

# Echolocation click discrimination for three killer whale ecotypes in the Northeastern Pacific

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## ABSTRACT:

Three killer whale ecotypes are found in the Northeastern Pacific: residents, transients, and offshores. These ecotypes can be discriminated in passive acoustic data based on distinct pulsed call repertoires. Killer whale acoustic encounters for which ecotypes were assigned based on pulsed call matching were used to characterize the ecotype-specific echolocation clicks. Recordings were made using seafloor-mounted sensors at shallow (~120 m) and deep (~1400 m) monitoring locations off the coast of Washington state. All ecotypes' echolocation clicks were characterized by energy peaks between 12 and 19 kHz, however, resident clicks featured sub peaks at 13.7 and 18.8 kHz, while offshore clicks had a single peak at 14.3 kHz. Transient clicks were rare and were characterized by lower peak frequencies (12.8 kHz). Modal inter-click intervals (ICIs) were consistent but indistinguishable for resident and offshore killer whale encounters at the shallow site (0.21–0.22 s). Offshore ICIs were longer and more variable at the deep site, and no modal ICI was apparent for the transient ecotype. Resident and offshore killer whale ecotype may be identified and distinguished in large passive acoustic datasets based on properties of their echolocation clicks, however, transient echolocation may be unsuitable in isolation as a cue for monitoring applications. © 2022 Author(s). All article content, except where otherwise noted, is licensed under a Creative Commons Attribution (CC BY) license (<http://creativecommons.org/licenses/by/4.0/>). <https://doi.org/10.1121/10.0010450>

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## I. INTRODUCTION

In the Northeastern Pacific Ocean, several populations of killer whales (*Orcinus orca*) inhabit overlapping ranges from the Aleutian Islands to Southern California (Ford, 1989; Hoelzel and Dover, 1991; Steiner *et al.*, 1979). Each of these populations belongs to one of three ecotypes that are genetically, behaviorally, and morphologically distinct (Dahlheim *et al.*, 2008; Deecke *et al.*, 2005; Ford, 1991; Hoelzel *et al.*, 1998; Morin *et al.*, 2010): residents, transients (also known as Bigg's killer whales), and offshores. Although these ecotypes inhabit many of the same areas, they are rarely observed together, and some observations indicate they may actively avoid each other (Baird and Dill, 1995).

Killer whales play an important ecological role as top predators, but face threats from oil spills, the biomagnification of organic pollutants, vessel disturbance and noise, and the depletion of prey species from anthropogenic causes, such as overfishing and dams (Krahn *et al.*, 2004). Because each killer whale ecotype has unique prey preferences, habitat use, and behaviors, they each occupy separate ecological niches, and therefore these threats have the potential to affect each ecotype in different ways.

Killer whales use three types of acoustic signals for orientation, navigation, communication, and prey acquisition: whistles, pulsed calls, and echolocation clicks (Ford, 1989; Holt *et al.*, 2013; Simonis *et al.*, 2012; Thomsen *et al.*, 2001).

Whistles, which can be low frequency or ultrasonic, are primarily used for short range communication within pods and family groups (Samarra *et al.*, 2010; Simonis *et al.*, 2012). Similarly, pulsed calls are thought to function in group recognition and cohesion (Ford, 1989; Miller *et al.*, 2004); several studies have assembled catalogs of pulsed calls unique among populations of each ecotype (Barrett-Lennard *et al.*, 1996; Deecke *et al.*, 2005; Ford, 1991). Echolocation clicks are used primarily for foraging and spatial awareness (Au, 2004). They are 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 differences in prey and habitat preferences may influence how and when echolocation occurs.

Residents are the most studied killer whale ecotype in the Northeast Pacific. Offshore of Washington, the resident ecotype is observed relatively close to shore, and consists of two populations: northern residents and southern residents. Residents live in stable matrilineal social groups ranging from 5 to 50 individuals which feed primarily on Chinook salmon (*Oncorhynchus tshawytscha*) (Au, 2004; Ford *et al.*, 1998; Ford and Ellis, 2006; Nichol and Shackleton, 1996; Parsons *et al.*, 2009). These salmon are known to have poor hearing abilities, therefore, there is little cost to residents being highly vocal while foraging (Ford and Ellis, 2006).

The transient ecotype is found throughout the Northeast Pacific and is commonly studied from Alaska to Washington (Baird and Dill, 1996; Ford *et al.*, 1998). The population

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found offshore of Washington is known as the West Coast transients (Bigg, 1982; Wiles, 2016). Like residents, the transient ecotype also has a matrilineal social structure, but with group sizes ranging from 1 to 15 individuals (Baird and Dill, 1995). Additionally, they are observed to have more range dispersal from the matriline and are commonly seen hunting in groups of three individuals (Baird and Whitehead, 2000; Ford *et al.*, 1998). They prey predominantly on marine mammals which include smaller delphinids in coastal and deep waters and pinnipeds along coastal habitats (Baird and Whitehead, 2000; Barrett-Lennard *et al.*, 1996; Deecke *et al.*, 2005; Ford *et al.*, 1998; Saulitis *et al.*, 2000). Since marine mammal prey have acute underwater hearing, transient killer whales have been observed restricting echolocation during hunting and will produce pulsed calls and whistles mainly after a kill and during surface activities for food sharing and communication (Barrett-Lennard *et al.*, 1996; Riesch and Deecke, 2011).

