BRILL Behaviour (2017) DOI:10.1163/1568539X-00003451 Behaviour brill.com/beh

The baroque potheads: modification and embellishment in repeated call sequences of long-finned pilot whales

Elizabeth M.J. Zwamborn * **and Hal Whitehead**

Department of Biology, Dalhousie University, 1355 Oxford Street, Halifax, NS, Canada B3H 4J1

*Corresponding author's e-mail address: elizabeth.zwamborn@dal.ca

Received 27 February 2017; initial decision 5 June 2017; revised 24 August 2017; accepted 28 August 2017; published online **???**

Abstract

Vocal variation within calls that are generally stereotyped suggests multiple simultaneous functions. These vocal cues may be especially important for group-living species. We describe two fundamental call transition types within repeated call sequences of long-finned pilot whales (*Globicephala melas*): embellishment — discrete changes to a specific part of a call — and morphing — non-discrete small changes across a call. Of transitions between consecutive calls, 31% were embellished and 20% morphed. Modifications between pairs of consecutive calls were often followed by another modification of the same type, with sequences of embellished transitions generally alternating between ornamentation and simplification. Ten classes of embellishment varied in rate of occurrence as well as temporal location within a call. Most common were the addition/deletion of pulsed or tonal elements. Functions of these modifications could include conveying information on location or the emotional state of the signaller, or they could be products of vocal innovation.

Keywords

long-finned pilot whale, *Globicephala melas*, communication, vocal modification, embellishment, vocalizations, cetacean.

1. Introduction

Vocal variation — specifically in reference to changes among stereotyped calls produced in succession by an individual or set of individuals — has been described in a number of species. These changes range from calls with increasingly 'aggressive' features made by the northern cricket frog (*Acris crepitans*) when approached by intruders (Wagner, 1989) to the learned development of stereotyped whistle sequences during the first year of life for

© Koninklijke Brill NV, Leiden, 2017

beluga whales (*Delphinapterus leucas*) (Vergara & Barrett-Lennard, 2008). One type of vocal variation, which we refer to as embellishment throughout this study, is the addition or removal of details or features from a call. Also described as ornamentation, this form of call modification is perhaps best known from studies of bird song, where it has found to be correlated with cognitive abilities such as vocal learning (Boogert et al., 2008; Sewall et al., 2013). In some species, the females show a preference for males with more complex song, leading to the hypotheses that when choosing mates, they use ornamentation as an indicator of the intellectual performance of the singer (Nowicki & Searcy, 2011; Sewall et al., 2013). Embellishment is also seen in anurans, as in the calls of the Tungara frog (*Engystomops pustulosus*). This species is found to make a basic 'whine' vocalization, that can be made more complex with an addition of up to six 'chucks' afterwards (Rand & Ryan, 1981). The chucks are added to the call in the presence of other singing males, as females are not as attracted to the individuals producing only whines.

Large portions of the known vocal repertoire of several cetacean species are made up of highly stereotyped vocalizations. These range from the temporally stable individual signature whistles of bottlenose dolphins (*Tursiops truncatus*) (Caldwell et al., 1990) and the dialects of different families of 'resident' killer whales (*Orcinus orca*) (Ford, 1989, 1991), to the distinctive sets of click patterns produced by sperm whale (*Physeter macrocephalus*) units and clans (Gero et al., 2016). Perhaps due to the often stereotypic nature of cetacean calls, the concept of embellishment has not been extensively explored within this taxon despite there being a number of studies that have described modifications to calls. One example of cetacean vocal modification observed in bottlenose dolphins, termed 'looping', happens when individuals alter their signature whistles through varying the number of repetitive elements, known as 'loops', within the whistle (Caldwell et al., 1990). This has been linked to stress, and may relay other important information about emotional state (Esch et al., 2009). Another possible expression of embellishment in cetaceans is the production of multi-component calls, where the individual components can be heard by themselves at other times. Killer whales have been found to produce compound vocalizations like these, where the relative positions of the sections remain unchanged even though not all sections are used every time the call is produced (Strager, 1995). For many cases of vocal variation in cetaceans we do not understand the purpose of the modifications being made. This is because understanding the function of call modification in this taxon is challenging due to the difficulty of linking vocalizations to individual callers and their behaviours in the field. However, by looking at cetacean vocal modification types — such as embellishment — and how they manifest themselves, we can begin to gather clues as to the kinds of information being transferred by different types of acoustic signals.

