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Acoustic classification of echolocation clicks of three killer whale ecotypes in the Northeastern Pacific

A thesis submitted in partial satisfaction of the requirements for the degree Master of Science

in

Marine Biology

by

Amanda Ann Leu

Committee in charge:

Kaitlin E. Frasier, Chair
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2021

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2021

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ABSTRACT OF THE THESIS

Acoustic classification of echolocation clicks of three killer whale ecotypes in the Northeastern Pacific

by

Amanda Ann Leu

Master of Science in Marine Biology

University of California San Diego, 2021

Kaitlin E. Frasier, Chair

Three distinct ecotypes of killer whale are found in the Northeastern Pacific, residents, transients, and offshores. These ecotypes have previously been discriminated in passive acoustics using distinct pulsed call repertoires that are shared within each ecotype. This type of discrimination process is strenuous and inefficient as it requires an analyst to manually review individual calls. Echolocation click features have been used in previous studies to identify some delphinids to the species level using a semi-automated process. A dataset consisting of manually labeled killer whale encounters identified to ecotype based on pulsed call matching was used to generate echolocation click archetypes for resident, transient and offshore killer whales to test if this process reveals discriminatory echolocation features for each ecotype in the Northeastern Pacific. Results indicate that resident and offshore killer whales can be distinguished acoustically based on the spectral shape and inter-click intervals of their echolocation clicks. Efficient, automated identification will allow expanded use of passive acoustic monitoring for management of these populations.

Introduction

In the Northeastern Pacific Ocean, several populations of killer whales (*Orcinus orca*) inhabit over-lapping ranges from the Aleutian Islands to southern California (John K B Ford 1989; A. Rus Hoelzel and Dover 1991; Steiner et al. 1979). Of these killer whale populations, there are three ecotypes that are genetically, behaviorally, and morphologically distinct: residents, transients (also known as Bigg's killer whales), and offshores (M. A. Bigg et al. 1990; J. K.B. Ford 1991; A. R. Hoelzel, Dahlheim, and Stern 1998; Barrett-Lennard 2000; Dahlheim et al. 2008; Deecke, Ford, and Slater 2005; Morin et al. 2010). These ecotypes inhabit many of the same areas, though they are rarely observed together, and some observations indicate they may actively avoid each other (R. W. Baird and Dill 1995).

Since each killer whale ecotype has different prey preference, habitat use, and behaviors, they each occupy separate ecological niches. Killer whales are top predators, and as such, face threats from biomagnification of organic pollutants, oil spills, prey species depletion from numerous anthropogenic causes including overfishing and dams, and interference from vessels, as well as vessel associated noise (Krahn et al. 2004). These threats have the potential to affect each ecotype in different ways.

Killer whales utilize four types of acoustic signals for communication and prey acquisition: whistles, pulsed calls, high-frequency modulated signals, and echolocation clicks (John K B Ford 1989; Thomsen, Franck, and Ford 2001; Samarra et al. 2010; Simonis et al. 2012). Whistles, which can be low frequency or ultrasonic, are primarily used for short range communication within pods and family groups (John K B Ford 1989). Similarly, pulsed calls are thought to function in group recognition and coordinate communication (John K B Ford 1989; Miller et al. 2004); several studies have assembled catalogs of pulsed calls unique to each ecotype (J. K.B. Ford 1991; Barrett-Lennard, Ford, and Heise 1996; Deecke, Ford, and Slater

2005). High-frequency modulated signals are ultrasonic tonals and their function is unknown but may be used in communication or possibly echolocation (Simonis et al. 2012). Echolocation clicks are used primarily for foraging and spatial awareness. They are characterized by short duration, high energy, ultrasonic, broadband signals that can occur in repetitive series. These are produced in a narrow beam directed in front of the animal. Echolocation clicks are used by all three ecotypes but variation in prey preferences and preferred habitats may be a driver for differences in how and when echolocating occurs.

The resident ecotype is among the most studied killer whale types, with habitat ranges observed relatively close to shore from British Columbia to Northern California (John K B Ford 1989; Deecke, Ford, and Slater 2005). There are four populations that make up the resident ecotype: northern residents, southern residents, southern Alaska residents, and western Alaska North Pacific residents. Each population within this ecotype lives in stable matrilineal social groups ranging from 5 to 50 individuals which feed only on teleost fish, primarily on select species of salmon (Parsons et al. 2009; Nichol and Shackleton 1996; Au et al. 2004). These prey fish are known to have poor hearing abilities thus there is little cost for the residents to be highly vocal while foraging (John K.B. Ford and Ellis 2006).

Transient ecotypes are found throughout the eastern North Pacific Ocean and are commonly studied from the Gulf of Alaska to Washington state (Robin W. Baird and Dill 1996; John K.B. Ford et al. 1998). There are five populations that make up the transient ecotype in the Northeastern Pacific; west coast transients, Gulf of Alaska transients, AT1 transients, Aleutian transients, and Bering Sea transients (M. Bigg 1982; Wiles 2016). The transient ecotype also has a matrilineal social structure, with group sizes ranging from 1 to 15 individuals (Baird and Dill 1995). They are observed to have more dispersal from the matriline and are commonly seen hunting in groups of three individuals (Robin W. Baird and Whitehead 2000; John K.B. Ford et

al. 1998). They prey exclusively on marine mammals which include smaller delphinids in coastal and deep waters and pinnipeds along coastal habitats (Robin W. Baird and Whitehead 2000; Saulitis et al. 2000). Since these marine mammal prey species have acute underwater hearing, transient killer whales have been observed restricting echolocation during hunting and will produce pulsed calls and whistles mainly during post kill and surface activities for food sharing and communication (Riesch and Deecke 2011).

Offshore ecotypes, termed for their tendency to be found in outer continental shelf waters, are the least understood of the three ecotypes that inhabit the Northeastern Pacific Ocean (Dahlheim et al. 2008). They undertake regional movements from southern California to eastern Alaska and are thought to feed mostly on pelagic fish with a preference for sharks (Dahlheim et al. 2008; John K.B. Ford et al. 2011). Social structure is relatively unknown, but they have been reported to travel in groups ranging from 75 to 100 individuals (Dahlheim et al. 2008) that may represent temporary aggregations. They have been observed to be very vocal, (similar to the residents) producing whistles and pulsed calls for communication as well as echolocation clicks simultaneously while foraging (Dahlheim et al. 2008).

The employment of passive acoustic monitoring (PAM) has proven successful in improving marine mammal data collection. PAM allows for acoustic recording in habitats that are difficult to access, for marine mammal species that are often only visible at the ocean surface.

