Changes in the frequency structure of echolocation clicks across behavioral states in Southern Resident killer whales (Orcinus orca)

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Abstract:

Southern resident killer whales are found throughout the Salish Sea during the summer months. They are known to produce a wide range of phonations, and echolocation clicks in particular are utilized continuously across a wide range of behaviors and for different tasks. Clicks were measured using a four hydrophone array, with data analysis using a single CRT hydrophone with a flat response up to 30 kHz. The data was collected using a 16 bit depth, and sampling at a rate 192,000 kHz. Observational data on the behavior state and orientation of the whale was taken with all recordings. Data was tested using a One- way ANOVA for differences in the frequency structures across various behavior states. Clicks were tested by using the measurements of center frequency, RMS bandwidth, and Q-value. Significant differences were found for all three measurements with respect to the behavior states foraging, milling, and traveling. The Q-value was significantly different for each of the behaviors and this confirms a difference in the overall structures for each type of click. A Significant difference in the frequency structure has been demonstrated, and it suggests killer whales have the ability to adjust the structure of their calls with respect to a particular task or behavior. These differences also confirm the importance of controlling for behavior state when studying SRKW killer whale populations.

Introduction:

The killer whale (*Orcinus orca*) is the largest member of the delphinid family, and belongs to the group of cetaceans known as Odontocetes. It is a highly social animal that forms complex social structures called pods, which are based on small and tight matrilineal relationships (NMFS, 2008). There are three distinct ecotypes of killer whale found in the Northeast Pacific: offshore, transient, and resident populations. Each ecotype has unique characteristics, however, for this study I will focus on the Southern Resident killer whale (SRKW) population found in the coastal waters of Washington State within the Salish Sea during the summer months (NMFS, 2008). These whales are of interest because they have been listed as endangered under the Endangered Species Act of 1973 since November 2005. Current threats to the SRKW's include decreased prey availability, environmental contaminants, and increased ambient noise from recreational and commercial (ferry, cargo, and whale watching) vessels throughout their critical habitat. Ambient noise is a serious concern for this population because the critical habitat for the summer months directly overlaps with popular boating grounds, as well as important shipping lanes between the US and Canada. The extensive use of acoustics for foraging, communication, and navigation results in high levels of susceptibility to disturbance and stress from sources of anthropogenic ambient noise. A study by Erbe (2002) used an acoustic impact model in order demonstrate the distances at which whales could detect noise, encounter masking, show avoidance behaviors, and experience hearing loss with respect to whale watching boats. This paper found that 400 m was a sufficient distance to prevent permanent hearing loss; however the law currently requires only 100 m of space for private and commercial whale-watching boats (Erbe, 2002).

Killer whales produce three primary types of phonations including echolocation clicks, tonal whistles, and pulsed calls (NMFS, 2008). Their most sensitive hearing is in the range of 18-42 kHz, with peak sensitivity at 20 kHz (Szymanski, 1999). Some of the energy in echolocation clicks fall outside of this range, and a click consists of high amplitude, broad band frequency spectrum, and they last for a very short duration of time. Au (2004) found 97% of the analyzed clicks had center frequencies between 45-80 kHz, RMS frequency bandwidths from 35-50 kHz, and Q-values ranging from 0.9 to 1.4 (Au et al, 2004). This study focused on similar measurements based on echolocation clicks produced during various behavioral states from free-ranging SRKW.

Foote and Nystuen (2008) demonstrate that there are differences in the frequencies of clicks and calls that are used by killer whale ecotypes with respect to ambient noise levels. Killer whales that hunt primarily off shore utilize minimum frequencies that are much higher than the inland resident populations. This is thought to compensate for the high levels of low-frequency background noise that is produced by the higher wind speeds in the open ocean environment. This demonstrates the ability of the species to modulate the frequencies of their clicks in response to various conditions. In addition, a study by Houser (1999) examined the degree of adaptive control over click production demonstrated by the Atlantic bottlenose dolphin. Classified echolocation clicks were analyzed with respect to animal specific differences, changes in predominant click type for various click trains, and clicks from task specific activities. Houser found different classifications of clicks corresponded to various locations within a given click train, and differences in frequency structures also arose with respect to different echolocation tasks (Houser, 1999). This is important because it provides evidence that individual animals are capable of using shifts in echolocation frequencies when faced with different tasks and situations. This information was used as a basis to predict differences in the frequency structures for echolocation clicks from killer whales in different behavioral states. Clicks are also used for both forging and socializing, and this parallel utilization across different behaviors suggests they differ in function. I predicted variations would be found in the frequency structures for individual clicks across phonations recorded across different behavior states.