Relatively little is known about the vocalizations of long-finned pilot whales (*Globicephala melas*), a voluble delphinid species found in temperate waters of the North Atlantic and Southern Oceans. Though pilot whales are generally thought to have a very fluid, graded repertoire, where distinctions between specific call types are hard to establish (Taruski, 1979), we observed that stereotyped repeated call sequences — formally defined as the same call made three or more times in sequence with roughly even spacing and a maximum of six seconds between them — make up a substantial portion of this species' acoustic repertoire in a population off Cape Breton, Nova Scotia, Canada (Zwamborn & Whitehead, 2017). The calls in sequence are generally non-overlapping and have similar amplitude, supporting the hypothesis that the sequences are generally made by a single whale (Busnel & Dziedzic, 1966; Sayigh et al., 2013). While broad descriptions of both pulsed calls (Nemiroff & Whitehead, 2009) and whistles (Taruski, 1979) are available, there has been very little work on the function of different parts of this species' vocal repertoire.

In this study we describe and characterize for the first time the transitions found between repeated calls within sequences. We also develop descriptive categorization tools that can be used in the investigation of call modification for other cetacean species. If non-random, characterizable forms of modification are found in pilot whale repeated call sequences, then it would suggest that call alteration may be intentional and have specific functions, rather than simply being the result of a fluid repertoire.

2. Materials and methods

2.1. *Field work and data collection*

Recordings of a population of long-finned pilot whales found in the Gulf of St. Lawrence off Cape Breton Island, Nova Scotia, Canada were collected opportunistically during the months of July and August during 1998, 1999, 2000, 2013 and 2014. The research used whale-watching vessels based in the ports of Bay St. Lawrence (47°02′N, 60°29′W) from 1998–2000 and Pleasant Bay (46°50′N, 60°47′W) from 2013–2014, which are separated by 31 km. Many individual whales were photo-identified in both areas using established protocols (see Ottensmeyer & Whitehead, 2003; Auger-Méthé & Whitehead, 2007). 1231 individual whales have been identified, through markings on and around their dorsal fins, with approximately 51% of the population being identifiable (Augusto et al., 2017). Many identified whales return to the study area in multiple years (Augusto et al., 2017). In Bay St. Lawrence recordings were collected using a VEMCO hydrophone (10 Hz–20 kHz) and a Sony TCM 5000 eV analogue cassette tape recorder. Those collected in Pleasant Bay used a Cetacean Research C55 hydrophone and a Zoom H4n 4-channel Handy Recorder. Early recordings made on cassette tapes were digitized using CoolEdit Pro (ver. 2.0). All audio files used in this study had a 16-bit sample size and a 44.1 kHz sampling rate. Recordings were taken after the vessel had encountered a group of pilot whales and the engine had been turned off. Hydrophones were deployed to a depth of 10–15 m. A total of 62 h of recordings were used for this analysis.

2.2. *Recording analysis*

Raven Pro (ver. 1.5) (Bioacoustics Research Program, 2014) was used to create spectrograms with a 600-point (13.6 ms) Hann window (3 dB bandwidth = 106 Hz), with a 50% overlap and 1024-point DFT. All recordings were visually scanned and any repetitive vocalizations that matched the definition of repeated call sequences were extracted. Repeated call sequences are defined as the same call type made three or more times at roughly regularly spaced intervals with up to six seconds in between calls (as in Zwamborn & Whitehead, 2017). These sequences had to have a good signal to noise ratio and minimal or no overlap with other calls for at least three calls in succession. Out of 188 repeated call sequences that met these criteria, 174 were scored for transition type for both the first and second call transitions as either stable, embellished, or morphed (Table 1, Figure 1). The remaining fourteen sequences could not be accurately categorized as they showed discrete as well as non-discrete changes and these sequences were omitted from further analysis.

Statistical analysis used IMB SSPS Statistics (IBM, 2013). Contingency tables were used to look at the relationship between the first and second transition types (i.e., the transitions between the first and second, and second and

Table 1.
Definitions of transition type classifications for long-finned pilot whale repeated call sequences.