The offshore ecotype, named for its tendency to be found in outer continental shelf waters, is the least understood of the three ecotypes that inhabit the Northeastern Pacific Ocean (Dahlheim *et al.*, 2008). Offshores 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; Ford *et al.*, 2011). Although their social structure is relatively unknown, they have been reported to travel in groups ranging from only a few to hundreds of individuals (Dahlheim *et al.*, 2008; Gassmann *et al.*, 2013) 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).

Passive acoustic monitoring (PAM) has expanded opportunities for marine mammal observation, by facilitating monitoring in inaccessible habitats and over long time periods (Sousa-Lima *et al.*, 2013). However, this approach relies on knowledge of distinct acoustic characteristics of certain marine mammal vocalizations from which identity may be inferred. It has been possible to identify some odontocete species in PAM datasets by quantifying species-specific echolocation click spectral characteristics (Frasier *et al.*, 2017; Roch *et al.*, 2011). However, echolocation click spectra are also affected by environmental factors such as orientation, distance to the recording instrument (Au *et al.*, 2012; Ivanov, 2004), and animals' apparent ability to shift their spectral click content (Ivanov, 2004; Wisniewska *et al.*, 2012).

Inter-click intervals (ICIs), or time intervals between clicks, have been used alongside spectral characteristics in previous studies to differentiate echolocation clicks of odontocete species (Frasier *et al.*, 2017). Species tend to have characteristic clicking rates that vary based on body size, group size, and distance from the object of interest (Ivanov, 2004). However, it has also been shown that odontocetes change their click rates during different stages of foraging (Aguilar de Soto *et al.*, 2012; Holt *et al.*, 2019; Madsen *et al.*, 2005; Wisniewska *et al.*, 2012). Typically, a slower

click rate is used during the initial search for prey and click rate increases once in pursuit of prey, until the onset of buzzing, immediately preceding prey capture (Arranz *et al.*, 2016; Wisniewska *et al.*, 2012). A modal ICI, likely associated with the search phase (Holt *et al.*, 2019), has been observed in many species and may be a useful feature for classification (Baumann-Pickering *et al.*, 2014; Frasier *et al.*, 2017).

A previous study of killer whales in the Northeastern Pacific (Rice *et al.*, 2017) used several years of data recorded offshore of Washington State to identify ecotypes by matching acoustic encounters containing pulsed calls to call catalogs (Deecke *et al.*, 2005; Ford, 1989, 1991). Using preexisting labels of ecotype encounters from Rice *et al.* (2017), the aim of this study was to determine if ecotype discrimination is possible using echolocation clicks. Establishing click parameters for each ecotype will allow efficient, automatic detection of these ecotypes in order to more effectively manage killer whale populations.

## II. METHODS

### A. Data collection

Acoustic data were collected using high-frequency acoustic recording packages (HARPs) moored to the sea floor with a hydrophone suspended approximately 20 m above (Wiggins and Hildebrand, 2007). Representative systems were calibrated at the Navy's Transducer Evaluation Center (TRANSDEC).

Recordings were collected intermittently from June 2008 to August 2013 at two sites off the coast of Washington (Fig. 1). One recording site was located on the Cape Elizabeth (CE) shelf about 35 km from shore at a depth of ~120 m (Table I). The other recording site was located in Quinault Canyon (QC), 75 km from shore at a depth of ~1400 m (Table I). Three deployments, which varied in duration (Table I), were examined from each of these two sites. 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-01 recorded for 5 min every 30 min between June 2008 and June 2009, Table I).

### B. 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 min elapsed without the presence of pulsed calls (Rice *et al.*, 2017). This pre-existing record of encounters was used as the starting point for the present analysis, to find periods that contained echolocation signals in addition to the pulsed calls associated with each ecotype (Table I).

Recordings were extracted for each identified encounter containing echolocation clicks, with a 20-min buffer prior to and following the onset of the first and end of the last pulsed call. One deployment (CE-01) was duty-cycled with 5 min