In general click beam patterns are known to have a strong directionality in their structures, and the horizontal beam is much narrower than the vertical beam (Au, 1995). This had important implications for producing accurate recordings of clicks for acoustical analysis in studies such as this one. As the axial alignment moves from 0 degrees to 5 degrees differences begin to arise in the structures of the waveform and frequency spectrum of the click. The center frequency and bandwidth also decreases in value as the click is turned off axis (Madsen, 2004). In a study by Madsen (2004), it was determined that in general axially aligned clicks show the greatest amplitudes relative to adjacent clicks. These characteristic allowed for me to sort clicks initially based on alignment and relative amplitude. Once these clicks were isolated further analysis of the spectrum structures, as well as the duration of the wave form gave further indication of the clicks axially alignment (Madsen, 2004).

This investigation of click structures across behavioral states will serve to develop a baseline of understanding for the abilities of killer whales to alter the frequencies structures of their clicks for different uses and situations. This information will be used to better understand the physiological, behavioral, and evolutionary significance of killer whale bio sonar systems. As ambient noise and other disturbances continue to increase throughout the SRKW's critical habitat, the possible impacts will need to be heavily considered for future recovery plans. A deeper understanding of when and how whales use specific phonations will help policy makers produce effective management guidelines, and it will allow for empirical measurements of differences in the behavior states for these killer whales. This study provided a crucial start to gaining a more detailed understanding to what degree free-ranging killer whales modulate the frequency structures of their clicks in real world situations. Overall, this has led to a better understanding of the whale's ability to avoid masking of their calls due to ambient noise and other disruptions.

Methods:

The data collection for this project was in the waters of the Salish Sea, and it was primarily centered on the West coast of San Juan Island in Haro Strait, and surrounding San Juan Islands south of Point Roberts. The research platform was the Gato Verde, a 42 foot sailing catamaran with a hybrid bio-diesel electric propulsion system. A bank of lead acid batteries was used to power two electric motors that allow the catamaran to run with minimal acoustical interference while recordings are being made. Five hydrophones are deployed for recordings, with an array of four Labcore 40 hydrophones off the port stern, and a single CRT (Cetacean Research Technology) C54 XRS/266 hydrophone off the starboard stern. Array hydrophones are separated by approximately 10 m of cable, and the final hydrophone is attached to the terminal end of the cable. Gain settings were fixed at 43.5 dB for the array, and 37.3 dB for the CRT, and all hydrophones were calibrated using the Interocean Systems, Model 902 Hydrophone Calibration System. The CRT was used in place of the second Labcore 40 hydrophone in the array for making recordings. The two sets of hydrophones were weighed down to a depth of 1.85 m, with a 12 lb. finned weight on the Labcore 40 hydrophone array and a 10 lb. finned weight for the CRT. Then they were deployed to avoid acoustic interference from the surface. The CRT trailed behind the boat on a 28.05 m cable. All four hydrophones were connected to two Sound Device 702 High Resolution Digital Audio Recording Units, and all hydrophones were initially sampled at 192 kHz, with a 16 bit depth rate. The audio channel with the CRT data was also saved as a mono file for frequency analyses. After collection, the data was down sampled to 48 kHz using a Matlab script. The Labcore 40 hydrophones have a peak frequency response at 5 kHz with sensitivity dropping from there. The CRT has a flat response curve from 1 kHz to 30 kHz, plus or minus three dB along the response line.