Transition	Definition
Stable	Call remains conserved with no major changes
Embellished	Discrete additions or subtractions made to call. Can include gaps, buzzes, inflections, new tonal sections, etc.
Morphed	A combination of non-discrete small changes made across call, often involving simultaneous changes in fundamental frequency, length, number of inflection points, and other elements

third, calls in the sequence), with a Pearson Chi Square test being performed to test the null hypothesis that the second call transition type is being made independently of the first transition type. Further, both contingency tables and Chi Square tests were used to investigate patterns of embellishment in sequences where both the two transitions looked at were classified as embellished, testing the null hypothesis that the second embellished transition type

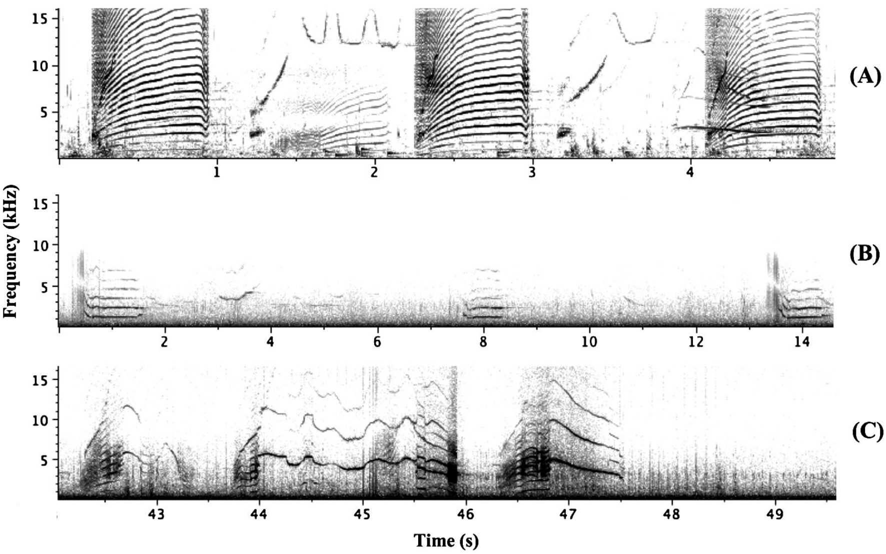

Figure 1. Spectrogram examples of sequences with (A) stable (B) embellished — with a buzz before the first and last calls — and (C) morphed transition types for repeated call sequences made by long-finned pilot whales (audio included as supplementary material).

Table 2.
Classifications for long-finned pilot whale repeated call sequence embellishment transitions.

Embellishment type	Definition of addition/subtraction
Biphonation	Addition of upper or lower frequency component resulting in biphonation and an increased complexity of the call
Buzz/pulse	A buzz, brief pulsed component, or click
Change	An already existing section of call is modified, while the rest remains the same and the change does not fit into one of the other categories
Gap	Call is segmented by a gap where the whale briefly stops emitting the call
Lengthening	One section of the call is significantly lengthened or shortened
Looping	Akin to what has been described in signature whistles, where the number of repetitive elements — 'loops' — are varied within a call
Step	A jump up or down in the fundamental frequency of the call which is visualized as a step-like contour on a spectrogram
Upsweep	An upwards sweep in frequency of a call
Wobble/hump	Inclusion of new inflection points to create fluid wobble or hump in a section of the call
Unclassified add/sub	A new section is added to or subtracted from call that does not fit into any of the other add/sub categories mentioned

— ornamentation or simplification — is independent of that in the embellished transition found before it.

Embellished transitions were then categorized according to class, which are defined and shown in Table 2 and Figure 2, and the location of these embellishments within the call was noted. This was done by dividing the call into thirds and then determining whether the embellishment was made at the beginning, middle, or end.

To test the repeatability of the categorizations for transition types and embellishment classes, two untrained volunteers were given a random subsample of spectrograms of calls ($N = 15$), along with definitions of transition types and embellishment classes (see Tables 1 and 2; Figures 1 and 2 for examples of these), and asked to complete the same task. In these trials, 83% of the classifications as to type matched those of the primary study, as did 83% of the classification of embellishment classes. This small sample thus showed general agreement that call transition types and classes can be reliably distinguished according to the classification methods used in this study.