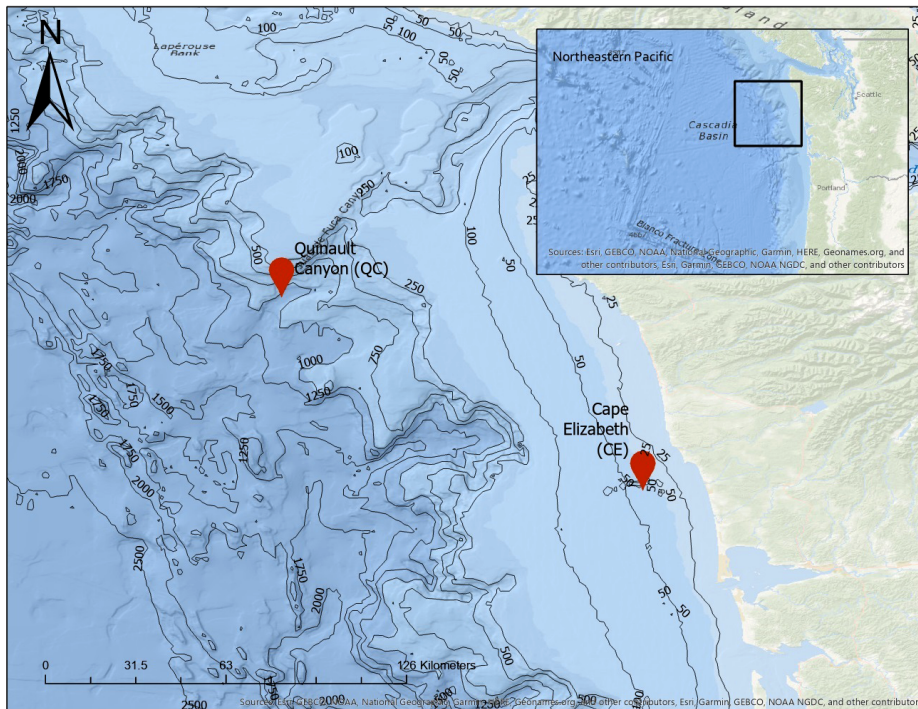


FIG. 1. (Color online) Locations of acoustic recording sites offshore of Washington state. CE: Cape Elizabeth, and QC: Quinault Canyon. (Map created using ARCGIS software by ESRI; ESRI 2015.)

of recording and 30 min of suspension. Encounters from this deployment were considered separate, since 30 min elapsed between recordings, unless there were multiple ecotypes present in a single 5 min recording, in which case the encounter was discarded. The transient ecotype is known to restrict echolocation during hunting and to produce pulsed calls primarily as post-kill communication (Barrett-Lennard *et al.*, 1996), therefore for this ecotype we collected data up to one hour prior to and 20 min following their pulsed call encounters to increase the likelihood of capturing echolocation produced during hunting.

Signal analysis was performed with custom-written software implemented in MATLAB (MathWorks, Natick, MA) including two tools within TRITON (Wiggins, 2003), a permissive echolocation click detector and a two-phase clustering process for grouping similar signals (Frasier *et al.*, 2017), and DETEDIT, a custom-written graphical user-interface for visualization of detections (Solsona-Berga *et al.*, 2020). The click detector was used to search for all signals within the frequency band from 1 to 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 high frequency signals outside the range of killer whale echolocation (Au, 2004). Detections within 20 ms of each other were excluded to reduce inclusion of signal reflections, closely overlapping signals from numerous animals, and high frequency buzzes, which are described as click trains with an ICI below 10 ms (Holt *et al.*, 2019). Detected signals were reviewed using DETEDIT, and false positives arising from non-target species and noise sources were manually flagged for removal. This process resulted in a subset of manually verified detections for each ecotype.

A two-step clustering process (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 each ecotype to further refine types by excluding additional false detections, as well as dissimilar and poor-quality detections embedded in bouts of clicking, which had not been removed manually. In the first phase of clustering, a distance matrix was computed based on spectral shape and waveform, capturing pairwise comparisons between all detections contained within successive one-minute time bins. Correlation distance (Székely *et al.*, 2007), a metric designed to compare the shapes of two vectors, was used to compute a distance score between each pair of clicks. Large distance scores between two detections indicate low similarity using this approach. Correlations between spectra and waveforms for each pair were computed independently, and then multiplied to produce a single distance score between paired detections (Frasier *et al.*, 2017). The result of many comparisons can be viewed as a network in which clicks are visualized as “nodes,” with similar nodes clustering together, while dissimilar nodes are repelled. An unsupervised network-based

TABLE I. Deployment site details including latitude, longitude, depth, and time periods of data collection analyzed for this study. Dates are given as mm/dd/yy.

Site	Latitude (N)	Longitude (W)	Depth (m)	Data start	Data end
CE-01	47° 21.48'	124° 41.00'	100	06/17/08	06/09/09
CE-02	47° 21.12'	124° 43.26'	118	05/21/11	11/06/11
CE-03	47° 21.14'	124° 43.28'	150	12/07/11	01/17/12
QC-01	47° 30.00'	125° 21.20'	1400	01/27/11	10/07/11
QC-02	47° 30.03'	125° 21.21'	1394	12/07/11	07/11/12
QC-03	47° 30.03'	125° 21.22'	1394	09/14/12	06/30/13



TABLE II. Encounter counts and durations are shown for each ecotype including the number of encounters reviewed, average encounter durations, and total encounter numbers and cumulative durations for each ecotype within each HARP deployment at the shallow site (CE) and deep site (QC). These encounters were manually identified based on ecotype-specific pulsed calls, and these encounter times are based on the duration of calling activity. The number of encounters that resulted in representative echolocation clicks for the ecotype after applying a similarity-based clustering and exclusion process are listed in parentheses.