I assisted in the collection of additional metadata on the behavioral states of the whales while recordings were being made. Five behavior states, resting, traveling, foraging, playing, and milling, as described in the 2004 National Oceanographic Atmospheric Administration (NOAA) SRKW workshop, were used to classify the whales behaviors throughout the time recordings were being made. Resting was defined by close contact between whales (flank or nonlinear formation), and slow but directional movement with high breathing synchronization, and very few clicks or calls. Traveling was characterized by directional movement with the whales swimming at any speed with relatively little space between individuals. Foraging behavior was more difficult to characterize, and it was classified as essentially any orientation, spread distance, direction, or speed that could be observed at the surface. Any observable lunge or chase events were also included in the foraging classification. Foraging by resident killer whales was defined as erratic high-speed swimming, lunging, and chasing fish near the surface in a study by Barrett-Lennard et al. (2004). Playing behavior consisted of three categories for any distance, orientation, and speed which include: object play (kelp and floats), social interactive play (touching, breaching, and percussive behaviors), and solitary play. The last classification was milling, and this was characterized as a nonlinear orientation where the whales were spread at any distance and moving with a slow or medium pace (NOAA 2004). These guidelines were based on definitions drawn from the 2004 SRKW Behavior Workshop and the 2004 Barrett-Lennard et al. paper (NOAA 2004, Barrett-Lennard et al. 2004).

The metadata that was recorded includes time, behavior state of the whales, orientation to the boat, pod size, and any additional notes about that time period. The data was synchronized with the hydrophone recording times so that the data sets could be applied to one another. The time and date was collected using a GPS, and a waypoint was used to mark the start and stop times of acoustic recordings. Behavior was recorded at time intervals of five minutes. The orientation of the whales to the boat was collected with respect to a clock face system with 12 o'clock pointing out of the bow, and continuing clockwise around the boat. A behavior state was assumed to be constant for all groups surrounding the boat; activities tend to be the consistent for all members of a pod despite different group orientations in the immediate area (Hoelzel 1993). All data was collected while following whale wise guidelines and abiding by the current laws.

Acoustical recordings were spliced into one minute long segments when they were down sampled to make the data more accessible. This data was then used to listen and observe the recordings initially. Once a click was located within the recordings and it showed the characteristics of an on axis click (Mansteen, 2004), I then exported the spectrum using, the program Audacity 1.3 Beta, in a .csv file format to excel for further frequency analysis. I compared the frequency structures of clicks known to be off axis with ones known to be on axis in order to test my sampling approach. Plots of the data then allowed me to compare its frequency structure to those found in Madsen (2004) to determine which clicks were most axially aligned, and therefore the most appropriate for further analysis. Next I converted dB values, exported from Audacity, into Intensity using excel:

[1] $\text{Intensity} = 10^{(dB/10)}$

A correction was made for the dB values in the upper frequencies of each click in order to compensate for the diminishing sensitivity of the CRT hydrophone. A graph was obtained that provided information on the sensitivity for the hydrophone across all frequency levels, and appropriate values were added above 20 kHz to each click, before it was analyzed using Excel. The Intensity values were used to calculate the center frequency and RMS bandwidth for each click using equations derived from Au (2008):

[2] $Fo = \sum Frequency * Intensity / \sum Intensity$

[3] $RMS\ Bandwidth = \sqrt{\sum Frequency^2 * Intensity / \sum Intensity - Fo^2}$

A Q-value was calculated by using both the center frequency and RMS bandwidth (Au, 2004):

[4] Q-Value = Fo / RMS Bandwidth

The data consisted of multiple clicks sampled from individual click trains, as well as single isolated clicks. In order to control for any bias from including multiple clicks from specific click trains I randomly selected 50 data points from my full data set using the random number generator in Excel. I then checked for significance using the One-way ANOVA in Sigmaplot, and I compared these values to my final results. I repeated this subsample test ten times, and each test produced results that were similar to my full data set. The main data set also failed to pass a normal distribution test in Sigmaplot, so I used a histogram and a normal probability test to better determine the distribution characteristics of the data. By using these techniques I determined the data was a sufficient representation of a normal distribution, and I used Sigmaplot to run a One-way ANOVA with a Holm-Sidak multiple comparison test. Behavioral states were used as the independent variable in every ANOVA, and the center frequency, RMS bandwidth, and Q-values were compared across these states as the dependent variables.