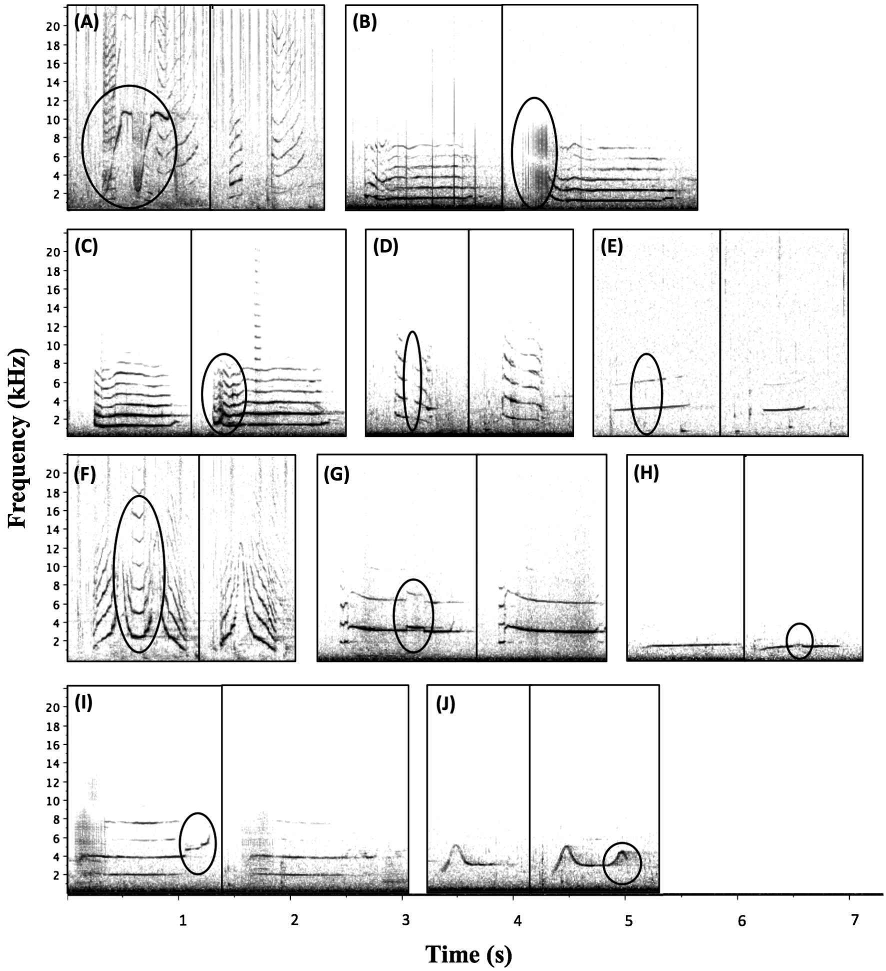

Figure 2. Spectrograms of different classes of embellishment found in the repeated call sequences of long-finned pilot whales including (A) biphonation (B) buzz/pulse (C) change (D) gap (E) lengthening (F) looping (G) step (H) wobble/hump (I) upsweep and (J) unclassified tonal additions presented in the order in which they were found (embellished areas circled).

3. Results

3.1. Transition types in repeated call sequences

Transitions between stereotyped calls within a repeated sequence were frequently stable, with little or no differences between consecutive calls occurring in 49% ($N = 170$) of transitions, but modification between calls was

Table 3.
Contingency table of first (A → B) and second (B → C) transition types with Pearson Chi-Square value of the null hypothesis that first and second transition types in the repeated call sequences of long-finned pilot whales are made independently of one another.

		B → C			Row total
		Stable	Embellished	Morphed	
A → B	Stable	63	21	4	88
	Embellished	13	35	3	51
	Morphed	6	2	27	35
Column total		82	58	34	174

$\chi^2_4 = 126.8$, $p < 0.001$.

also frequent with embellishment of a call occurring in 31% ($N = 109$) of transitions and morphing found in 20% ($N = 69$). When looking at the second transition in relation to the preceding one in the sequence, whales tend to use the same type of transition more often than expected by chance (Table 3). If a whale begins the repeated call sequence using a stable transition it most often continues that way, if it embellished then it continues to do so, and if it morphed the call it often will continue in the second transition with the same type. Morphed transitions between calls were rarely followed by stable ones, and even less commonly by embellished transitions, with these patterns in reverse being uncommon as well. However, stable transitions were followed by embellished ones occasionally and embellished by stable, though these were less frequent then repeated call sequences where only a single transition type was noted. Therefore, transition types within a sequence do not appear to be made independently of one another.

3.2. Embellishment patterns and categorization

In the majority of the 35 sequences where an embellished transition was followed by another of the same type, there was an alternating addition and subtraction pattern, where a call would be ornamented, then simplified or vice versa (Table 4). Only seven sequences did not have this alternating pattern.