Site-deployment	Offshores			Transients			Residents		
	Total duration (h)	Average duration (h)	Number of encounters	Total duration (h)	Average duration (h)	Number of encounters	Total duration (h)	Average duration (h)	Number of encounters
CE-01	N/A	N/A	0	3.42	0.04	142 (1)	1.95	0.04	45 (14)
CE-02	2.82	1.13	4 (4)	7.22	0.45	16 (1)	2.43	1.22	4 (4)
CE-03	N/A	N/A	0	1.52	0.25	6	N/A	N/A	0
QC-01	0.55	0.14	4	0.55	0.14	4	0.02	0.02	1
QC-02	2.57	0.64	4 (4)	4.27	0.53	8 (1)	0.12	0.04	3
QC-03	2.28	0.57	4 (2)	4.33	0.54	8 (1)	N/A	N/A	0
All	8.22	0.62	15	21.3	0.33	184	4.52	0.33	51

clustering algorithm known as Chinese Whispers (Biemann, 2020) was used to identify one or more clusters of similar nodes within each successive one-minute bin. Nodes which were not associated with a cluster were excluded from further analyses. In the second clustering step, the mean bin-level spectra and ICI distributions of the one-minute clusters identified in the first step were clustered again to identify the dominant recurring “click type” present across the set of encounters associated with each ecotype. Clusters consisting of 50 or more one-minute bins were retained and merged to characterize the overall click type. Summary features for each ecotype’s echolocation clicks, including mean and variance of spectra, peak frequencies, 3 dB bandwidths, and ICI distributions, were computed across the merged set, and compared when possible between the deep and shallow sites.

### III. RESULTS

Of the 443 encounters reported by Rice *et al.* (2017), 250 encounters that were recorded with the 200 kHz sampling rate were chosen to compare spectral parameters across deployments (Table II). Of the encounters examined, 33 encounters containing echolocation clicks with high enough quality and in large enough quantities to be retained by the two-phase clustering process were used to calculate the click types (Table III). Resident encounters produced the largest number of one-minute bins with good quality echolocation clicks while the transient encounters had the least. Ultimately, representative click types were developed from 7087 clicks for residents, 226 clicks for transients, and 26 396 clicks for offshores.

The click types identified for each killer whale ecotype had similar mean spectra with small differences in the overall shape and peak frequencies. Each ecotype’s mean spectra were characterized by a broad energy peak between 12 and 19 kHz with small differences in overall shape and peak frequency. Modal ICI patterns were apparent for the two ecotypes that commonly produce clicks (residents and offshores), whereas no distinguishable pattern in ICI was apparent for the transient ecotype (Table III).

#### A. Resident

Overall, pulsed call encounters of resident killer whales examined in our study had a mean duration of 0.33 h (Table II) with high concentrations of echolocation. For resident encounters, 95% of analyzed recording time and 90% of analyzed echolocation clicks were recorded at CE (the shallow site). Following the clustering process, echolocation detections during the few encounters from QC (the deep site) were discarded due to poor quality and low numbers, therefore the description of this type is based only on shallow site recordings.

For residents, click peak energy was concentrated below 25 kHz [Figs. 2(A) and 2(B)]. The mean spectrum consisted of a broad energy peak consisting of two sub-peaks at  $13.7 \pm 2.6$  kHz and  $18.8 \pm 2.2$  kHz, respectively [Figs. 2(A) and 2(B)], separated by a shallow spectral notch at 16 kHz. Resident ecotype echolocation had a fairly consistent modal ICI at CE, with an overall mean modal value of  $0.21 \pm 0.09$  s [Figs. 2(C) and 2(D)].

#### B. Transient

Of 184 encounters identified as the transient ecotype based on pulsed calls, four included high-quality echolocation clicks

TABLE III. Summary of echolocation click features, including number of encounters, one-minute bins, and clicks used for each click type, as well as the associated mean peak frequency, standard deviation (SD) of the mean peak frequency, and mean of the modal inter-click interval (ICI) across all contributing one-minute time bins ( $\pm$  SD).

	Residents	Transients	Offshores
Number of encounters	19	4	10
Bins (one-min)	96	11	346
Number of clicks	7087	226	26 396
Peak frequency	Peak 1: $13.7 \pm 2.6$	CE: $13.2 \pm 2.7$	CE: $15.4 \pm 2.9$
Mean $\pm$ SD (kHz)	Peak 2: $18.8 \pm 2.2$	QC: $12.6 \pm 2.6$	QC: $14.3 \pm 2.4$
3 dB bandwidth	Peak 1: $4.3 \pm 3.4$	CE: $5.4 \pm 2.6$	CE: $3.7 \pm 2.1$
Mean $\pm$ SD (kHz)	Peak 2: $4.5 \pm 2.6$	QC: $6.9 \pm 2.7$	QC: $7.2 \pm 2.2$
Modal ICI (s)	$0.21 \pm 0.09$	N/A	CE: $0.22 \pm 0.09$ QC: $0.33 \pm 0.25$