Echolocation clicks previously have been used to identify odontocete species (Frasier et al. 2017; Roch et al. 2011) using Triton, a MATLAB-based (Mathworks, Natick, MA) acoustic data display and analysis software application (S. M. Wiggins and Hildebrand 2007), along with programs for semi-automatic analysis of parameters such as spectral shape, inter-click interval (ICI), and waveform envelopes.

Several species-specific echolocation click spectral characteristics have been quantified in acoustical data (Frasier et al. 2017; Roch et al. 2011). With some parameters of these spectral shapes of echolocation clicks affected by orientation of the animal producing the pulse to the recording instrument (Ivanov 2004; Au et al. 2012a), and the animals' ability to shift their spectral click content dependent on context (Ivanov 2004; Danuta Maria Wisniewska et al. 2012). However, echolocation clicks' overall spectral shape and peak frequencies have enough differences for discrimination between odontocetes species in acoustic data (Soldevilla et al. 2008).

Inter-click intervals (ICIs), or time intervals between clicks, have been used alongside spectral characteristics in previous studies to differentiate odontocete species echolocation clicks (Frasier et al. 2017). Species tend to have characteristic clicking rates that may vary based on body sizes, group sizes, and distance from the object of interest (Ivanov 2004). It has also been shown that odontocetes change their click rates during different stages of foraging (Danuta Maria Wisniewska et al. 2012; Arranz et al. 2016; Holt et al. 2019; Madsen et al. 2005). Typically, the initial search for prey is predominantly a slower click rate which increases once in pursuit of prey, until the onset of buzzing, immediately preceding prey capture (Danuta Maria Wisniewska et al. 2012; Arranz et al. 2016). Despite this variability, a modal ICI has been observed in many species (Roch et al. 2011; Frasier et al. 2017).

A previous study of killer whales in the Northeastern Pacific (Rice et al. 2017) utilized data from two HARP locations off the coast of Washington and killer whale pulsed call catalogs (J. K.B. Ford 1991; Thomsen, Franck, and Ford 2001; John K B Ford 1989) to identify ecotypes in several years of recorded data, matching each pulsed call acoustic encounter to the repertoire catalog for each ecotype. This study generated a labeled dataset of acoustic encounters for each

of the three ecotypes. From these preexisting labels, we explored echolocation click differences, compiling parameters useful for their distinction in acoustic data.

Methods

i. Data Collection

For this study, acoustic data was collected using High-frequency Acoustic Recording Packages (HARPs) moored to the sea floor with a hydrophone suspended about 20 meters above (S. M. Wiggins and Hildebrand 2007). These HARPs allow for continuous broadband (100 kHz) recording and their data can be analyzed for acoustical presence of marine mammals.

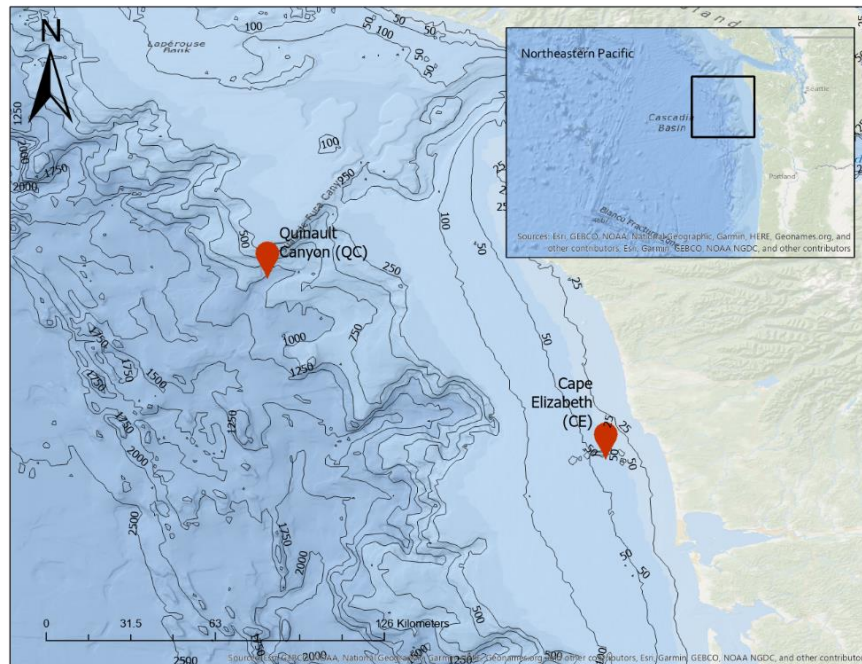


Figure 1. Locations of acoustic recordings sites off Washington state. CE: Cape Elizabeth, and QC: Quinault Canyon.

Acoustic data were collected intermittently from June 2008 to August 2013 at two sites off the coast of Washington state (Figure 1). One recording site was located near Quinault Canyon (QC), 75 km from shore at depths of 1394 m or 1400 m, depending on deployment (Table 1). The other recording site was located on Cape Elizabeth (CE) shelf about 35 km from

shore at a depth of 100 m to 140 m depending on deployment (Table 1). At each site, a single HARP was deployed, with a 16-bit resolution and sampling rate of 200 kHz. All but one deployment collected continuous recordings (CE-08 recorded for 5 minutes every 30 minutes).

Table 1. High-frequency acoustic recording package deployments. Listed as latitude, longitude, depth and time periods of data collection analyzed for this study. Dates given as mm/dd/yy.

Deployment	Lat (N)	Lon (W)	Depth (m)	Data Start	Data End
08 CE	47° 21.48'	124° 41.00'	100	6/17/08	6/9/09
13 CE	47° 21.12'	124° 43.26'	118	5/21/11	11/6/11
14 CE	47° 21.14'	124° 43.28'	150	12/7/11	1/17/12
12 QC	47° 30.00'	125° 21.20'	1400	1/27/11	10/7/11
14 QC	47° 30.03'	125° 21.21'	1394	12/7/11	7/11/12
15 QC	47° 30.03'	125° 21.22'	1394	9/14/12	6/30/13

ii. Data Analysis

Previous work by Rice et al., (2017) identified the presence of resident, transient, and offshore killer whale ecotypes in these data using their pulsed call repertoires. Encounter times and durations were logged when a pulsed call was identified; encounters were considered separate if 15 minutes elapsed without presence of pulsed calls (Rice et al. 2017). This pre-existing record of encounters was used as the starting point of the present analysis, to find periods that contained echolocation signals in addition to the pulsed calls associated with each ecotype (Table 2).

