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Acoustic Communication of the Killer Whale, *Orcinus orca*

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ABSTRACT

Functional use of killer whale pulsed calls is an important facet of their communication. The complexity of their vocalizations presents opportunities for theoretical and structural analysis of such calls. This study seeks to answer questions regarding social and behavioral context of monophonic and biphonic calls, how they can be classified using computer science technology, and what possible mechanisms for sound modulation exist anatomically in varying populations of *Orcinus orca*. The method used to guide this review is described by Arksey and O'Malley as the scoping review method (Pham et al., 2014). All research included in this review is organized into a data table for reference. Features of killer whale communication were broken down into multiple definitive groups including clicks, whistles, pulsed, discrete, aberrant, variable, monophonic, and biphonic calls. Computer network analysis of the vocalizations has provided a framework for comparing and classifying both similar and dissimilar calls. Restricted study of the anatomy of vocal producing organs in this species has limited true understanding of both sound generation and the extent of vocal manipulation, but distinct biological structures have been identified and their significance discussed. Concrete conclusions over niche usage of calls in killer whale society have not been made, however, it is known that most calls are too complex to only be associated with a singular behavioral or social context. Rather, their complexity has furthered the need for additional research to be conducted.

Introduction

Communication is a strong component of social interactions as observed in numerous terrestrial and aquatic animals. Humans communicate using a combined form of spoken and written language, varying across geographical and cultural settlements. In cetaceans, communication takes the common form of whistles, clicks, and pulsed calls. Killer whales, in particular, are highly intelligent marine mammals who widely inhabit the world's oceans (Forney and Wade 2007 as cited in Filatova et al., 2012). Their intelligence has provoked the usage of a complex variety of vocalizations, as outlined in this paper. Essentially, what are killer whales talking about? While this question is an extremely anthropomorphic view of their vocalizations, it is a digestible way to think about their communication. If killer whales are socializing amongst each other, then it can be fascinating to imagine their language as something humans could learn to understand. Killer whale matrilineal groups, as well as pods, have a unique dialect specific to that group of individuals (Ford 1991 as cited in Filatova, 2020). Evidence like this gives an insightful taste of how orca society uses communication in niche ways, much like human language. This review aims to understand the vocalizations orcas use to communicate, and does so by organizing the information into sections that support the objective. An overview of the different types of vocalizations are described, with references to the studies that have begun to classify them. Following that is the brief section concerning the mechanisms for vocal production and other anatomical information. The last section attempts to compile the research concerning context and usage of both monophonic and biphonic calls, and begins to examine other prospective social functions of vocalizations.

Methods

This literature review was guided by the scoping review process, as originally defined by Arksey and O'Malley (Pham et al., 2014). Such a format was chosen because killer whale communication, while broadly studied, has significant gaps in understanding. A systematic review was not applicable based on the nature of the research, so a scoping review was better suited to map the literature regarding acoustic communication of orcas. The five key stages of the scoping review approach are: "(1) identifying the research question, (2) identifying relevant studies, (3) study selection, (4) charting the data, and (5) collating, summarizing, and reporting the results" (Arksey and O'Malley, 2005 as cited in Pham et al., 2014). The sixth, optional stage to conduct a consultation exercise was omitted for this review.

Based on this model, the first step was to identify the research questions: What are killer whales communicating about? What are the mechanisms for these vocalizations? How are they being classified? These questions were synthesized on the basis of interest, without prior knowledge on the subject matter. The second step was to identify relevant studies and select these applicable articles for further research.

This literature review used online databases accessible through Google Scholar and the University of New Hampshire online library. There was no determined limitation for the time frame of published research, but selected articles happened to have been published between 2001 and 2020. Overall, there was little inclusion criteria aside from applicable key words. Studies selected were written in English and had to be accessed either from a free online journal, or through the UNH online library portal. Keywords that were used to locate studies consisted of, but were not limited to, vocal communication, cetaceans, vocal sharing, directionality, killer whales, vocal anatomy, calling, *Orcinus orca*, behavior, acoustic communication, marine mammal, discrete calls, biphonation, dialect, culture, vocal learning, cetacean culture, odontocete communication, vocalizations, and acoustic behavior.

Once the information had been gathered, it was then organized into a subsequent data table (Table 1). Using the data table as a reference for the review, the summarization began. The discussion of this body of research was divided into chapters of content, as opposed to the methodologies or type of study conducted. Guided by the research topics of the summarized studies, the sections of this review are Classifying, Recording, and Analyzing Calls, Vocal Anatomy, and Context and Usage of Vocalizations.