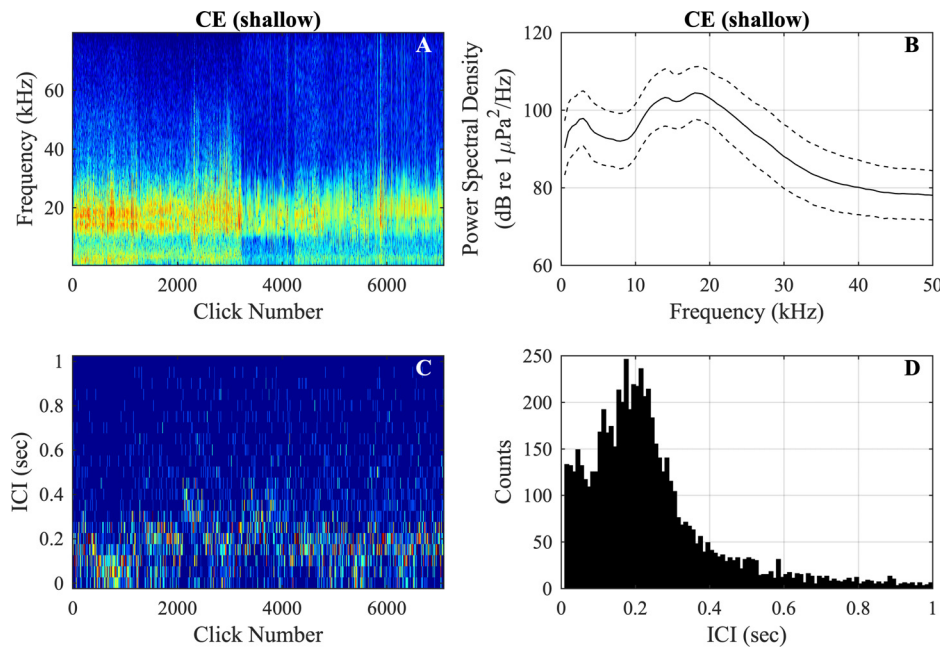


FIG. 2. (Color online) Resident ecotype echolocation click spectral and temporal features: (A) Concatenated mean spectra of all representative resident clicks, sorted by detection time, are shown for the shallow monitoring site (CE) only, because no good quality, representative clicks were retained from resident encounters at the deep monitoring site (QC) in our analysis. (B) The mean resident click spectrum (solid line) with 25th and 75th percentiles (dashed lines) for CE was computed across all representative clicks. Inter-click interval (ICI) distributions are shown in 2 views: In (C) as an ICIGram in which the distribution of ICIs is computed within successive batches of ten sequential clicks; and in (D) as an overall histogram of ICIs computed between successive pairs of clicks.

that were used to describe the click type (Table II). Transients produced the lowest number of echolocation clicks in this dataset (Table III). Overall transient pulsed call encounters had a mean duration of 0.33 h. The majority (80%) of transient echolocation clicks retained to describe the type were recorded at QC. Click spectra recorded at the deep and shallow sites were similar in shape, however, spectra were generally smoother for deep site detections. The mean spectrum was similar in shape and frequency content between the two sites, consisting of a broad energy peak with mean peak frequency of  $13.2 \pm 2.7$  kHz at CE and  $12.6 \pm 2.6$  kHz at QC, and 3 dB bandwidths of  $5.4 \pm 2.6$  kHz and  $6.8 \pm 2.7$  kHz, respectively [Table III; Figs. 3(A)–3(D)]. No distinguishable modal ICI was seen for the transient ecotype, and few clear click trains were visible in the data [Figs. 3(E)–3(H)].

### C. Offshore

Of 15 encounters identified as the offshore ecotype based on pulsed calls, 10 included good quality echolocation clicks. Offshore pulsed call encounters were typically longer in duration with a mean of 0.62 h across all 15 encounters (Table II) and contributed a higher number of echolocation clicks per time bin analyzed. Of the high quality subset of detections retained and used to describe this type, 93% of the detections occurred at QC. Click spectra were comparable across the deep and shallow sites [Figs. 4(A)–4(D)]. As in the transient case, smoother, more consistent spectral shapes were typical of detections at QC with greater variability observed at CE. The mean spectrum at both sites consisted of a single broad peak with a slightly higher peak frequency of  $15.4 \text{ kHz} \pm 2.9 \text{ kHz}$  at CE, compared with  $14.3 \pm 2.4$  kHz at QC. Measured mean 3 dB bandwidths were considerably lower at CE ( $3.7 \text{ kHz} \pm 2.1 \text{ kHz}$ ) due to irregular spectral shapes, compared to  $7.2 \pm 2.2$  kHz at QC

(Table III). A mean modal ICI of  $0.22 \pm 0.09$  s was visible within the CE detections; however, the value and strength of the modal ICI at QC was highly variable with a mean of  $0.33 \pm 0.25$  s [Figs. 4(E)–4(H); Table III].

## IV. DISCUSSION

By utilizing isolated killer whale acoustic encounters identified to ecotype using established pulsed call libraries, we were able to extract associated echolocation clicks for this comparative study. Despite broad similarities in echolocation click types between these three northeastern Pacific ecotypes, differences in spectral features may support discrimination between them. Minor site specific differences in mean click peak frequency were identified for the two ecotypes which were detected at both the shallow and deep sites. These are likely associated with differences in transmission loss, as detailed within the ecotype-specific discussions below. In general, it is important to note that this study differs from earlier efforts to describe killer whale echolocation, in that it describes the signals as recorded in an offshore, uncontrolled environment. The parameters reported in this study are likely generalizable to similar open water passive acoustic monitoring studies with free-ranging groups of variable sizes engaging in variable behaviors, positioned and oriented semi-randomly relative to a sensor recording at depth (approximately 100 m or more).