We extracted recordings for each identified encounter containing echolocation clicks, with a 20-minute buffer prior to and following the onset of the first and end of the last pulsed call. Since the transient ecotype is known to restrict echolocation during hunting and to produce pulsed calls primarily as post kill communication (Riesch and Deecke 2011), we collected data up to one hour prior to their pulsed call encounters.

Table 2. Ecotype Encounters. Lists for each ecotype and encounter, the count of encounters per deployment, the average duration of an encounter in hours, and the total encounters and total encounter time per deployment as well as tallied encounter durations for each ecotype.

Deployment	Resident			Transient			Offshore			Totals		
	Encounters (cnt)	Average Encounter Duration (hrs)	Total Encounter Duration (hrs)	Encounters (cnt)	Average Encounter Duration (hrs)	Total Encounter Duration (hrs)	Encounters (cnt)	Average Encounter Duration (hrs)	Total Encounter Duration (hrs)	Encounters (cnt)	Average Encounter Duration (hrs)	Total Encounter Duration (hrs)
08 CE	32	0.042	2.77	42	0.05	3.50	n/a	n/a	n/a	74	n/a	6.27
12 QC	n/a	n/a	n/a	3	0.16	0.48	4	0.55	0.55	7	0.55	1.03
13 CE	8	0.58	4.03	34	0.38	12.63	3	0.94	2.82	45	0.94	19.48
14 CE	n/a	n/a	n/a	10	0.23	2.28	n/a	n/a	n/a	10	n/a	2.28
14 QC	3	0.039	0.12	10	0.46	4.58	4	0.64	2.57	17	0.64	7.27
15 QC	n/a	n/a	n/a	10	0.59	5.90	9	5.42	5.42	19	5.42	11.32
Total per Ecotype	43	0.66	6.92	109	0.31	29.38	20	0.58	11.35	172	0.58	20.13

Signal analysis was performed with custom-written software using MATLAB (MathWorks, Natick, MA) employing *Triton* (S. Wiggins 2003) and three additional tools; a permissive echolocation click detector as described in Frasier et al., (2017), *DetEdit*, a custom-written graphical user-interface for visualization of detections (Solsona-Berga et al. 2020), and a two-phase clustering tool that compiled reoccurring signals as described in Frasier et al., (2017). The click detector was used to search for all signals within the frequency band from 1 - 80 kHz with peak to peak amplitudes of 110 dB or higher. The 1 - 80 kHz band was chosen to exclude low frequency noise as well as higher frequency signals that are outside the range of killer whale echolocation (Au et al. 2004). Detections within 0.02 seconds of each other were excluded to reduce capturing signal reflections, closely overlapping signals from numerous animals, and partial signals from high frequency buzzes, which are described as clicks with a repetition rate less than 10 microseconds (Holt et al. 2019). The minimum peak to peak threshold of 110 kHz was selected to analyze encounters that were close enough to the recorder to capture a large number of nearby clicks without capturing the more distant lower amplitude signals.

Detected signals were analyzed using *DetEdit* (Solsona-Berga et al. 2020) to visualize all signals identified by the click detector. This allowed manual removal of false positives arising from anthropogenic noise, non-target species, and other noise sources. This process produced a subset of manually verified detections to represent each ecotype's echolocation clicks.

A two-step clustering tool designed to identify the most common signal types detected in a data set, as described in Frasier et. al., (2017), was used to find the most common echolocation click features for each ecotype. The clustering process described below was repeated independently for all detections associated with ecotype. In the first phase of the

clustering process, a distance matrix was computed based on spectral shape and waveform, capturing pairwise comparisons of all detections within one-minute time bins across all data for each ecotype. An unsupervised network-based clustering algorithm known as Chinese Whispers (Biemann 2020) was used to identify one or more clusters of clicks with similar spectra within each successive one-minute bin. In the second step, the mean bin-level spectra and ICI of the clusters identified in the first step were clustered again to identify dominant recurring “click types” present across the set of encounters associated with each ecotype. These recurrent types were summarized by calculating mean spectra, ICI distributions, and mean waveform envelopes summarizing important frequency and temporal features. With this information, an echolocation click archetype was constructed for each killer whale ecotype. A minimum of 50 1-minute bins containing clicks with these similar summary features were required to be retained to characterize the click archetype.

Results

Of the 443 encounters reported in Rice et al. 2017, those that were recorded with the 200kHz sampling rate that were not duty cycled were chosen for consistency and accuracy in comparing spectral parameters across deployments, (Table 1). Of the encounters examined, only those echolocation clicks with high enough quality to be retained by the two-phase classifier were used to calculate an archetype, (Table 3). An individual echolocation archetype was defined for each of the three ecotypes and all statistics were calculated using bin level averages that contributed to each archetype.

Table 3. Ecotype click parameters including, number of bins used in each archetype; number of clicks used to make each archetype; number of encounters that generated a click for each archetype; mean peak frequency of the archetype; standard deviation of the mean peak frequency; means of the modal inter click interval of each bin from 0.01s; and standard deviation mean of the modal inter click interval.

	Resident		Transient	Offshore
Bins present in archetype	299		94	273
Clicks present in archetype	15197		1044	25049
Encounters present in archetype	14		12	11
Peak Frequencies (kHz)	13.45	17.40	13.78	13.66
St Dev Peak Frequencies (kHz)	± 1.7	± 1.7	± 4.24	± 2.42
Modal ICI (s)	0.22 ± 0.07		NA	0.36 ± 0.14

Residents had the largest number of one-minute bins with good quality echolocation clicks at 299, while the transients had the least at 94. The offshore ecotype however, produced the most echolocation clicks overall which is reflected in Table 3 even though their encounters and time bins of 273 were similar to residents. The offshore ecotype had 273 one-minute bins over 11 encounters that were retained (similar to residents) but with 25,049 clicks in the archetype which is about 40% higher than that of the other ecotypes with similar number encounters (Table 3). Conversely, the transient ecotype had 1,044 echolocation clicks, about 5% of the averages of the offshore and resident ecotype's echolocation clicks but from a similar number of encounters, (Table 3).