All embellished transitions in this study were categorized into classes and the relative locations within the calls were noted (Table 5). The most common classes of embellishments in repeated call sequences were general tonal

Table 4.
Contingency of embellishment for first (A → B) and second (B → C) transition types (addition and subtraction) with Pearson Chi-Square value of the null hypothesis that the second embellished transition type — addition or subtraction — is made independent of that which was used in the first embellished transition.

		B → C		Row total
		Addition	Subtraction	
A → B	Addition	4	17	21
	Subtraction	11	3	14
Column total		15	20	35

$\chi_1^2 = 12.2$, $p < 0.001$.

additions and subtractions that did not fit into defined categories, as well as buzzes and pulses. Other embellishment modifications observed were: the addition of a higher or lower frequency component, a specific section of the call being changed, the addition of a gap, a significant increase in length of a section of the call, looping patterns, addition of steps, upsweeps at the beginning or end, and finally a wobble in one section of the call. Some embellishment classes were seen in specific locations within the call, such as buzzes which were almost always observed at the beginning, looping and

Table 5.
Chart of types of embellishment contrasted with location in the call for embellished transitions in repeated call sequences of long-finned pilot whales with the most commonly observed location within a call indicated by an asterisk.

	Beginning	Middle	End	All	Other	Total
Biphonation	0	1	0	5*	0	6
Buzz/pulse	19*	0	1	0	0	20
Changed	3*	0	3*	0	0	6
Gap	5	8*	1	0	0	14
Length	1	2	3*	0	0	6
Looping	0	2	7*	0	0	9
Step	1	3*	3*	0	0	7
Upsweep	3	0	7*	0	0	10
Wobble	2	10*	2	0	0	14
Unclassified add/sub	6	4	8*	0	2	20
Column total	40	30	35	5	2	112

upsweeps at the end, and wobbles in the middle (Table 5). Others seemed to be relatively equally distributed over the length of a call, such as the unclassified tonal additions and subtractions and the step embellishment. For three call transitions there were two embellishments made to the call simultaneously, which resulted in a total number of 112 embellishments categorized.

4. Discussion

Although the repeated call sequences produced by long-finned pilot whales are often stable in nature, this study found that modification — embellishment or morphing — between repeated calls occurs in over 50% of transitions. These vocal repetitions show characteristic patterns — particularly the use of a single transition type over consecutive transitions within a repeated call sequence and the alternating of embellished transitions between simplified and more complex calls — yet at the same time the amount of variation found within these sequences is remarkable. The ubiquity and arrangement of embellishment, along with the non-independence of transitions in repeated call sequences, leads us to consider whether there are underlying functions behind these patterns or whether these modifications are simply artefacts of the pilot whale's fluid vocal repertoire (Taruski, 1979; Weilgart & Whitehead, 1990).

4.1. Patterns and potential functions of embellishment

Perhaps the most intriguing observation of this study is the high frequency of the embellished transition type, where only one section of the call is altered. Vocal sequences produced by other species, including examples amongst cetaceans (Ford, 1989; Janik et al., 2013; Sayigh et al., 2013), pinnipeds (Stirling et al., 1987) and birds (McGregor et al., 1981), are often found to contain repeated calls or phrases that are nearly identical to each other. Why then is call modification, particularity embellishment, so common in the repeated call sequences of long-finned pilot whales? The high rates of modification could result directly from the fluid nature of their vocal repertoire (Taruski, 1979). Alternatively, the embellishment of calls may relay specific information to signal receivers. If this is the case, the patterns and nature of these transitions may give insight into the reason behind these modifications.