### A. Resident ecotype

Our findings for resident killer whales align with previous studies, which have documented highly vocal foraging of both whistles and echolocation (Au, 2004; Heimlich-Boran, 1988; Holt *et al.*, 2019). Previously reported resident killer whale clicks (Au, 2004) have a similar spectral shape to the resident clicks reported here. However, Au (2004) report maximum energy peaks between 20 and 40 kHz,

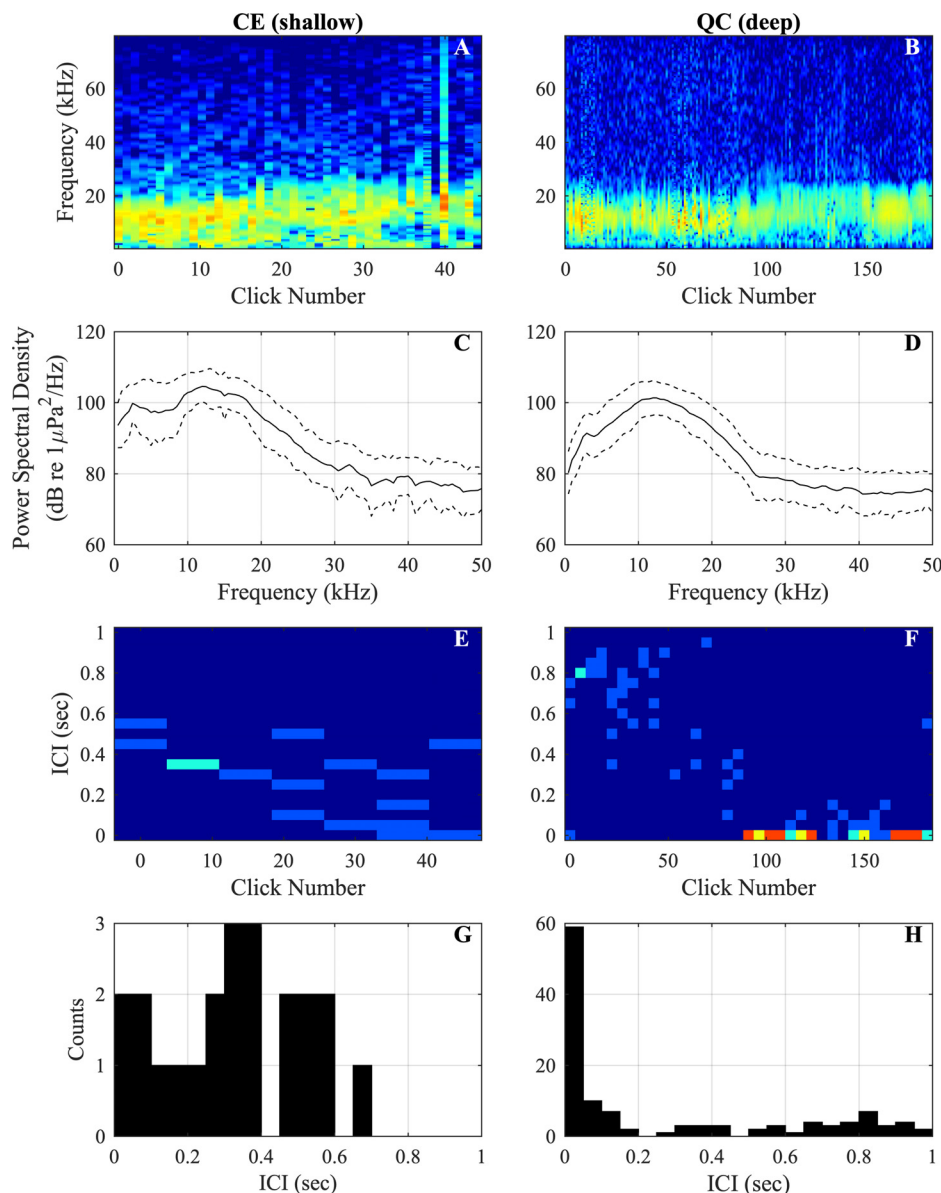


FIG. 3. (Color online) Transient eco-type echolocation click spectral and temporal features: Concatenated mean spectra of all representative transient clicks, sorted by detection time, are shown for the shallow monitoring site, CE (A), and deep site, QC (B). Mean click spectra (solid line) with 25th and 75th percentiles (dashed lines) for CE (C) and QC (D) were computed across all representative clicks. Inter-click interval (ICI) distributions are shown in two views: First, as an ICIgram in which the distribution of ICIs is computed within successive batches of five sequential clicks at CE (E) and QC (F); and second, as an overall histogram of ICIs computed between successive pairs of clicks at CE (G) and QC (H).