The click archetypes identified for each killer whale ecotype had similar mean spectra with small differences in the overall shape and peak frequencies. Each ecotype's spectra were characterized by an energy peak, with the peak of energies in frequencies below 20 kHz (Figure 2A, 3A, 4A). The two ecotypes that commonly produce clicks (residents and offshores), had clear modal peaks in their ICI, whereas the transient ecotype showed no distinguishable pattern in ICI (Table 3).

i. Resident

Encounters of resident killer whales in our study had a mean duration of 0.66 hours (Table 2) with high concentrations of echolocation. The click archetype for residents was constructed with 15,197 clicks from 299 one-minute time bins spanning 14 encounters over 3 deployments (Table 3). Resident encounters were primarily recorded at the shallow site (CE),

which accounted for 95% of the total encounter duration and 90% of the 15,197 clicks used to generate their archetype.

The click peak energy was concentrated below 20 kHz, (Figure 2A and B). The mean spectrum consists of a broad energy peak with a ± 3 dB bandwidth spanning between 11.5 kHz to 22 kHz and two sub-peaks; the first with a mean frequency of 13.5 ± 1.7 kHz and the second with a mean frequency at 17.5 ± 1.7 kHz (Figure 2A), resulting in a dip in normalized amplitude, centered around 16 kHz.

Resident ecotype echolocation has a clear modal ICI of 0.22 ± 0.07 seconds, (Figure 2C), seen across most time bins and encounters (Figure 2D).

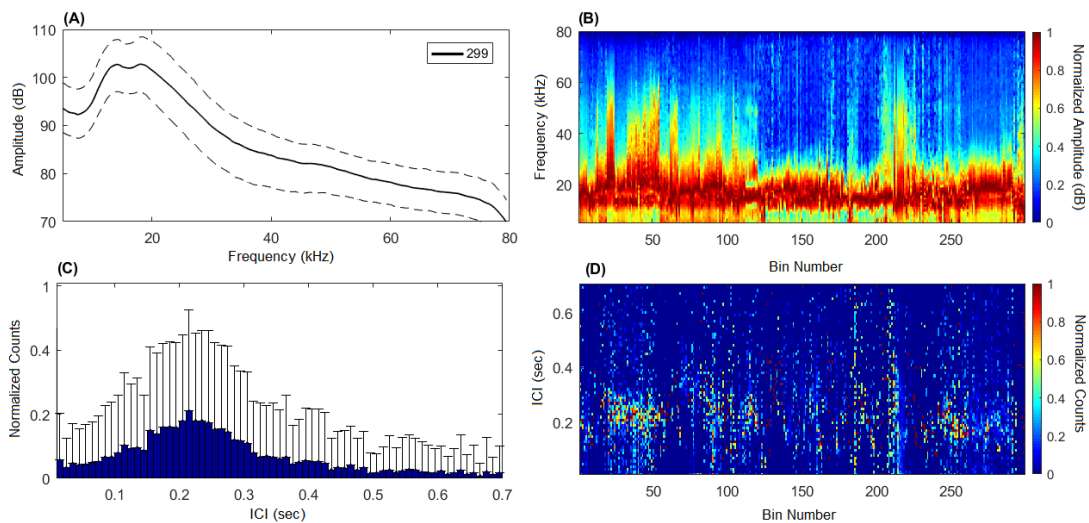


Figure 2. Resident click archetype: (A) mean spectrum (solid line) with 25th and 75th percentiles (dashed lines). (B) Concatenated mean spectra for each 1-minute time bin. (C) Histogram of ICI with error bars indicating the standard deviation across bin number for each ICI 0.01 second range. (D) ICIGram showing ICIs across time bins with the maximum value in each bin number normalized to 1 to remove the effects of total detection counts.

ii. Transient

Although more encounters (109) were analyzed for the transient ecotype than for the other ecotypes (Table 2), the results retained the least number of echolocation clicks (Table 3).

Transient encounters had a mean duration of 0.31 hours. Their click archetype is made up of

1,044 clicks from 94 one-minute time bins spanning 12 encounters over 6 deployments (Table 3). We found that 66% of transient echolocation clicks used to make the archetype were recorded at the shallow site (CE) and 34% were recorded at the deeper site (QC). The mean spectrum has a broad energy peak with an ± 3 dB bandwidth spanning from 8 kHz to 19 kHz and a mean peak frequency centered at 13.78 ± 4.24 kHz (Figure 3A).

No distinguishable modal ICI was seen for the transient ecotype (Figure 3C). The lack of a distinct modal ICI is also apparent across time bins and encounters (Figure 3D).

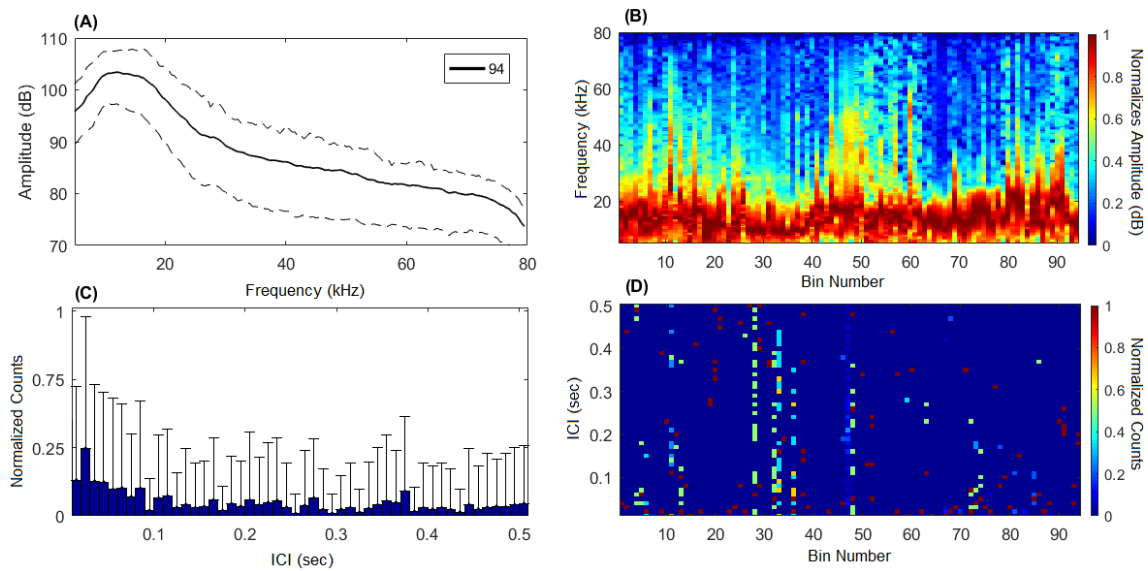


Figure 3. Transient click archetype : (A) mean spectrum (solid line) with 25th and 75th percentiles (dashed lines). (B) Concatenated mean spectra for each 1-minute time bin. (C) Histogram of ICI with error bars indicating the standard deviation across bin number for each ICI 0.01 second range. (D) ICIgram showing ICIs across time bins with the maximum value in each bin number normalized to 1 to remove the effects of total detection counts.