Results

In total, twenty-one research articles were read and analyzed for the purpose of this review. They were organized alphabetically by the author into the data table below as a reference for summarizing the literature. These articles discussed varying topics that were important factors of killer whale communication. Common themes included: the acoustic repertoires of certain populations, with emphasis on their varying social multi-pod aggregations in context of their vocalizations, behavioral and contextual patterns of discrete calls, usage of monophonic and biphonic calls in mixed-pod groupings, using dynamic time warping to classify vocalizations, extent of vocal learning in the species, and the means for sound production in killer whales.

Table 1. Compilation of the research articles referenced in this study.

Author(s)	Research Questions, Objectives, Purpose	Analysis, Results, and Conclusions	Implications for Future Research

Abramson, J. Z., Hernández-Lloreda, M. V., García, L., Colmenares, F., Aboitiz, F., & Call, J.	Are killer whales capable of vocal learning and imitation? Are the vocal variants observed in natural populations of orcas socially learned by imitation?	Copies were made accurately for most sounds and then confirmed by both external independent blind observers and dynamic time warping analysis (Abramson et al., 2018). Sounds had great variability between copies. DTW showed that copies of novel conspecific and human sounds were made more accurately than the copies of familiar sounds. Acoustic dialects of killer whales are likely obtained through social learning and imitation (Abramson et al., 2018). Killer whales have the ability to control sound production and can copy sounds outside of their typical repertoire.	Future studies must explore the limitation of underwater sounds, as this was conducted in-air which is not the typical acoustic habitat for this species.
Bergler, C., Schröter, H., Cheng, R. X., Barth, V., Weber, M., Nöth, E., Hofer, H., & Maier, A.	How can deep neural networks be trained to identify reappearing communication patterns in large bioacoustic archives?	Architecture was chosen and trained to organize the sounds from the data set into killer whale sounds, and other noise. It proved successful at determining whether or not a recording should be classified as “noise” or “killer whale noise.”	More work must be done to determine patterns in killer whale vocalizations, beyond the two most basic classifications.
Bowles, A. E., Grebner, D. M., Musser, W. B., Nash, J. S., & Crance, J. L.	How do disproportionate bubble streams from stereotyped pulse calls compare? What is their perspective function?	Out of 1206 divergent high frequency component calls (DHFC), 51% were produced simultaneously with bubble streams, but only 1.3% of non-DHFC calls were bubbled (Bowles et al., 2015). This was a significant difference. Bubbling explained less than 15% of the variance in acoustic features (Bowles et al., 2015). Bubbling is associated with a variety of activities and functions. Bubbling would draw attention to calls containing a high frequency component (HFC), making these vocalizations easier to localize and follow, particularly for group members outside of the directionality beam (Bowles et al., 2015).	Further research should be made regarding specific social or behavioral instances where bubbling is present.
Brown, J. C., Hodgins-Davis, A., & Miller, P. J. O.	How can dynamic time warping and a dissimilarity matrix be used to compare and dissect killer whale vocalizations?	57 sounds were grouped into nine call types, and only one inconsistency was observed between the perceptual and automated methods which occurred (Brown et al., 2006). Dynamic time warping has proved extremely helpful and successful for the automatic classification of killer whales vocalizations (Brown et al., 2006).	More testing with diverse call repertoires recorded in wild, natural conditions is needed to determine the full potential of dynamic time warping.
Deecke, V. B., Ford, J. K., & Slater, P. J.	How has the sensitive hearing ability of mammalian prey impacted vocal behavior of the transient killer	Residents produced more calls than non-residents for all activity types. Transients are silent while hunting and vocal during and after an attack. Vocal activity was significantly elevated after the seven confirmed kills (Deecke et al., 2005). Transient killer whales vocalize less during hunting in	Data was collected from only seven confirmed kills, so more research should be done with other observations.