considerably higher than the 12 to 19 kHz reported here (Table III). This difference in reported peak frequencies is likely attributable to frequency-dependent transmission loss over greater distances between the animals and acoustic sensors in our open water, seafloor-mounted sensor configuration, and to variable click arrival angles in our data. For Au (2004), recordings were taken near the sea surface, with sensors deployed from a small boat, and manually positioned 150 m to 200 m directly ahead of vocalizing individual animals, at depths between 1.2 m and 1.5 m. Only on-axis echolocation clicks were selected for analysis. In the present study, hydrophones were positioned near the seafloor at depths of either 100–140 m or 1400 m with no control on orientation of the animals relative to the hydrophone. Detection ranges were limited indirectly by the minimum received level threshold of the detector, which could allow detection ranges up to 5 km for on-axis clicks in deep water, assuming source levels near 200 dB re:1  $\mu$ Pa peak-to-peak

(Au, 2004; Frasier *et al.*, 2016). However, most detected clicks are likely produced at significantly shorter ranges (Frasier *et al.*, 2016). In general, higher amplitude clicks showed greater high frequency energy [Fig. 2(A)], further supporting the assumption that propagation loss is reducing the higher frequency content of clicks received from greater distances.

Echolocation beam patterns are narrow, and spectra of signals received even slightly off-axis may appear to have reduced high-frequency content and lower overall amplitude relative to on-axis signals (Au *et al.*, 2012). There is a relatively low probability of receiving large numbers of directly on-axis signals with our recording design, particularly at close ranges where animals would have to orient strongly toward the seafloor to produce an on-axis click with respect to our seafloor sensor.

Our modal ICI for residents at CE is also consistent with prior findings. Holt *et al.* (2019) report that residents



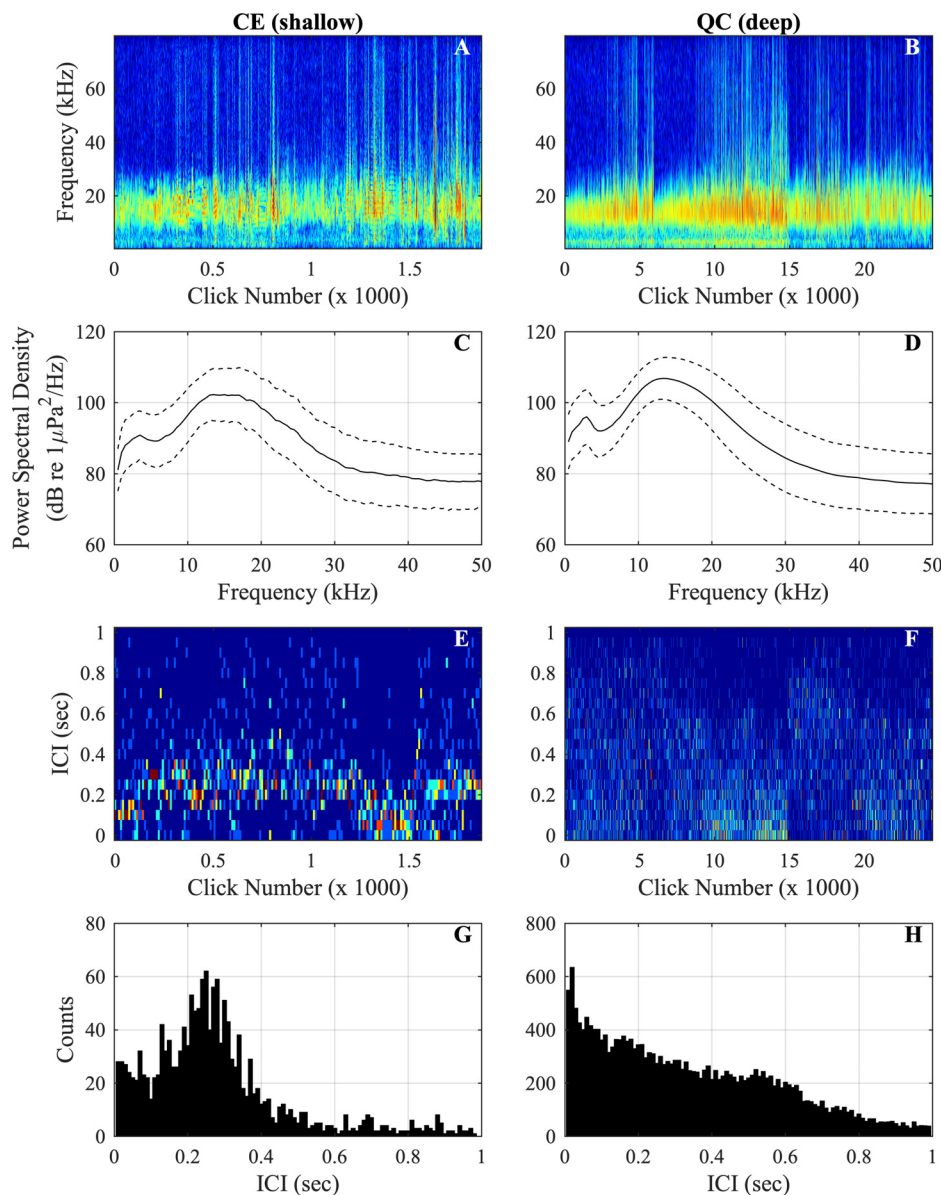


FIG. 4. (Color online) Offshore ecotype echolocation click spectral and temporal features: Concatenated mean spectra of all representative offshore clicks, sorted by detection time, are shown for the shallow monitoring site, CE (A), and deep site, QC (B). Mean click spectra (solid line) with 25th and 75th percentiles (dashed lines) for CE (C) and QC (D) were computed across all representative clicks. Inter-click-interval (ICI) distributions are shown in two views: First, as an ICIGram in which the distribution of ICIs is computed within successive batches of 10 sequential clicks at CE (E) and QC (F); and second, as an overall histogram of ICIs computed between successive pairs of clicks at CE (G) and QC (H).