iii. Offshore

We examined fewer encounters of the offshore ecotype (20); however, encounters were typically longer in duration with a mean of 0.58 hours (Table 2) and contributed a higher number of echolocation clicks per time bin analyzed. The archetype is a composite of 25,049 clicks from 273 one-minute time bins spanning 11 encounters from 4 deployments (Table 3). We found that 100% of time bins used in the offshore echolocation archetype were from the deep recording site (QC). The mean spectrum has a band of peak energy with an ± 3 dB bandwidth 10 kHz to 18 kHz and a mean peak frequency of 13.66 ± 2.42 kHz (Figure 4A). There are distinguishable ICI patterns mean of the modal ICI's of 0.36 ± 0.14 seconds (Figure 4C) with the value and strength of the ICI mode varied somewhat between encounters (Figure 4D).

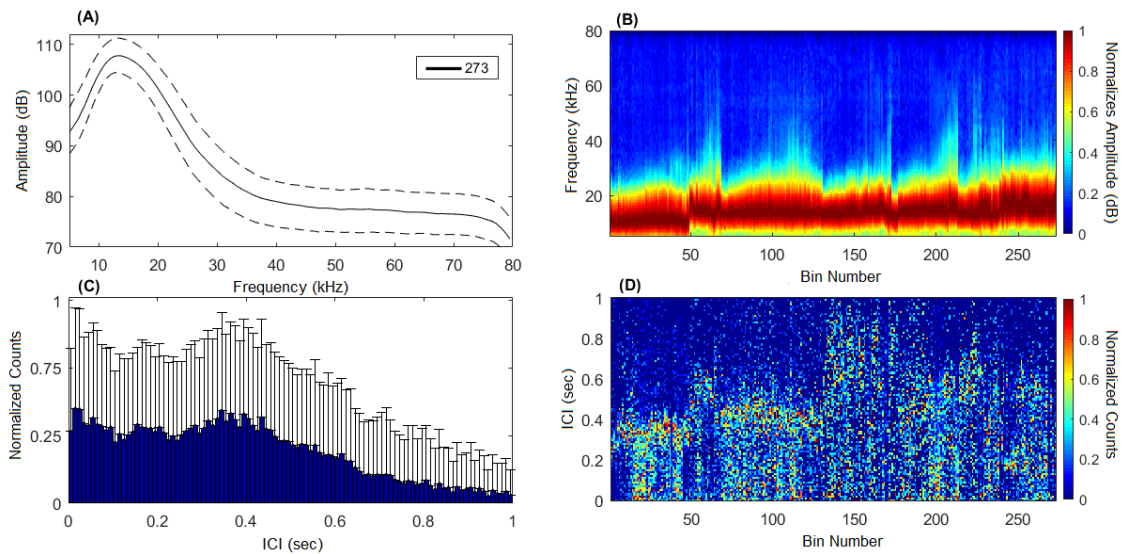


Figure 4. Offshore click archetype : (A) mean spectrum (solid line) with 25th and 75th percentiles (dashed lines). (B) Concatenated mean spectra for each 1-minute time bin. (C) Histogram of ICI with error bars indicating the standard deviation across bin number for each ICI 0.01 second range. (D) ICIgram showing ICIs across time bins with the maximum value in each bin number normalized to 1 to remove the effects of total detection counts.

Discussion

i. Resident Archetype

Our findings align with previous studies of resident killer whales which have documented their highly vocal foraging (Heimlich-Boran 1988; Holt et al. 2019; Au et al. 2004). Au et al. (2004) recorded resident killer whales using near-surface echolocation signals received on-axis. Their findings show a similar spectral shape, with frequency peaks ranging between 20 kHz to 60 kHz, higher than identified in this study (13.5 ± 1.7 kHz and 17.5 ± 1.7 kHz), (Figure 2A). These differences in peak frequencies are likely attributable to the variable click arrival angles in our data. For Au et al. (2004), recordings were taken near the sea surface (1.2 m to 1.5 m) and positioned 150 m to 200 m directly ahead of vocalizing individual animals and clicks were selected for analysis with on-axis echolocation receive. In the present study, hydrophones are positioned on the seafloor at depths of either 100-140 or 1400 m with no control on orientation of the animals relative to the recording hydrophone. Since echolocation is

highly focused energy, attenuation for signals received off-axis from the direct front of the animal's head would lower the peak frequencies as seen in previous studies (Au et al. 2012b).

Holt et al. (2019) show that residents foraging on salmon do so in waters ranging from 10-100 m depths, where salmon are abundant (Candy and Quinn 1999). They describe an ICI of >100ms as the most abundantly used click rate at surface depths and up to 200 m (Holt et al. 2019). Our modal inter-click interval of 0.22 ± 0.07 seconds is comparable to these findings in similar depths for resident killer whales.

ii. Transient Archetype

Although more encounters were analyzed for transients than for other ecotypes (Table 1), these encounters yield fewer echolocation clicks, presumably because of the transient ecotype's foraging strategies. Studies have documented transients restricting the use of echolocation as a hunting strategy since their prey have acute underwater hearing (Deecke, Ford, and Slater 2005), and producing clicks that are less distinguishable from background sound levels by lowering amplitude and generating space irregular clicks (Barrett-Lennard, Ford, and Heise 1996). This strategy of blending echolocation clicks with background noise levels may have caused a lower number of detections, which contribute to a low sample size, which is reflected in the 25th and 75th percentiles seen in the mean spectrum (Figure 3A).

It is presumed that the transient ecotype use randomly spaced, sparse and lower amplitude echolocation signals because it is less likely for a prey species to recognize (Barrett-Lennard, Ford, and Heise 1996). This strategy may explain the lack of click trains and clear ICI seen in our findings. These types of echolocation clicks may have been missed during the detection process by capturing partial, or possible, whole click trains.

iii. Offshore Archetype

Analysis of offshore killer whales' echolocation revealed robust spectral shape and a somewhat ambiguous modal ICI. Low variability in the spectral shape (Figure 4A), is most likely attributable to the larger sample size for this ecotype and overall strong similarity of clicks. Since these clicks are all from the deeper site (QC), it is also likely that there is greater attenuation in frequencies above 40 kHz.