There are several possible explanations for the alternating addition-subtraction pattern of ornamentation and simplification, which relate to the kind of embellishment that was added. Embellished call modification may be related to the emotional state of the signal producer. In 8% of embellished transitions we observed a variation in the number of repetitive elements that the call which was being repeated contained, similar in nature to what has been described as looping in the signature whistles of bottlenose dolphins (Caldwell et al., 1990). Though these made up only a small percentage of categorized embellishments, it is possible that they could operate in a similar manner to looping, which has been linked to stress (Esch et al., 2009). Another possible explanation for the observed pattern of ornamentation and simplification found in embellished call sequences is that whales add certain features to their calls in order to send locational information to other whales. It was observed that the upper frequency component of the biphonated calls made by killer whales was directional, leading to the hypothesis that these calls are used to help with coordination (Miller, 2002). Clicks and buzzes — which can be used for communicative purposes beyond their well-established echolocation functions (Whitehead & Weilgart, 1991; Rankin et al., 2007) — are also directional in nature (Bradbury & Vehrencamp, 2011), and could be therefore used to give other individuals information on the location and orientation of the caller. An artefact of recording with an omnidirectional hydrophone is that there is the possibility that in some instances these directional vocalizations may only be heard when the whale is oriented suitably. Because of the alternating patterns of ornamentation and simplification found in many sequences along with the consistent amplitude and rhythmic repetition of calls, few sequences were likely included in our study where whales were changing direction with enough consistency to produce these interchanging repetitions. This being said, directional changes by the signal producer resulting in the loss or gain of high frequency components provide a possible explanation for some transitions observed in these sequences — further studies into the directionality of pilot whale calls and the resulting recorded signals are needed to determine to what degree directionality of call elements affects recorded signals. Together buzzes and pulses, along with biphonation, accounted for 23% of embellished transitions observed in this study. Given that pilot whales are a very social species living in a group setting where coordination would be important, a reasonable explanation for embellishments involving buzzes or clicks as well as upper frequency components is that these modifications function in conveying locational information to signal receivers.

The alternating pattern of ornamentation and simplification may also be explained in some cases by two whales producing similar, but at the same time distinctive, versions of the same call in a non-overlapping rhythmic pattern. Similarly, two whales producing a similar vocalization at significantly different depths could also result in a difference of amplitude and call duration (Jensen et al., 2011). The latter explanation is unlikely for differences observed in this study, as pilot whales in our area were rarely recorded in coastal waters deeper than 80 m, within which range Jensen et al. (2011) found little variation in call measures. Additionally, our definition of repeated call sequences includes only those where calls are roughly equally spaced, have similar amplitude, and are without any overlap — thus likely excluding the majority of sequences where two or more whales are vocalizing. However, we may have included a few vocal interactions between two (or more) whales where timing between calls was evenly spaced and both individuals produced the same call type that achieved similar received amplitudes at the hydrophone. Though antiphonal duetting (two individuals vocally interacting with each other in a reciprocal manner (Hall, 2004)) has not been well established or studied in cetaceans, call-matching (one individual makes a sequence of calls, and another attempts to match each call of the first) has been observed in a variety of species and has an assortment of proposed functions ranging from providing locational information (Janik, 2000; Miller et al., 2004) to social bonding (Schulz et al., 2008). In order to determine whether some of these cases, such as that of sperm whales, are coordinated duets rather than simply the response of one individual to another's signal, studies focusing on timing and specific context of both individuals are needed. While considering the possibility of two signallers in some sequences, it is important to note that mimicry has been well documented in a variety of cetacean species. Mimicry is found in bottlenose dolphins, which have been found to mimic not only another individual's signature whistle (Tyack, 1986), but sounds found outside the vocal repertoire of this species such as human voice (Lilly, 1965) and computer generated sounds (Richards et al., 1984). Belugas have also been found to imitate human speech (Ridgway et al., 2012). The precision of the vocal imitations observed in cetaceans suggest that in a few cases it may be difficult to differentiate between one whale modifying calls and the alternative where one whale is imitating the call of another if the latter happens to be in a stereotyped temporal pattern with similar amplitude.

4.2. Potential functions of morphing

Morphed transitions between consecutive calls in sequence were less common than both stable and embellished, but nonetheless made up a substantial portion of transitions. Possible reasons for the high frequency of morphing include the phenomenon of infant babbling and alteration due to the emotional state of the individual. In regard to infant babbling, we know that many species, including cetaceans and primates (Elowson et al., 1998; Vergara & Barrett-Lennard, 2008), show vocal development in young that involves learning calls over time (Fripp et al., 2005). Young individuals produce sequences of calls that at first are quite variable, becoming more stereotyped as the age of the animal increases (Vergara & Barrett-Lennard, 2008). It is possible that some repeated call sequences with morphed transitions are the result of vocal learning in pilot whale calves, as many groups are seen with young. Repeated call sequences as a whole are not more commonly heard from groups with calves (Zwamborn & Whitehead, 2017), but a more specific study of transition types in relation to group composition is needed to determine whether pilot whale calves may be a predictor for the presence of sequences with morphed transitions.