	whales in British Columbia?	order to avoid the detection/eavesdropping of mammalian prey (Deecke et al., 2005).	
Filatova, O. A.	What are the potential functions of biphonic calls in R-type killer whales? What is the long range detectability of the LFC and HFC?	Biphonic calls are a directionality cue. The lower frequency component (LFC) is better for long range communication. Higher frequency component (HFC) was not detectable over long distances due to transmission loss. The two components may serve for recognition on different levels, LFC family level and HFC clan level (Filatova, 2020).	This research must be conducted in other populations to determine whether or not the function of biphonic calls is the same or different.
Filatova, O. A., Deecke, V. B., Ford, J. K., Matkin, C. O., Barrett-Lennard, L. G., Guzeev, M. A., Burdin, A. M., & Hoyt, E.	Is repertoire diversity related to population size? Is the evolution of monophonic and biphonic calls caused by random processes and directional selection?	There is no direct relationship between call repertoire similarity and geographical distance. Dialect evolution is a process influenced by an interaction between directional selection, horizontal transmission, and founder effects (Filatova et al., 2012). The diversity of monophonic calls was higher than the diversity of biphonic calls, suggesting that monophonic and biphonic calls have different principles of evolution that are shared among the different resident populations (Filatova et al., 2012).	More research overall should be conducted regarding the complexity of monophonic calls.
Filatova, O. A., Fedutin, I. D., Nagaylik, M. M., Burdin, A. M., & Hoyt, E.	How does the emission of monophonic and biphonic calls depend on multi-pod groupings and type of activity?	The usage of monophonic and biphonic calls depends on the number of pods in the area and is less dependent on the type of activity (Filatova et al., 2009). Discrete calls may have more complex functions. Perhaps it is the sequence of calls rather than isolated calls that is of importance in coordinating group movements within specific activities (Filatova et al., 2009).	More research must be conducted to determine the function of monophonic calls, as well as the true function of all discrete calls.
Filatova, O. A., Guzeev, M. A., Fedutin, I. D., Burdin, A. M., & Hoyt, E.	Based on the roles of type of activity and social context, and number of pods, which types of killer whale stereotyped calls could have a specific communicative function?	The rate of monophonic calls was significantly lower when mixed pod groupings were present. The usage of biphonic calls was significantly higher during mixed-pod groupings (Filatova et al., 2013). Mixed pod grouping was a more significant variable than type of activity. Low frequency monophonic and biphonic calls have different niche roles in killer whale acoustic communication. Type of activity did not significantly influence call usage and stereotyped calls may have a more complex function.	Conduct similar research with other populations to compare and contrast the functional use of the same calls.
Filatova, O. A., Samarra, F. I., Deecke, V. B., Ford, J., Miller, P. J., & Yurk, H.	Is cultural evolution of killer whale calls a random process with accumulated errors? Does temporal change occur at dif-	The cultural evolution of killer whale sounds is not a random process driven by steady error accumulation. The similarity of repertoires is not necessarily proportional to the time that passes since divergence of their ancestors (Filatova et al.,	Future studies should focus on revealing standards that define the speed of change of both call categories and syllables.

	ferent speeds in different components of killer whale repertoires?	2015). Acoustic similarity does not always indicate relatedness and may vary across call types and syllables (Filatova et al., 2015).	
Foote, A. D., Osborne, R. W., & Rus Hoelzel, A.	Is there a relative production of call types over varying times and multiple social contexts?	There is overall stability in the relative production of call types in each pod's repertoire. Proportional call production in the repertoires is conserved over more than 30 years. Diversity and production of call types varied between social and milling behavioral contexts.	Future research should be conducted to specifically study the other groups in the area, not just the Southern Resident population.
Graham, M. A., & Noonan, M.	What are the consistent vocal patterns during an agonistic chase of captive orcas, and what are those call types, who produces the calls?	There were two distinct behavioral patterns. There were periods of both intense aggressive chase and less intense inter-chase intervals. Vocalizations during chase appeared to be modified versions of similar, non chase calls which can be an analogy to human tone of voice. Some call types were categorically different during agonism.	More research must be done on killer whales in the wild to determine the true rate of aggression in this species and which calls produced during these periods are aggressive or distress signals.
Kremers, D., Lemasson, A., Almunia, J., & Wanker, R.	Is vocal divergence and convergence compulsorily exclusive? Is acoustic divergence not systematically controlled? Is it due to individual morphological differences?	Four out of 12 call types were shared by all four orcas, two call types were only shared by the males, whereas the females did not have their own call structure. Four call types were individual specific. Some call types showed similarity with Canadian and Icelandic ancestors of these orcas. Sex appears to be important in vocal sharing patterns. Captive male orcas show higher call matching and stronger convergence of their vocal repertoires than females. Vocal learning also plays a part in producing certain call types.	There is a need for more research to determine the functional significance of having several calls.
Kuroda, M. Miki, N., & Matsuishi, T. F.	What are the organs involved in the sound production of echolocation clicks? How do those structures affect click frequency characteristics?	CT scans revealed the three dimensional topography of different species of small toothed whales. They displayed the melon, dorsal bursae, vestibular sac, connective tissue, and other structures in the head of odontocetes. The structures in the vestibular sacs and morphological features of the melon may determine click frequency (Kuroda et al., 2020).	More research must be done to increase the knowledge of the overall head anatomy and the functional morphology for all vocalizations in odontocetes, not just clicks. Research should also determine the physical properties of the melon's terminal branch.
McKenna, M. F., Cranford, T. W., Berta, A., &	How does the melon vary across odontocete taxa? Can	Melon boundaries were discerned using the CT scans. They were determined by the gradients in density, beginning with a lower density core com-	Future research must determine the true function of melon characteristics rather