Some bins throughout the concatenated spectra (Figure 4B, bins 1 - 50 and 170- 175) show a lower peak frequency with a mean of $12.7 \text{ kHz} \pm 1.5 \text{ kHz}$, compared to the remainder of the concatenated spectra that had a mean peak of $14.3 \text{ kHz} \pm 1.4 \text{ kHz}$. Since these different peaked signals were not all generated from the same encounters, these distinctions may be due to differences among offshore pods and is worthy of further investigation. These different spectral peaks also attribute to the higher peak frequency standard deviation ($\pm 2.4 \text{ kHz}$) for the offshore archetype, (Figure 4A).

Offshore ecotype ICI distribution has an ambiguous modal mean of 0.36 ± 0.14 seconds (Figure 4C). Their overall larger group sizes likely contribute to this ambiguity, as it is difficult to identify click trains from a single animal, leading to saturation in the lower ICI values with multiple animals echolocating simultaneously. Several studies have shown that the ICIs of other odontocetes are highly variable depending on behavior and distance from target (Holt et al. 2019; Danuta M. Wisniewska et al. 2014; Arranz et al. 2016). However, modal ICI is often a reliable characteristic feature of species in offshore environments (Roch et al. 2011; Frasier et al. 2017). Our results show that there are distinct modal ICIs visible within about half of the individual encounters (Figure 4D), which do not correlate with the lower peak frequencies. This variability could be attributed to differences in behavior, foraging depths, target prey, or other unknown factors such as different pod groups.

iv. Common Attributes

The spectral bandwidth of echolocation clicks for each archetype may be reduced with distance from the recording instrument, due to the attenuation of higher frequency content with distance. Peak frequencies may also differ from those reported in near surface studies due to the position of the recording instrument on the seafloor and the inclusion of all detected clicks. Low amplitude, highly off-axis clicks are less likely to be detected on the seafloor systems because the distances between the animals and the sensor are large, therefore we expect that most received signals are near on-axis, but with some angle variability.

The number of clicks detected per unit time varied between the three ecotypes, and this likely represents some combination of differences in group size, cue production rate, and vocalization probability. Ecotype-specific estimates of cue rate parameters could be used to estimate acoustic group sizes and densities of the respective ecotypes at each monitoring location (Frasier et al., 2016; Hildebrand et al., 2015).

Our results show that when averages of clicks are considered across encounters, the differences between ecotypes are consistent enough across multiple detections to support ecotype level click classification for both residents and offshore, using methods such as deep neural nets. In cases where these ecotypes echolocate without accompanying pulsed calls, it may be possible to use this classification system to more efficiently determine ecotype presence.

Conclusions

Differences in echolocation click features for three Northeast Pacific killer whale ecotypes may allow for efficient ecotype identification in long-term acoustic data. While it seems feasible to discriminate between the echolocation clicks of residents and offshores, based on differences in their spectral characteristics and ICIs, identification using echolocation may be more difficult for transients due to the low numbers of clicks typically captured in passive

acoustic data. However, the results of this analysis reveal the potential to classify encounters of killer whale ecotypes in acoustic data where animals are using echolocation alone. By developing efficient acoustic classifiers using click archetypes, it will be possible to more efficiently document the occurrence of these ecotypes in autonomously collected passive acoustic data and aid in effective monitoring efforts.

Bibliography

- Arranz, P., S. L. DeRuiter, A. K. Stimpert, S. Neves, A. S. Friedlaender, J. A. Goldbogen, F. Visser, J. Calambokidis, B. L. Southall, and P. L. Tyack. 2016. "Discrimination of Fast Click-Series Produced by Tagged Risso's Dolphins (*Grampus Griseus*) for Echolocation or Communication." *Journal of Experimental Biology* 219 (18): 2898–2907. <https://doi.org/10.1242/jeb.144295>.
- Au, Whitlow W. L., Brian Branstetter, Patrick W. Moore, and James J. Finneran. 2012a. "The Biosonar Field around an Atlantic Bottlenose Dolphin (*Tursiops Truncatus*)." *The Journal of the Acoustical Society of America* 131 (1): 569–76. <https://doi.org/10.1121/1.3662077>.
- . 2012b. "Dolphin Biosonar Signals Measured at Extreme Off-Axis Angles: Insights to Sound Propagation in the Head." *The Journal of the Acoustical Society of America* 132 (2): 1199–1206. <https://doi.org/10.1121/1.4730901>.
- Au, Whitlow W. L., John K. B. Ford, John K. Horne, and Kelly A. Newman Allman. 2004. "Echolocation Signals of Free-Ranging Killer Whales (*Orcinus Orca*) and Modeling of Foraging for Chinook Salmon (*Oncorhynchus Tshawytscha*)." *The Journal of the Acoustical Society of America* 115 (2): 901–9. <https://doi.org/10.1121/1.1642628>.
- Baird, R. W., and L. M. Dill. 1995. "Occurrence and Behaviour of Transient Killer Whales: Seasonal and Pod-Specific Variability, Foraging Behaviour, and Prey Handling." *Canadian Journal of Zoology* 73 (7): 1300–1311. <https://doi.org/10.1139/z95-154>.
- Baird, Robin W., and Lawrence M. Dill. 1996. "Ecological and Social Determinants of Group Size in Transient Killer Whales." *Behavioral Ecology* 7 (4): 408–16. <https://doi.org/10.1093/beheco/7.4.408>.
- Baird, Robin W., and Hal Whitehead. 2000. "Social Organization of Mammal-Eating Killer Whales: Group Stability and Dispersal Patterns." *Canadian Journal of Zoology* 78 (12): 2096–2105. <https://doi.org/10.1139/cjz-78-12-2096>.
- Barrett-Lennard, Lance G. 2000. "Population Structure and Mating Patterns of Killer Whales." University of British Columbia.
- Barrett-Lennard, Lance G., John K.B. Ford, and Kathy A. Heise. 1996. "The Mixed Blessing of Echolocation: Differences in Sonar Use by Fish-Eating and Mammal-Eating Killer Whales." *Animal Behaviour* 51 (3): 553–65. <https://doi.org/10.1006/anbe.1996.0059>.
- Biemann, Chris. 2020. "Chinese Whispers - An Efficient Graph Clustering Algorithm and Its Application to Natural Language Processing Problems." *Proceedings of TextGraphs: The 1st Workshop on Graph-Based Methods for Natural Language Processing*, 73–80.
- Bigg, M. A., P. F. Olesiuk, G. M. Ellis, J. K.B. Ford, and K. C. Balcomb. 1990. "Social Organization and Genealogy of Resident Killer Whales (*Orcinus Orca*) in the Coastal Waters of British Columbia and Washington State." *Report - International Whaling*

Commission, Special Issue 12 (12): 383–405.

