 7 for the three elevation angles, 0°, 22.5° and 45°. Only in the broadside aspect are the echoes relatively similar in shape. The differences in the waveforms for aspect angles other than 90° are in the arrival time of the different highlights and in the total duration of the returns. This is not surprising because of asymmetry in the shape of swimbladders would affect both the backscatter process and the internal propagation paths that the incident signal take after entering the body of the salmon.

Polargrams, which are the frequency spectra of the echoes as a function of the polar angle about one side of each fish species, are shown in Fig. 8. The amplitude of each spectra is coded in color as shown in the color bar to one side of the figure. A similar kind of polargram can be drawn in which the envelope of the echo for each polar angle can be drawn as was done by Reeder *et al.* (2004). Perhaps the best way to visualize the polargrams is to step back and look at the pattern of changes in the spectra as the polar angle varies. Each polargram has a slightly different pattern as the echo spectra change with angle and this pattern may be used by killer whales to discriminate a specific species of salmon. One feature of the polargrams is the presence of diagonal stripes that indicate how information from different frequencies varies in a pattern as the fish aspect angle changed.

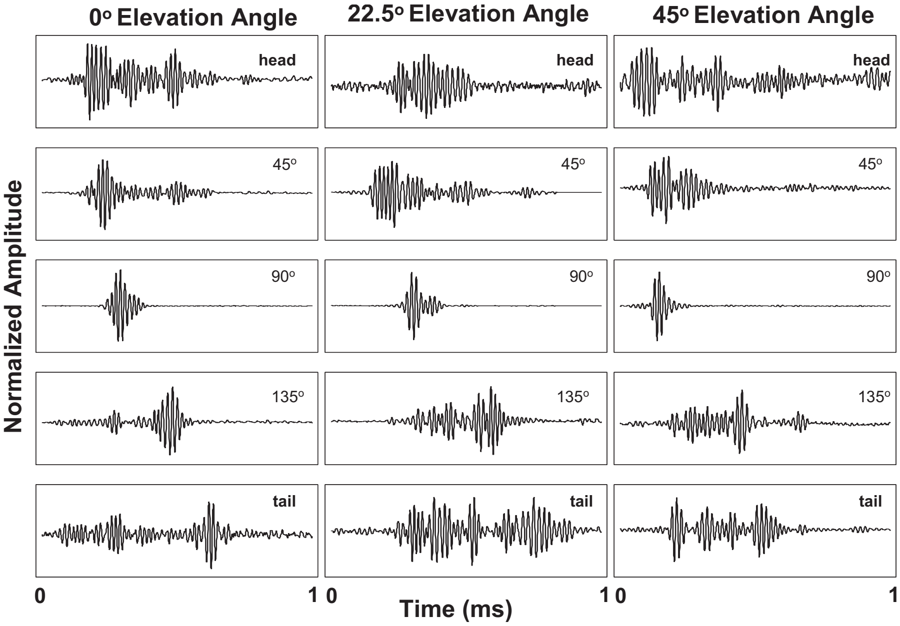

FIG. 7. Echo waveform from a Chinook salmon for elevation angles of 0°, 22.5° and 45° and for five different aspect angles.

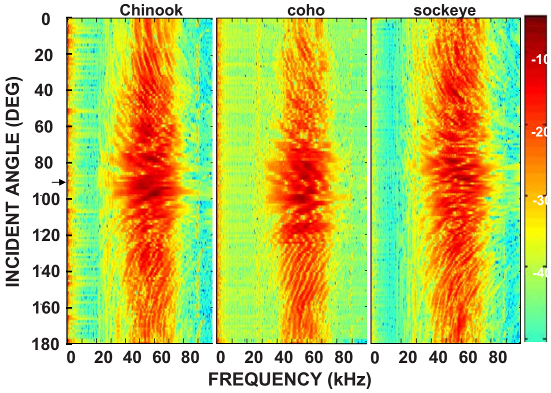

FIG. 8. (Color online) Polargrams (frequency spectra versus polar angle of the echoes) for the three species of salmon obtained with the orca-like biosonar signal. The frequency spectra for different polar angles are shown with the amplitude color coded according to the color bar on the right.

These are caused by changes in the high-light separations time as the polar angle changes which will cause local maxima and minima in the spectrum to shift. The shift in local maxima and minima in the spectrum are reflected by the diagonal stripes. The polargrams clearly show differences in the spectra of the echoes from the difference salmon species that can be utilized by killer whales in discriminating between these three species of salmon. In a natural environment, the predator-prey geometry will constantly change from ping to ping and the polargram can be used to gain an appreciation of how the spectra of the echoes will change as the predator-prey geometry changes dynamically.