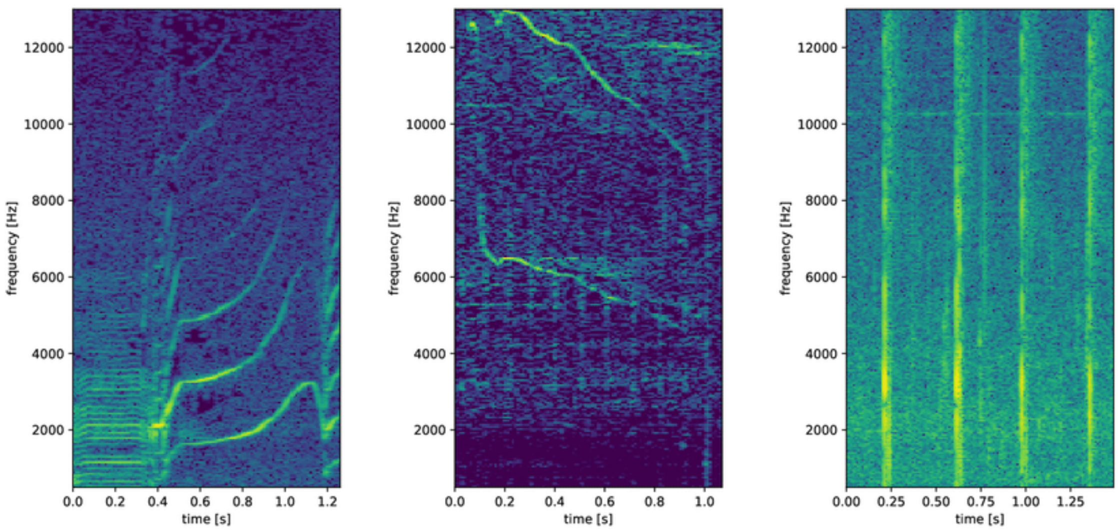
Pyenson, N. D.	standardized definitions of the melon be determined using computed tomography scans? What is the perspective function of the melon?	posed of lipids, to the higher density shell of connective tissue (McKenna et al., 2011). Melon functions and features discussed were biosonar beam formation, pathways for sound transmission, and the likelihood of click frequencies being propagated and refracted through the melon. The pathways of sound in the head are incredibly dependent on the relationship between the melon and sound sources such as the phonic lips, or dorsal bursae (McKenna et al., 2011). The diameter of the melon may restrict low frequencies, functioning as a noise filter.	than just perspective function.
Thomsen, F., Rehn, N., & Teichert, S.	How are variable calls used by killer whales? How can the structural and temporal patterns of these calls be defined? What is the potential functional use of variable calls?	642 variable calls were recorded and were found in 98 sequences (Thomsen et al., 2007). Variable calls can be categorized into distinct groups, even though the name variable suggests otherwise. Variable calls in killer whales are a form of graded communication. These calls are also more complex than discrete calls and are not suited for functioning as long range communication signals. The sequences of variable calls are general indicators of the emotional state of each individual (Thomsen et al., 2007). Duration and number of calls within each sequence most likely depends on the state of the sender.	One specific call type, the V4 call category, may have been too broad and future studies should focus on determining the true division of the vocalizations.
Miller, P.	Are killer whale stereotyped calls a direction of movement cue?	Killer whale call types containing a high frequency component (HFC) are directional at high frequencies (Miller, 2002). Call structure reflects signaler orientation and direction of movement. The HFC may be a necessary feature for the generation of a possible direction of movement cue in killer whale calls (Miller, 2002). At least a subset of killer whale calls are broadly directional at high frequencies (Miller, 2002).	Future research should use playback experiments to test how killer whales respond to directional cues and whether familiarity is necessary for receivers to interpret such signals.
Tyack, P. L., & Miller, E. H.	This is a review presented as a chapter in a publication. It discusses the vocal anatomy, communication and echolocation of marine mammals, often in comparison to terrestrial animals.	The scope of acoustic communication is discussed, with relevant inclusion of research concerning sound production. Anatomical information for various cetaceans like pinnipeds, sirenians, and odocontes is also a highlighted point. Potential source filtering is also included. Echolocation is its own subsection with regards to multiple species. The section on communication is very broad and does not offer much insight into killer whale communication specifically.	In the chapter of this book, it is apparent that more research must be done to fully understand the mechanisms for sound productions in all types of cetaceans, but also in odontocetes specifically.