Results:

Nine days of measurements were obtained between September 13, 2010 and October 23. I analyzed clicks from recordings on all nine days, and across five behavioral states. However, only Foraging, Milling, and Traveling were used for final analysis, this was due to restraints from the total sample sizes of three clicks for socializing and resting. Every click was handpicked from the recordings, and only clicks that were considered to be on axis with the hydrophone array were used for final analysis. Only clicks with high relative amplitudes to adjacent clicks, smooth spectrum, and good wave form structures were used for analysis. It has been shown in other closely related species that clicks are directional and distortion in the frequency structures occur when they are received off axis (Madsen 2004 and Au, 1995). Three spectrum and the wave forms of echolocation clicks from the encounter behavior states are shown in Fig 1. The spectra on the left are representations of the mean values calculated with the ANOVA's for each of the behavioral states, and the plot on the right is the same click represented as a wave form. This highlights the broad band frequencies and short durations that are normally associated with echolocation clicks.

A.

B.

C.

Figure 1:

The frequency spectra and wave forms for three different behavior states. A. Spectrum and wave form from a foraging killer whale. B. Spectrum and wave form from a milling killer whale. C. Spectrum and wave form from a traveling killer whale.

The results from the ANOVA for the center frequency are shown in Fig. 2a, and I included the histogram as a graphical representation for the distribution of the data in Fig 2b. Center frequency is defined as the frequency value that splits the energy from the spectrum into two equal parts (Au, 2008).

A.

B.

Figure 2.

Results from the One-way ANOVA statistical test for the center frequency across behavior states. A. Scatter plot of the mean center frequency across three behaviors. B. Histogram of the center frequency data to represent the normal distribution of the data.

Clicks taken from foraging killer whales had the highest center frequencies with a mean of 25,407 Hz, followed by traveling at 24,421 Hz, and milling was the lowest with 23,737 Hz. The ANOVA produced $F_{618,619} = 7.144$, $P = < 0.001$, and the multiple comparisons test only found a significant difference between foraging and milling killer whales with $P = < 0.001$.

The results for the RMS bandwidth test are represented in Fig. 3a, and the histogram for the data is included in Fig 3b for the same reasons stated above. The RMS bandwidth is used to describe the spectral standard deviation around the center frequency of the spectrum (Madsen, 2004). The RMS bandwidth gives a better bandwidth representation for bimodal clicks, and I chose to use this measurement due to findings in a study on SRKW by Whitlow Au in 2004 that found 89% percent of clicks had bimodal structures (Au, 2004). Traveling whales were found to have the highest mean RMS value at 9266 Hz, followed by foraging whales at 9266 Hz, and milling was the lowest with a value of 8308 Hz.

A.

B.

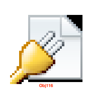
Figure 3.

Results from the One-way ANOVA statistical test for the RMS bandwidth, across behavior states. A. Scatter plot of the mean RMS bandwidth across three behavior states. B. Histogram of the RMS bandwidth data to represent the normal distribution of the data.

Significant differences can be seen in Fig 3a for both traveling and foraging with respect to milling behavior: $F_{618,619} = 12.196$, $P = < 0.001$. For the multiple comparisons tests both P-values for traveling vs. milling and foraging vs. milling were < 0.001.

Q-values are used to describe the overall frequency structure of clicks with respect the center frequency and the RMS bandwidth. High Q-values correspond with sharp and narrow spectrum, while lower values represent a broad and wide frequency spectrum. The Q-value was highest when the whales were milling with a mean of 3.026, this was followed by foraging at 2.819, and traveling had the lowest value of 2.613. The distribution of all the values is displayed as a histogram in Fig. 4b.

A.



B.

Figure 4:

Results from the One-way ANOVA statistical test for the Q-value, across behavior states. A. Scatter plot of the mean Q-value across three behavior states. B. Histogram of the Q-value data to represent the normal distribution of the data.

The initial results for the ANOVA, $F_{618,619} = 14.334$, $P = <0.001$, showed a large level of significance. The multiple comparisons test showed all of the differences across the behavioral states were significant. Milling vs. foraging and milling vs. traveling each had $P = <0.001$, and foraging vs. traveling had a $P = 0.008$.

Discussion:

Hearing and reference other figures

This study has found significant differences across various measurements of the frequency structures, with respect to the behavior states of SRKW. My prediction for changes in click structures was supported by all three measurements and Fig. 4a shows significant differences for all three behavior states. These findings suggest killer whales have a certain degree of control over all of their phonations, not just calls. It has been demonstrated that on average whales have higher center frequencies while they are foraging when compared to milling. This is an important difference because it suggests the whales are actively changing their calls for different tasks, and each behavior could have its own specific purpose that is paired with a certain click structure. It also validates the separation of milling and foraging as different behavior states even though they often appear very similar on the surface. However, it is hard to determine what the higher center frequency is being used for during foraging, and why they shift the frequency for milling behavior.