The target strength from the dorsal-tilt aspect of a Chinook and a coho salmon is shown in Fig. 9. Backscatter measurements with the salmon in the dorsal-tilt axis had the lowest priority in our study and so good echoes were collected from only these two specimens. Similar to measurements done in the lateral plane, the lowest echo levels were collected from the head and tail aspect and the highest levels were collected when the longitudinal axis of the swimbladder was perpendicular to the path of the incident signal. The measurements done in the dorsal-tilt plane were used to simulate a situation in which a salmon at depth is swimming directly away from an echolocating killer whale close to the surface. The echoes returning to the killer whale would come from different parts of the dorsal surface of the salmon. This geometry would be similar to the one used by Au *et al.* (1974) in modeling the detection range of a killer whale foraging on a salmon. However, the target strength values between 90° and 180° for the Chinook salmon in Fig. 9 are approximately 10 to 15 dB larger than the theoretical calculations in Au *et al.* (1974). The reason for this difference is not known except that the target strength in our measurements were based on energy of the broadband signals whereas in Au *et al.* (1974) target strength values were based on the peak-to-peak values of a tonal signal. As the horizontal range between the killer whale and the salmon decreases, different portions of the dorsal surface of the salmon would be ensonified. The echo structure for a Chinook and coho salmon for different incident angles is shown in Fig. 10. The results suggest that in this geometry, the echo structure for the Chinook and coho salmons are different and can probably be attributed to differences in the anatomical shape and geometry of the swimbladder.

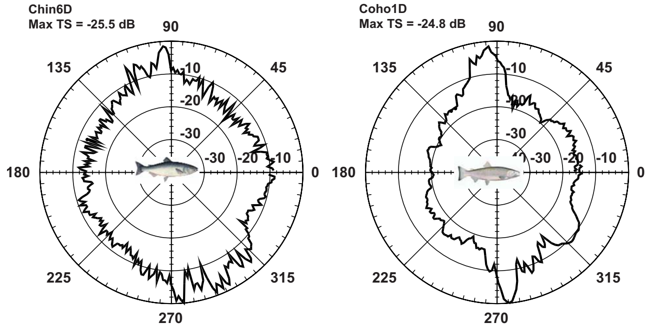

FIG. 9. (Color online) Polar plots of the target strength of a Chinook and a coho salmon with the salmon rotated in the dorsal tilt plane.

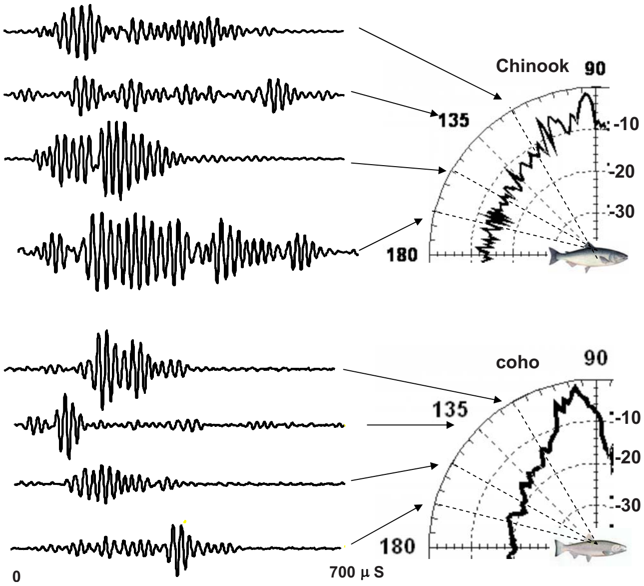

FIG. 10. (Color online) Echo waveforms from a simulated perspective of a killer whale approaching a salmon from the rear at various elevation angles.

IV. DISCUSSION AND CONCLUSIONS

The specific setup was chosen to minimize extraneous echoes and keep the fish alive throughout the measurement process. Therefore, the salmon could not be mounted in a very rigid fashion which introduced some unmeasurable amount of uncertainty in the precise orientation of the salmon; the fish were not mounted exactly vertically in the roll plane and the longitudinal axis of the salmon were close to but not exactly parallel to the horizontal. However, we were willing to accept these minor sources of uncertainty realizing the inherent difficulties of working with live salmon. We also wanted to simulate a natural condition as best as possible. If the salmon happened to expire in the course of the measurement, data from that session were not accepted. On some occasions, the salmon would "wake" up from its anesthetized state and start to thrash about. On those occasions, we waited until the subject relaxed and remain relatively still before continuing with the measurements or we terminated the measurement.

The results were analyzed and discussed mainly from an echo structure perspective; frequency spectra information was not used. The multiple highlight feature of the echoes made analysis and interpretation in the time domain more insightful than in the frequency domain. It suffice to state that the all the information present in one domain are also present in the other domain. The auditory system of mammals probably utilize simultaneous time-frequency information rather than information in only one domain. Two logical follow-on to this study include the determination how a mammalian auditory model would respond to the echoes collected in this study and to conducted human listener experiments as has been done for echoes collected with other targets (Au, 1993; DeLong *et al.*, 2007).