Wellard, R., Erbe, C., Fouda, L., & Blewitt, M.	What is the acoustic repertoire of killer whales in Australian waters? How do they compare to vocalizations of other populations?	Sounds were grouped into whistles, burst-pulse sounds and clicks. Whistles were defined as continuous frequency modulated tonal sounds. Burst-pulse sounds were defined as rapidly repeated pulses that appeared as a wave on a spectrogram. 142 vocalizations were suitable for categorization out of the 2376 vocalizations recorded. Whistles were grouped into four different groups with different characteristics and burst-pulse sounds were placed into five different call types. Australian killer whale vocalizations have a similar repertoire to that of other regions. Some calls were strikingly similar to calls recorded in Antarctica.	Future research should determine whether or not different ecotypes of killer whales exist in the Australia region. Also, further analysis and comparison can expand the knowledge of this population.
Williams, R., Clark, C. W., Ponirakis, D., & Ashe, E.	What are the ocean noise levels? What are the intensities of anthropogenic activities? How does that impact the endangered Canada's Pacific Ocean fin, humpback, and killer whale? Sound is a critical element of killer whale habitats so how is that deteriorating with human noise pollution?	Commercial shipping can create chronic noise in low frequencies (Williams et al., 2013). The recorded noise levels are large lost opportunities for acoustic communication. 62% is lost for killer whales at a median level, and 97% under noisy conditions (Williams et al., 2013).	Future research must better quantify the temporal patterns and distances at which whales actually use these communication signals. Additional research must also be completed to understand physiological stress responses to the noise.

Discussion

Classifying, Recording, and Analyzing Sounds and Calls

In order to understand the language, or dialects, of killer whales, the different vocal components must be understood and subsequently classified. On the most basic level, orca vocalizations can be broken down into three umbrella categories consisting of whistles, clicks, and pulsed calls (Awbrey et al. 1982; Ford 1989 as cited in Deecke et al., 2005). These sounds all serve a different functional purpose in the society of *Orcinus Orca*. Figure 1 depicts these vocalizations on a spectrogram. Whistles vary in frequency, but consist of a tonal sinusoidal pattern (Brown et al., 2006). They are most commonly used in social contexts and may facilitate short term communication (Ford 1989; Thomsen et al. 2002 as cited in Deecke et al., 2005). Whistles have frequencies ranging between 1.5 and 18 kilohertz with durations between 50 milliseconds to 12 seconds, however, it has been found that whistles can reach the ultrasonic range at up to 75kHz in certain Atlantic populations (Ford 1989; Samarra et al. 2010 as cited in Bergler et al., 2019). Echolocation clicks are a series of short, broadband pulses from 01 milliseconds and 25ms with a repetition rate of up to 300 per second (Ford 1989 as cited in Bergler et al., 2019), primarily used for signaler orientation and prey detection (Brown et al., 2006; Deecke et al., 2005). Pulsed calls are extremely complex sounds that can include multiple harmonics which are referred to as the low frequency component and high frequency component (Brown et al., 2006), hereinafter referred to as LFC and HFC. These two independently modulated features provide evidence for multiple sound sources (Miller, 2002; Filatova et al.,2007 as cited in Bowles et al., 2015). When pulsed calls do not include both a LFC and HFC they are considered to be monophonic, opposite to their biphonic counterpart. Other classifications of pulsed calls include discrete, aberrant, and variable calls (Ford 1989 as cited in Deecke et al., 2005). Discrete calls are stereotyped to a specific population and can be assigned to either individuals, matrilines, or clans, based on their structural properties. Aberrant calls are based on the discrete calls but have varying degrees of modification. Variable calls are not stereotyped and are commonly shared amongst populations. All pulsed calls have been linked to group recognition and communication, both within populations as well as intermingling with others (Deecke et al., 2005; Filatova, 2020), although studies have found that high frequency pulsed calls can also convey signaler orientation and provide a direction of movement cue (Miller, 2002).



a) Killer whale pulsed call **b)** Killer whale whistle **c)** Killer whale echolocation click

Figure 1. Example of the three different types of killer whale vocalizations visible on a spectrogram (Bergler et al., 2019).