A similar trend appeared for traveling and foraging with respect to RMS. Whales that were milling had a significantly lower RMS value, which means their clicks were narrow and the energy was more concentrated at lower values. These differences in mean values continue to suggest the whales are doing something drastically different while they are milling. The mean center frequency for milling is also the closest to peak sensitivity of hearing for the killer whales. All of the means fall within the sensitive hearing range, but it could be important that mean for milling is the closest to the peak sensitivity (Szymanski, 1999).

The final measurement, the Q-value, gives an overview of a click's structure by taking the ratio of center frequency and RMS. The continued trend for significant differences in milling from foraging and traveling also appears in the Q-values. Overall, clicks associated with milling have narrow clicks centered on lower frequencies, traveling has the broadest clicks in the middle frequencies, and foraging has the highest frequencies but they are not as wide or narrow as the other two. These findings suggest the whales are making specific changes to their clicks depending on the task they are performing. Significant differences in the Q-values can lead to the overall conclusion that the fundamental shape of the clicks is significantly different across behavior states. This study provides evidence that killer whales have the ability to actively adapt to different situations and circumstances. Future research should focus on differences between populations, individual whales, and opposite sexes in order to better understand how much control killer whales have over the phonations they produce.

When I compared my values to those obtained by Au in 2004, some major differences arose instantly. I attempted to compensate for differences in sampling rates and equipment by correcting for the sensitivity loss in the CRT; however our values are still very different. Au's study focused on killer whales that were only foraging, and he used data from whales that came within 5 to 15 meter of his array. The data in this study was collected from a wide range of distances, and it focused on distinct shifts in behavioral states. I found foraging to have a center frequency at 25,407 Hz, RMS of 9266, and Q-value of 2.819. The mean center frequencies from Au's paper are 50 kHz, the mean RMS is 40 kHz, and the Q-values range from 0.9 to 1.4. I believe these differences are a combination of equipment, methods, and the behavioral state of the whales. Au mentions the whales turn their heads toward his array and the source level of their clicks decrease as they approach; which suggests the whales are echolocating on the array itself. I believe this will cause changes in the structures of the clicks and that it is not an accurate measurement of clicks from free-ranging killer whales. The bimodal structures of clicks collected by Au are most likely responsible for the higher center frequencies and RMS bandwidths. I think these differences highlight the importance of controlling for the whales behavior, and studying the animals in a natural setting without influencing their behavior.

Possible sources of error range from data collection to analysis. Deciding which clicks were on axis required a combination of observational data and hand picking wave forms and spectra. Many of the clicks that were known to be on axis from observational data were clipped due to the gain settings of the hydrophones at the time of the recordings. A conservative approach was taken and only a small number of the recorded clicks were used for the final analysis. Using FFT windows for analyzing clicks is hard because the smallest FFT window is still bigger than the average click, and as a result a small amount of extra data is analyzed. Measures were taken to control for this and it was determined that the FFT window had minimal effect on the spectral analysis. Clicks have high frequency components, and electronic interference can have an impact on the upper frequencies of the spectrum. A conservative approach was taken and only a small number of the recorded clicks were used for the final analysis. Collecting behavioral data is also a judgment call, and that could be a possible source of human error. Also on days with low visibility the accuracy of behavioral data can be impacted. Finally small differences in clicks across individual whales or from whales of the opposite sex may exist, and these influences will need to be studied in the future in order to understand their possible impacts.

This study has provided empirical evidence that shows SRKW change the frequency structures of their clicks with respect to what behavior state they are in. Further understanding should be gained about the ability of these whales to adapt for different situations, and more clarity is needed in order to know if these differences appear on an individual or species level. Behavior has been shown to have a significant influence on the structure of specific phonations, and future studies should take this into account to minimize error. Passive studies on free-ranging animals provide drastically different and valuable information, and they will be crucial to further understanding the SRKW population in the Salish Sea.

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