Another possibility for the presence of morphed call sequences would be that the transitions are related to the emotional state of the signaller, with sequences displaying morphing perhaps indicative of an excited or stressed individual. Just as aberrant calls in killer whales were found associated with socializing and periods of high excitement (Ford, 1989), perhaps the more variable calls heard from pilot whales in repeated sequences are representative of emotional state. Further study into the context of morphed transitions is needed to determine if this is the case.

4.3. Innovation as an explanation for call modification in pilot whales?

There is also a possibility that call modification observed in repeated call sequences may be a product of innovation for innovation's sake. Just as innovation is popular in many human cultures today, it has also been observed in non-human species such as chimpanzees, *Pan troglodytes* (Ramsey et al., 2007) and swamp sparrows, *Melospiza georgiana* (Nowicki et al., 2001). In fact, many definitions of both culture and intelligence include innovation as a key component (Kummer & Loy, 1971; van Schaik & Pradhan, 2003). Innovation has not yet been studied in pilot whales, though examples from other cetacean species include the novel play behaviour of bottlenose dolphin calves, which is thought to have an important role in cultural innovation (Kuczaj et al., 2006), and the initiation of lobtail feeding amongst New England humpback whales (*Megaptera novaeangliae*) (Weinrich et al., 1992). An example of behavioural innovation for the sake of innovation was a short-lived fad seen amongst the southern 'resident' killer whales, where one whale began pushing dead salmon around with its head and it was not long before individuals from other pods were also seen exhibiting the same behaviour (Whitehead et al., 2004). If different kinds of innovation have been described amongst other species of cetaceans, might pilot whales be also doing this vocally?

4.4. Conclusions

Modification within the repeated call sequences of long-finned pilot whales occurs frequently, including morphed as well as a diverse range of embellished transitions. This vocal variation may be linked to the information being transferred through these call repetitions or innovation. Future research using a hydrophone array would make it possible to look at individual behaviour or location with respect to the larger group, and other data valuable for understanding call context. Studies using acoustically-recording suction cup tags on multiple whales within a group may also provide insight into the social and acoustic framework of these modified calls. Even at a group level, an investigation into context as it is related to the frequency of different transition types may give insight into whether there are differences in the situational use of stable, embellished and morphed transitions, including more specifically the classes of embellishments categorized in this study.

Acknowledgements

Thanks to everyone who was involved in the field and lab during the 16-years of this study, especially the graduate students, research assistants, coop students, and volunteers who collected, organized, and analysed much of the data leading up to this study. A special thanks to the captains and crews of the "Double-Hookup" (Captain Mark's Whale and Seal Cruise) and "Northern Gannet" (Captain Cox's Whale Watch), who helped facilitate these field studies. We also would like to thank the anonymous referees whose insight helped improve this manuscript. Finally, thanks to the Natural Sciences and Engineering Research Council of Canada (NSERC) for providing the funding required to run these field seasons.

References

Auger-Méthé, M. & Whitehead, H. (2007). The use of natural markings in the studies of long-finned pilot whales (*Globicephala melas*). — Mar. Mammal Sci. 23: 77-93.

Augusto, J.F., Frasier, T.R. & Whitehead, H. (2017). Social structure of long-finned pilot whales (*Globicephala melas*) off northern Cape Breton Island, Nova Scotia. — Behaviour 154: 509-540.

Bioacustics Research Program (2014). Raven Pro: interactive sound analysis software. The Cornell Lab of Ornithology, Ithaca, NY, available online at http://www.birds.cornell.edu/raven.

Boogert, N.J., Giraldeau, L.A. & Lefebvre, L. (2008). Song complexity correlates with learning ability in zebra finch males. — Anim. Behav. 76: 1735-1741.

Bradbury, J.W. & Vehrencamp, S.L. (2011). Principles of animal communication. — Sinauer Associates, Sunderland, MA.

Busnel, R.G. & Dziedzic, A. (1966). Acoustic signals of the pilot whale *Globicephala melaena* and of the porpoises *Delphinus delphis* and *Phocoena phocoena*. — In: Whales, dolphins, and porpoises (Norris, K.S., ed.). University of California Press, Berkeley, CA, p. 607-646.