With the advancements in computer science and technology, researchers have begun to train computer programs to classify killer whale vocalizations (Bergler et al., 2019; Deecke et al., 2005). These studies have collected recordings from different populations, one sourcing from captivity, and the other from British Columbia waters. Underwater hydrophones are the most common recording devices for such projects. Killer whales are one of the most wide ranging species on the planet, and they inhabit all oceans, therefore these processes must be applied to all populations to ensure accurate classifications. ORCA-SPOT is an automated program that distinguishes between killer whale sounds, environmental noise, and human sounds. It uses a Convolution Neural Network (CNN) which can classify spectrograms based on pattern recognition and generate an output that is either "killer whale noise" or "noise." The ORCA-SPOT network processes the data with other algorithms, to assist this study in organizing more than 19,000 hours of sound from a database known as the Orchive. This extremely large bioacoustic archive project was a very important step in understanding the communication and linked behavioral patterns of the killer whale species (Bergler et al., 2019). The other study referenced in this review that attempted to classify killer whale vocalizations used dynamic time warping, a process in which the melodic contours of killer whale calls were compared using a dissimilarity matrix (Deecke et al., 2005). Figure 2 illustrates a simplistic diagram where some structural components of killer whale vocalizations are labeled. The algorithm was constructed to compress and expand the time axis of a signal to determine the frequency overlap with a reference signal (Filatova et al., 2012), and this method of classification for pulsed calls proved very effective and should be tested further to expand on other population repertoires (Brown et al., 2006).

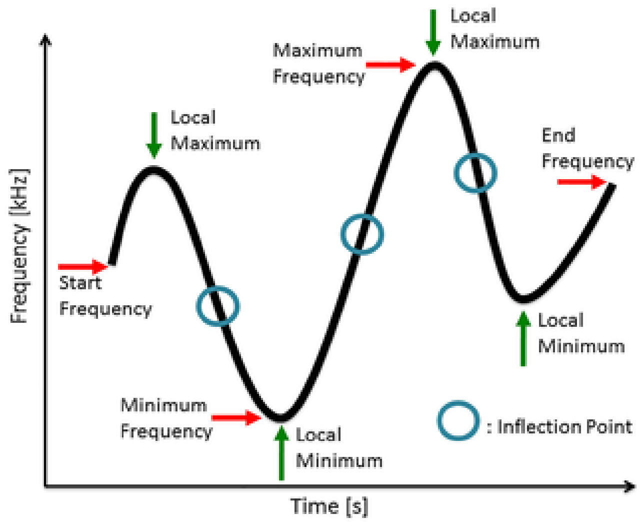


Figure 2. Parameters used to analyze killer whale calls (Wellard et al., 2015).

Vocal Anatomy

The vocal anatomy of cetaceans, and killer whales in particular is not comprehensively understood, with debates over the means of sound production in odontocetes (Tyack & Miller, 2002). It is assumed, however, that biphonic calls are evidence for two separate sound sources, (Miller, 2002; Filatova et al.,2007 as cited in Filatova et al., 2013). Scientists debate that unlike other mammals, the larynx is not the primary source of vocalizations in killer whales and instead the nasal passages are the anatomical structure which enable sound production (Tyack & Miller, 2002). One study provided evidence to support this hypothesis in dolphins by using an X-ray to determine movement in the nasal passages during vocalizations, while during the same period of time no motion was detected in the larynx (Dormer 1979 as cited in Tyack & Miller, 2002). While this experiment was performed on a different species, both killer whales and dolphins are part of the Delphinidae family, and the nasal passages may be homologous.

Further anatomical information is limited due to strict conditions of specimens used for analysis. However, other structures have been successfully studied, and their functional use theoretically explored. Within the nasal cavity, killer whales have a pair of phonic lips, which can operate as two independent sound sources, potentially responsible for the modulation of biphonic calls (Cranford et al. 1996 as cited within Abramson et al., 2018). When pressurized air passes through the phonic lips, vibrations are reflected by the skull, nasal air sacs, and dense tissue which all function as an acoustic mirror. These sound vibrations propagate into the environment as echolocation clicks (McKenna et al., 2011). In the rostrum of killer whales and most other cetaceans, there exists the melon, which is considered their acoustic lens (Harper et al. 2008; McKenna et al. 2012 as cited in Kuroda et al., 2020). It is composed of fat and connective tissue, which can often be mistaken for the blubber surrounding it, as it is of similar density (McKenna et al., 2011). The melon's primary function may be to focus sound and amplify components of the acoustic signal (Norris and Harvey 1974 as cited in McKenna et al., 2011).