- Bigg, M. 1982. “An Assessment of Killer Whale (*Orcinus Orca*) Stocks off Vancouver Island, British Columbia.” *Report of the International Whaling Commission* 36: 655–66.
[http://scholar.google.es/scholar?hl=en&q=An+assessment+of+killer+whale+\(Orcinus+orca\)+stocks+off+Vancouver+Island,+British+Columbia&btnG=&as_sdt=1,5&as_sdtp=#0](http://scholar.google.es/scholar?hl=en&q=An+assessment+of+killer+whale+(Orcinus+orca)+stocks+off+Vancouver+Island,+British+Columbia&btnG=&as_sdt=1,5&as_sdtp=#0).
- Dahlheim, Marilyn E., Alisa Schulman-Janiger, Nancy Black, Richard Ternullo, Dave Ellifrit, and Kenneth C. Balcomb. 2008. “Eastern Temperate North Pacific Offshore Killer Whales (*Orcinus Orca*): Occurrence, Movements, and Insights into Feeding Ecology.” *Marine Mammal Science* 24 (3): 719–29. <https://doi.org/10.1111/j.1748-7692.2008.00206.x>.
- Deecke, Volker B., John K.B. Ford, and Peter J.B. Slater. 2005. “The Vocal Behaviour of Mammal-Eating Killer Whales: Communicating with Costly Calls.” *Animal Behaviour* 69 (2): 395–405. <https://doi.org/10.1016/j.anbehav.2004.04.014>.
- Ford, J. K.B. 1991. “Vocal Traditions among Resident Killer Whales (*Orcinus Orca*) in Coastal Waters of British Columbia.” *Canadian Journal of Zoology* 69 (6): 1454–83.
<https://doi.org/10.1139/z91-206>.
- Ford, John K.B., and Graeme M. Ellis. 2006. “Selective Foraging by Fish-Eating Killer Whales *Orcinus Orca* in British Columbia.” *Marine Ecology Progress Series* 316: 185–99.
<https://doi.org/10.3354/meps316185>.
- Ford, John K.B., Graeme M. Ellis, Lance G. Barrett-Lennard, Alexandra B. Morton, Rod S. Palm, and Kenneth C. Balcomb. 1998. “Dietary Specialization in Two Sympatric Populations of Killer Whales (*Orcinus Orca*) in Coastal British Columbia and Adjacent Waters.” *Canadian Journal of Zoology* 76 (8): 1456–71. <https://doi.org/10.1139/z98-089>.
- Ford, John K.B., Graeme M. Ellis, Craig O. Matkin, Michael H. Wetklo, Lance G. Barrett-Lennard, and Ruth E. Withler. 2011. “Shark Predation and Tooth Wear in a Population of Northeastern Pacific Killer Whales.” *Aquatic Biology* 11 (3): 213–24.
<https://doi.org/10.3354/ab00307>.
- Ford, John K B. 1989. “Acoustic Behaviour of Resident Killer Whales (*Orcinus Orca*) off Vancouver Island, British Columbia.” *Canadian Journal of Zoology* 67: 727–45.
<http://www.eonet.ne.jp/~skado/book1/BCcg-RISKv3sheet.pdf>.
- Frasier, Kaitlin E, Marie A Roch, Melissa S Soldevilla, Sean M Wiggins, Lance P. Garrison, and John A Hildebrand. 2017. “Automated Classification of Dolphin Echolocation Click Types from the Gulf of Mexico.” *PLoS Computational Biology* 13 (12): 1–23.
<https://doi.org/10.1371/journal.pcbi.1005823>.
- Heimlich-Boran, J. R. 1988. “Behavioral Ecology of Killer Whales (*Orcinus Orca*) in the Pacific Northwest.” *Canadian Journal of Zoology* 66 (3): 565–78.
<https://doi.org/10.1139/z88-084>.
- Hoelzel, A. R., M. Dahlheim, and S. J. Stern. 1998. “Low Genetic Variation among Killer Whales (*Orcinus Orca*) in the Eastern North Pacific and Genetic Differentiation between

- Foraging Specialists.” *Journal of Heredity* 89 (2): 121–28.
<https://doi.org/10.1093/jhered/89.2.121>.
- Hoelzel, A. Rus, and Gabriel A. Dover. 1991. “Genetic Differentiation between Sympatric Killer Whale Populations.” *Heredity* 66 (2): 191–95. <https://doi.org/10.1038/hdy.1991.24>.
- Holt, Marla M., M. Bradley Hanson, Candice K. Emmons, David K. Haas, Deborah A. Giles, and Jeffrey T. Hogan. 2019. “Sounds Associated with Foraging and Prey Capture in Individual Fish-Eating Killer Whales, *Orcinus Orca*.” *The Journal of the Acoustical Society of America* 146 (5): 3475–86. <https://doi.org/10.1121/1.5133388>.
- Ivanov, M. P. 2004. “Dolphin’s Echolocation Signals in a Complicated Acoustic Environment.” *Akusticheskij Zhurnal* 50 (4): 550–62. <https://doi.org/10.1134/1.1776226>.
- Krahn, Margaret M., Michael J. Ford, William F. Perrin, Paul R. Wade, Robyn R. Angliss, M. Bradley Hanson, Barbara L. Taylor, Gina M. Ylitalo, Marilyn E. Dahlheim, John E. Stein and Robin S. Waples. 2004. *2004 Status Review of Southern Resident Killer Whales (Orcinus Orca) under the Endangered Species Act. NOAA Technical Memorandum NMFS*.
- Madsen, P. T., M. Johnson, N. Aguilar De Soto, W. M.X. Zimmer, and P. Tyack. 2005. “Biosonar Performance of Foraging Beaked Whales (*Mesoplodon Densirostris*).” *Journal of Experimental Biology* 208 (2): 181–94. <https://doi.org/10.1242/jeb.01327>.
- Miller, Patric J.O., A. D. Shapiro, P. L. Tyack, and A. R. Solow. 2004. “Call-Type Matching in Vocal Exchanges of Free-Ranging Resident Killer Whales, *Orcinus Orca*.” *Animal Behaviour* 67 (6): 1099–1107. <https://doi.org/10.1016/j.anbehav.2003.06.017>.
- Morin, Phillip A., Frederick I. Archer, Andrew D. Foote, Julia Vilstrup, Eric E. Allen, Paul Wade, John Durban, Robert Pitman, Lewyn Li, Pascal Bouffard, Sandra C. Abel Nielsen, Morten Rasmussen, Eske Willerslev, M. Thomas P. Gilbert, and Timothy Harkins. 2010. “Complete Mitochondrial Genome Phylogeographic Analysis of Killer Whales (*Orcinus Orca*) Indicates Multiple Species.” *Genome Research* 20 (7): 908–16.
<https://doi.org/10.1101/gr.102954.109>.
- Nichol, L. M., and D. M. Shackleton. 1996. “Seasonal Movements and Foraging Behaviour of Northern Resident Killer Whales (*Orcinus Orca*) in Relation to the Inshore Distribution of Salmon (*Oncorhynchus Spp.*) in British Columbia.” *Canadian Journal of Zoology* 74 (6): 983–91. <https://doi.org/10.1139/z96-111>.
- Parsons, K. M., K. C. Balcomb, J. K.B. Ford, and J. W. Durban. 2009. “The Social Dynamics of Southern Resident Killer Whales and Conservation Implications for This Endangered Population.” *Animal Behaviour* 77 (4): 963–71.
<https://doi.org/10.1016/j.anbehav.2009.01.018>.
- Rice, Ally, Volker B. Deecke, John K.B. Ford, James F. Pilkington, Erin M. Oleson, John A. Hildebrand, and Ana Širović. 2017. “Spatial and Temporal Occurrence of Killer Whale Ecotypes off the Outer Coast of Washington State, USA.” *Marine Ecology Progress*