(typically) forage in waters ranging from 10 to 100 m depth, where salmon are abundant (Candy and Quinn, 1999). They describe an ICI of  $>0.1$  s as the most abundantly used click rate from the surface to 200 m (Holt *et al.*, 2019). Additional research is needed to determine whether the observed ICI holds at deeper locations.

## B. Transient ecotype

More encounters were analyzed for transients than for other ecotypes (Table I), yet these encounters yielded far fewer echolocation clicks, presumably because of this ecotype's acoustically cryptic foraging strategies. Several studies have documented transients restricting the use of echolocation as a hunting strategy, since their prey have acute underwater hearing (Deecke *et al.*, 2005), and producing clicks that are less distinguishable from background sound levels by lowering amplitude and generating sparse, irregular clicks (Barrett-Lennard *et al.*, 1996). This strategy

of blending echolocation clicks with background noise levels may explain the lower number of detections we found for this ecotype as well as the lower peak frequency, may render the clicks less discernable relative to background noise, and may explain the lack of a clear modal ICI. In this study, transient echolocation signals were the most weakly parameterized of all ecotypes due to the limited number of confirmed detections. Additional research is needed to further refine our understanding of the typical features of these clicks. Based on these preliminary findings, echolocation clicks may only be weakly effective signals for long term autonomous monitoring of transient ecotype presence, and encounters with clear clicking activity are unlikely to be associated with the transient ecotype.

## C. Offshore ecotype

Analysis of offshore killer whales' echolocation revealed a consistent spectral shape across deep and shallow

encounters and a variable modal ICI, particularly at QC. The relatively large sample size for this ecotype allowed for comparison between the deep and shallow sites, revealing minimal between-site differences in overall spectral shape. The set of QC detections was relatively spectrally uniform, while the CE detections had greater spectral variability. Killer whales are relatively shallow divers, spending the majority of their time near the sea surface (Dahlheim *et al.*, 2008). At CE, larger numbers of highly off-axis clicks may have been detected above the minimum received level threshold because the near-surface animals are closer to the hydrophone than they would be in deep water. In contrast, in deep water, where an animal directly above the instrument is still over 1 km away from the hydrophone, highly off-axis signals may be too attenuated to be detected. The detectable signals may be closer to on-axis and more uniform as a result.

The offshore ecotype detections at CE exhibited a fairly clear model mean ICI, however, at QC the mode was often indistinguishable, and varied between encounters. Possible explanations include differences in group sizes, larger detection ranges at the deep site allowing more simultaneous detections of multiple individuals, or differences in animal size, behavior or between pods. Large group sizes can lead to saturation in the lower ICI values when overlapping click trains are simultaneously received from multiple animals. ICI is also related to search range, such that animals echolocating at a more distant target may wait longer to receive an echo before clicking again.

The usefulness of ICI for species identification is debatable. Several studies have shown that the ICIs of some odontocetes can be highly variable depending on behavior and distance from a target (Arranz *et al.*, 2016; Holt *et al.*, 2019; Wisniewska *et al.*, 2014). However, modal ICI has been shown to be stable for a number of odontocete species in offshore environments, in the context of large passive acoustic datasets (Frasier *et al.*, 2017; Roch *et al.*, 2011). In this study, modal ICI was a discernable feature within approximately half of the individual encounters. For both residents and offshore ecotypes, ICIs were generally longer than typically observed for smaller delphinids, and could likely be used to rule out a subset of other candidate species, but not to distinguish the two ecotypes.

#### D. General comments

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 group sizes and habitat use by the respective ecotypes acoustically 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 off-shores. 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. The addition of deep learning methods to future applications of the clustering algorithm used in this study may allow for more efficient and accurate click classification.

#### V. CONCLUSIONS

Similarities and differences in echolocation click features were elucidated for three Northeast Pacific killer whale ecotypes recorded in an offshore, uncontrolled passive acoustic monitoring study across two sites, one shallow and one deep. Distinctive spectral features were largely stable across sites for the two ecotypes for which good-quality detections occurred at both, with small differences in peak frequency attributed to effects of acoustic propagation and transmission loss. Findings of this study suggest that it is feasible to discriminate between the echolocation clicks of resident and offshore killer whales based on differences in their spectral characteristics and ICIs, and perhaps identify additional encounters without identifiable pulsed calls. However, identification of transients is limited due to low numbers of clicks typically captured in passive acoustic data. Development of acoustic classifiers using these click types will facilitate automatic detection of these ecotypes in autonomously collected passive acoustic data and aid in effective monitoring efforts, as well as expand opportunities for investigations into additional questions related to group size, densities, and habitat use for this endangered species.

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