Context and Usage of Vocalizations

When deciphering the language of killer whales not only is it important to classify these calls based on spectrogram parameters, but to also consider behavioral context. In the same way that we know humans use certain words, phrases, or tones for specific social or behavioral contexts, it would be interesting to know if orcas exhibit these anthropomorphic traits. Filatova et al. (2012) determined four different activities that calls could potentially be attributed to. Foraging was defined as the times in which whales were viewed carrying fish in their mouths or exhibited intensive swimming with changes in direction and irregular diving. Traveling was when all members of the observed pod were moving at a relative speed to each other in a consistent direction. Socializing was characterized by behaviors such as rolling, breaching, and flipper and fluke slapping. Resting was when the whales stayed close together in the same place and displayed minimal movement (Filatova et al., 2013). Research determined that these types of behaviors did not have a significant influence on the usage of different discrete calls. Call types were not exclusively correlated with any of these activities (Filatova et al., 2013; Ford 1989 as cited in Filatova et al., 2009). This data refuted the idea that monophonic and biphonic calls are only used in a specific context, which suggests that they have more complex functions.

Since these calls are used in a variety of circumstances, a potential alternative function is based on social presence of different pod groupings. Monophonic calls were used significantly less during multi-pod aggregation interactions and biphonic calls were used more frequently in these mixed-pod contexts (Filatova et al., 2013; Foote et al., 2008; Filatova et al., 2009). The monophonic calls used less often in multi-pod scenarios are used predominantly when those same pods are alone, continually reinforcing the idea that biphonic calls serve the purpose of group cohesion (Foote et al., 2008, Filatova, 2020). It can be hypothesized that biphonic calls serve as a pod affiliation vocalization to maintain contact when in the presence of other whales outside their pod. The two independent components of a biphonic call may be responsible for an increase in call type recognition, subsequently keeping members of a family closely connected while mingling with unfamiliar whales. Some syllables in these biphonic calls may be used as population markers and are used more conservatively, while others are matriline markers and are used far more frequently, resulting in stable and variable features of vocalization evolution (Filatova et al., 2015). Biphonic calls also have a strong mixed-directionality feature which signalers may use to provide a direction of movement cue to receivers of the call (Miller, 2002). It has been observed that killer whales vocalize immediately before a change in their swimming direction (Jacobsen 1986; personal observation as cited in Miller, 2002). As a result, biphonic calls could be used by orcas to signal their location and intended direction of movement to members of their matrilineal line in the presence of other pods. The higher frequency component of pulsed calls may also duplicate the matrilineal identity signal when environmental noise masks the identifying feature of the lower frequency components (Filatova, 2020). The acoustic variation of the HFC is an example of how killer whales have control over their vocalization production, which has been determined by other experiments as well (Abramson et al., 2018; Kremers et al., 2012). Such experiments have begun to determine the extent to which killer whales can manipulate their sound modulation by using novel conspecific sounds as something for the whales to recreate (Abramson et al., 2018; Kremers et al., 2012)..

Another example of vocal control is during agonistic periods, where calls were also structurally modified (Graham & Noonan, 2010). These calls resemble similar non-chase calls used in peaceful episodes of behavior, but were slightly altered and used in heated, conflict situations. Similarly, aberrant calls have been recorded in the wild as modified discrete calls. This can be theoretically compared to tone of voice in humans as vocal features may change during changes in an emotional state, even if the same words are produced (Wurm et al., 2001 as cited in Graham & Noonan, 2010). It is interesting to muse on the fact that some killer whale calls that vary in parameters such as frequency or amplitude may just be an outward example of expressing emotional state in their communication.

Furthermore, killer whale calls that have a divergent high frequency component are structurally specialized in long range communication (Miller 2006 as cited in Bowles et al., 2015), but another study found a correlation between these calls and bubble stream emission which may mean that they serve a function in a close contact range (Bowles et al., 2015). It is clear that these calls are extremely complex and require more research to entirely understand their function. It can be assumed that pulsed calls usually used for long range contact may also function to maintain contact in close range high activity states, as long as the DHFC is accompanied by synchronous bubbles (Bowles et al., 2015). Other instances of close range contact in killer whale behavior have involved the usage of variable pulsed calls (Thomsen et al., 2007). These particular calls were described as excitement calls, characterized by their swift changes in pitch (Ford 1989 as cited in Thomsen et al., 2007). It was proposed that these variable calls were used to coordinate interactions between whales when in close proximity to each other in one of two behavioral contexts; either traveling or socializing. Variable calls are most likely a grade signal consisting of different call types, each used for subtle changes in motivation or motion, and could also relate to the emotional state of the individual producing the call (Thomsen et al., 2007).