- Series 572*: 255–68. <https://doi.org/10.3354/meps12158>.
- Riesch, Rüdiger, and Volker B Deecke. 2011. “Whistle Communication in Mammal-Eating Killer Whales (*Orcinus Orca*): Further Evidence for Acoustic Divergence between Ecotypes.” *Behavioral Ecology and Sociobiology* 65 (7): 1377–87. <https://doi.org/10.1007/s00265-011-1148-8>.
- Roch, Marie A., Holger Klinck, Simone Baumann-Pickering, David K. Mellinger, Simon Qui, Melissa S. Soldevilla, and John A. Hildebrand. 2011. “Classification of Echolocation Clicks from *Odontocetes* in the Southern California Bight.” *The Journal of the Acoustical Society of America* 129 (1): 467–75. <https://doi.org/10.1121/1.3514383>.
- Samarra, Filipa I. P., Volker B. Deecke, Katja Vinding, Marianne H. Rasmussen, René J. Swift, and Patrick J. O. Miller. 2010. “Killer Whales (*Orcinus Orca*) Produce Ultrasonic Whistles.” *The Journal of the Acoustical Society of America* 128 (5): EL205–10. <https://doi.org/10.1121/1.3462235>.
- Saulitis, Eva, Craig Matkin, Lance Barrett-Lennard, Kathy Heise, and Graeme Ellis. 2000. “Foraging Strategies of Sympatric Killer Whale (*Orcinus Orca*) Populations in Prince William Sound, Alaska.” *Marine Mammal Science* 16 (1): 94–109. <https://doi.org/10.1111/j.1748-7692.2000.tb00906.x>.
- Simonis, Anne E., Simone Baumann-Pickering, Erin Oleson, Mariana L. Melcón, Martin Gassmann, Sean M. Wiggins, and John A. Hildebrand. 2012. “High-Frequency Modulated Signals of Killer Whales (*Orcinus Orca*) in the North Pacific.” *The Journal of the Acoustical Society of America* 131 (4): EL295–301. <https://doi.org/10.1121/1.3690963>.
- Soldevilla, Melissa S., E. Elizabeth Henderson, Gregory S. Campbell, Sean M. Wiggins, John A. Hildebrand, and Marie A. Roch. 2008. “Classification of Risso’s and Pacific White-Sided Dolphins Using Spectral Properties of Echolocation Clicks.” *The Journal of the Acoustical Society of America* 124 (1): 609–24. <https://doi.org/10.1121/1.2932059>.
- Solsona-Berga, Alba, Kaitlin E. Frasier, Simone Baumann-Pickering, Sean M. Wiggins, and John A. Hildebrand. 2020. “Detedit: A Graphical User Interface for Annotating and Editing Events Detected in Long-Term Acoustic Monitoring Data.” *PLoS Computational Biology* 16 (1): 1–10. <https://doi.org/10.1371/journal.pcbi.1007598>.
- Steiner, William W., James H. Hain, Howard E. Winn, and Paul J. Perkins. 1979. “Vocalizations and Feeding Behavior of the Killer Whale (*Orcinus Orca*).” *American Society of Mammalogists* 60 (4): 823–27.
- Thomsen, F., D. Franck, and J. K. B. Ford. 2001. “Characteristics of Whistles from the Acoustic Repertoire of Resident Killer Whales (*Orcinus Orca*) off Vancouver Island, British Columbia.” *The Journal of the Acoustical Society of America* 109 (3): 1240–46. <https://doi.org/10.1121/1.1349537>.
- Wiggins, Sean. 2003. “Autonomous Acoustic Recording Packages (ARPs) for Long-Term Monitoring of Whale Sounds.” *Marine Technology Society Journal* 37 (2): 13–22.

<https://doi.org/10.4031/002533203787537375>.

Wiggins, Sean M., and John A. Hildebrand. 2007. "High-Frequency Acoustic Recording Package (HARP) for Broad-Band, Long-Term Marine Mammal Monitoring." *International Symposium on Underwater Technology, UT 2007 - International Workshop on Scientific Use of Submarine Cables and Related Technologies 2007*, 551–57. <https://doi.org/10.1109/UT.2007.370760>.

Wiles, Gary J. 2016. "Periodic Status Review for the Killer Whale in Washington." Olympia.

Wisniewska, Danuta M., Mark Johnson, Paul E. Nachtigall, and Peter T. Madsen. 2014. "Buzzing during Biosonar-Based Interception of Prey in the Delphinids *Tursiops Truncatus* and *Pseudorca Crassidens*." *Journal of Experimental Biology* 217 (24): 4279–82. <https://doi.org/10.1242/jeb.113415>.

Wisniewska, Danuta Maria, Mark Johnson, Kristian Beedholm, Magnus Wahlberg, and Peter Teglberg Madsen. 2012. "Acoustic Gaze Adjustments during Active Target Selection in Echolocating Porpoises." *Journal of Experimental Biology* 215 (24): 4358–73. <https://doi.org/10.1242/jeb.074013>.