Results obtained in this study showing differences in the structure of echoes are not surprising since the shape, size and orientation of the swimbladder were expected to be different for the different salmon species. Morphology of the swimbladder within species also showed some variations, as one would expect for a biological organism and these variations would be reflected in the echoes from different individuals. For the Chinook and coho salmon examined in this study, there was a relatively consistent intraspecies geometry in the swimbladders. The interspecies differences in swimbladder geometry and size were much larger. Unfortunately, we did not have access to chum salmon, the other specie that killer whale forage on during the fall when Chinook salmon becomes rare in the Pacific northwest (Ford *et al.*, 1998; Ford and Ellis, 2006)

Species-specific differences in the echo structure of backscattered broadband acoustic signals from Chinook, coho and sockeye salmon have been observed in this study. The data indicate that the echo structure vary in amplitude, time separation between highlights, number of highlights and overall duration depending on the angle of incident of echolocation signals. These results suggest a very complex backscattering process with various types of aspect dependent information available. So the most obvious question is whether or not a killer whale can handle the aspect dependent fluctuations associated with reflection from a single salmon. From a slightly different perspective one could ask whether or not a killer whale can generalize from fluctuating broadband echoes that a potential prey is a Chinook salmon instead of some other salmon species. The task for a foraging killer whale is to detect, localize, recognize and track a moving Chinook salmon prey. Since both predator and prey are moving, the acoustic geometry will be continuously changing causing the echo structure to fluctuate. If a killer whale utilizes the echo structure information to hunt for Chinook salmon, then the whale would need to generalize and be able to determine that these echoes are from a Chinook salmon. Such a capability is not out of the question since dolphins and porpoises seem to be "acoustic" animals with large portions of their brain and nervous system devoted to the processing of acoustic information (Ridgway, 2000). Just as humans can assign objects to specific classes even without a prior experience with the specific object, dolphins may be able to assign fluctuating and varying echoes to a specific-species of salmon. Unfortunately, this issue cannot be adequately addressed without some controlled psycho-acoustic experiments with a dolphin subject. Nevertheless, the results obtained in this study indicate that species-specific differences are present in the echo structure.

There are two obvious issues that need to be addressed concerning this project. First, all the specimens were obtained from the Issaquah Salmon Hatchery, up river from Lake Washington and the Puget Sound. These fish would be completing their osmoregulatory transition from salt to fresh water (Koch 1968), which is energetically demanding (Hendry and Berg 1999). Changes in osmoregulation would influence the water content of the musculature in the fish body and could affect the volume of gas in the swimbladder. Both of these responses to life in fresh water could have some minor but unknown effects on the acoustic reflectivity of the fish body and swimbladder. We assumed that physiological responses to changes in osmoregulation will not affect the acoustic reflectivity of the subjects. Travel time from Puget Sound to the Issaquah Fish Hatchery is approximately one month and it is thought that adaptation to fresh water would occur during that period. Second, salmon are physostomes with a pneumatic duct connecting the swimbladder to the digestive tract so that geometry of the swimbladder is subject to changes cause by change in ambient pressure at different depths. Mukai and Iida (1996) showed that target strength decreased with depth in kokanee salmon in accordance with Boyle's law. However, Mukai and Iida (1996) did not address the issue of swimbladder geometry but merely swimbladder volume and its effect on target strength. Whether there are species-specific differences in swimbladder geometry and volume at depth has not been examined (see Horne *et al.*, 2009 for an example of a phisoclist). Connections of the swimbladder to the spinal column, ribs, and musculature also restrict labile surfaces to the ventral side of the swimbladder and could affect how the shape of swimbladders varies with depth. There is a distinct possibility that species-specific differences in the shape, size and volume of the swimbladder of salmon may still exist at depth. If this happens, the differences in echo structure close to the surface and at depth may be preserved to a certain extent. This issue is still an open question and further work is necessary to determine the dynamic behavior of the swimbladder at different ambient pressures.

It should be emphasized that although our results suggest that interspecies difference in echo structure exist in salmon, this type of information is probably not the only information used by an echolocating killer whale to detect, localize and recognize Chinook salmon. There are potentially a multitude of cues that would be available to a killer whale through the echolocation process. The swimming behavior and dynamics of potential prey can be determined by examining the change in the echo amplitude and timing as well as the echo structure from ping to ping. The depth of potential prey could also be determined by the echolocation process. A foraging killer whale will no doubt use as many available cues that are present. Furthermore, different cues may have different weight depending if the whales are foraging in relatively open waters or in the vicinity of islands and other land masses with steep cliff that protrude into the water. Chinook salmon have been observed "hiding" from foraging killer whales by swimming into narrow crevices along these steep cliffs (Ford, personal communications). This study should be the first of many attempting to dig deeper into the foraging behavior by echolocating killer whales.

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