It is interesting to note that different killer whale ecotypes vocalize more or less based on their social and dietary patterns. One study found that in the region of British Columbia, two different ecotypes of killer whales had drastically different temporal vocalization emission patterns (Deecke et al., 2005). Fish-eating resident killer whales of British Columbia produce pulsed calls far more frequently than the mammal-eating transient ecotype. These transients are silent while hunting for prey, which is regularly mammalian species that are known to have good underwater hearing. It is therefore in the interest of eavesdropping that the orcas do not vocalize during the hunt. After the prey has been captured and killed, the rate of vocalizations increases significantly (Deecke et al., 2005), signaling that the negative consequence of vocal behavior is lower in this context. The coordination of vocal behavior is a contextual behavioral decision of the killer whales to strategically hunt the acoustically sensitive prey (Deecke et al., 2005). This same phenomenon may occur in killer whales off the coast of Australia, but more research must be conducted to determine that and whether or not that dictates a separation in ecotype (Wellard et al., 2015). While some killer whales off the coast of British Columbia make strategic choices to reduce vocalizations, it may not become a choice for all populations as the anthropogenic sound levels in the area are continuing to increase. Orcas living in the noisiest sites of the region lose up to 97% of their acoustic communication space (Williams et al., 2013). This will limit the extent to which omnidirectional, burst-pulse, and social communication calls can be used, but more research must better define the importance of these calls and how ocean noise levels truly impact the ability for an orca to produce these vocalizations and have a receiver interpret that signal (Williams et al., 2013).

Strengths and Limitations

One strength of this study is that it provides a clear and concise overview of the information necessary to further understand killer whale communication. The background knowledge this review outlines is critical when approaching concepts that have not been fully studied by experts on the subject of orca vocalizations. This review will allow others to quickly gain a basis to expand on with this subject. It acts as a useful resource for people unfamiliar with the content to begin learning about cetacean communication. The limitations are as follows: Articles were only accessed through two online databases, which severely decreases the amount of information included. This limited the content that could be used, and that became apparent when morphological information included in the vocal anatomy section was predominantly sourced from articles about click generation and not pulsed call modulation. The timespan for the research was only spread over one semester, and summarizing a body of literature that begins in some subtopics' case, in 1970, makes it difficult to fully review all the details. Furthermore, a lack of background in physics limited the discussion of technical sound waves, spectrograms, and the true process of dynamic time warping.

Future Steps

Further research on the vocalizations and communication of killer whales should be focused on a few specific areas of study. First, the vocal anatomy of orcas should be definitively determined. This will allow for biphonation to be correctly attributed to certain vocal passages or filters, which will subsequently make classifying calls far easier. Comprehensive understanding of the anatomical structures that produce sound will also assist in measuring the vocal learning capacity of the species. Computer science technology, such as ORCA-SPOT should grow their programs to classify more niche differences in sound. Instead of only determining “orca noise” and “noise,” the network should categorize calls by different parameters. A few examples could include monophonic, biphonic, varying pods, and echolocation clicks or whistles. With a more complex automated classification system, sifting through large databases can be done faster, which will bring researchers closer to cracking the language barrier between killer whales and humans. Another notable mention for future research would be inventing ways in which more recordings can be obtained without excessive anthropogenic interference. In conjunction with automated programs, hydrophones can be trained to only record noise that is in fact audible killer whale vocalizations. This will increase the pool of recordings that can be studied while also minimizing excess recordings that only contain boat or environmental noise. Deeper and more intricate classifications will lead to a greater understanding of the function of pulsed calls, which vary immensely. Analyzing the sound contours of a spectrogram may find common syllables in discrete calls. Monophonic calls in particular are not well understood, so further research unrelated to behavioral context must be studied in relation to these calls in different populations.

Conclusion

Killer whale vocalizations are a deeply complex form of communication. The functional use of pulsed calls has been extensively explored, but no true conclusion has been made, and the same statement is true for vocal anatomy. Monophonic and biphonic calls are not simple enough to assign a function based on behavioral context, which is where structural framework must be investigated, as the frequencies and contours of both the LFC and HFC may provide more indications to decipher these calls. The effectiveness of automated computer programs used for the purpose of identifying vocalizations and classifying them has proved useful and must be expanded on. There is still not a comprehensive understanding of the common function of orca communication, but yet a strong foundation for more research.

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