Caldwell, M.C., Caldwell, D. & Tyack, P.L. (1990). Review of the signature-whistle hypothesis for the Atlantic bottlenose dolphin. — In: The bottlenose dolphin (Leatherwood, S. & Reeves, R.R., eds). Academic Press, San Diego, CA, p. 199-234.

Elowson, A.M., Snowdon, C.T. & Lazaro-Perea, C. (1998). Infant "babbling" in a nonhuman primate: complex vocal sequences with repeated call types. — Behaviour 135: 643-664.

Esch, H.C., Sayigh, L.S., Blum, J.E. & Wells, R.S. (2009). Whistles as potential indicators of stress in bottlenose dolphins (*Tursiops truncatus*). — J. Mammal. 90: 638-650.

Ford, J.K.B. (1989). Acoustic behaviour of resident killer whales (*Orcinus orca*) off Vancouver Island, British Columbia. — Can. J. Zool. 67: 727-745.

Ford, J.K.B. (1991). Vocal traditions among resident killer whales (*Orcinus orca*) in coastal waters of British Columbia. — Can. J. Zool. 69: 1454-1483.

Fripp, D., Owen, C., Quintana-Rizzo, E., Shapiro, A., Buckstaff, K., Jankowski, K., Wells, R. & Tyack, P.L. (2005). Bottlenose dolphin (*Tursiops truncatus*) calves appear to model their signature whistles on the signature whistles of community members. — Anim. Cogn. 8: 17-26.

Gero, S., Whitehead, H. & Rendell, L. (2016). Individual, unit, and vocal clan level identity cues in sperm whale codas. — Roy. Soc. Open Sci. 3: 150372.

Hall, M.L. (2004). A review of the hypotheses for the functions of avian duetting. — Behav. Ecol. Sociobiol. 55: 415-430.

IBM (2013). IBM SPSS Statistics for Mac. IBM, Armonk, NY.

Janik, V.M., King, S.L., Sayigh, L.S. & Wells, R.S. (2013). Identifying signature whistles from recordings of groups of unrestrained bottlenose dolphins (*Tursiops truncatus*). — Mar. Mammal Sci. 29: 109-122.

Janik, V.M. (2000). Whistle matching in wild bottlenose dolphins (*Tursiops truncatus*). — Science 289: 1355-1357.

Jensen, F.H., Perez, J.M., Johnson, M., Soto, N.A. & Madsen, P.T. (2011). Calling under pressure: short-finned pilot whales make social calls during deep foraging dives. — Proc. Roy. Soc. Lond. B: Biol. Sci. 278: 3017-3025.

Kuczaj, S.A., Makecha, R., Trone, M., Paulos, R.D. & Ramos, J.A. (2006). Role of peers in cultural innovation and cultural transmission: evidence from the play of dolphin calves. — Int. J. Comp. Psychol. 19: 223-240.

Kummer, H. & Loy, J. (1971). Social behaviour and habitat (book review: Primate societies: group techniques of ecological adaptation). — Science 174: 49-51.

Lilly, J.C. (1965). Vocal mimicry in *Tursiops*: ability to match numbers and durations of human vocal bursts. — Science 147: 300-301.

McGregor, P.K., Krebs, J.R. & Perrins, C.M. (1981). Song repertoires and lifetime reproductive success in the great tit (*Paris major*). — Am. Nat. 118: 149-159.

Miller, P.J.O., Shapiro, A.D., Tyack, P.L. & Solow, A.R. (2004). Call-type matching in vocal exchanges of free-ranging resident killer whales, *Orcinus orca*. — Anim. Behav. 67: 1099-1107.

Miller, P.J.O. (2002). Mixed-directionality of killer whale stereotyped calls: a direction of movement cue? — Behav. Ecol. Sociobiol. 52: 262-270.

Nemiroff, L. & Whitehead, H. (2009). Structural characteristcs of pulsed calls of long-finned pilot whale *Globicephala melas*. — Bioacoustics 19: 67-92.

Nowicki, S., Searcy, W.A., Hughes, M. & Podos, J. (2001). The evolution of bird song: male and female response to song innovation in swamp sparrows. — Anim. Behav. 62: 1189-1195.

Nowicki, S. & Searcy, W.A. (2011). Are better singers smarter? — Behav. Ecol. 22: 10-11.

Ottensmeyer, C.A. & Whitehead, H. (2003). Behavioural evidence for social units in long-finned pilot whales. — Can. J. Zool. 81: 1327-1338.

Ramsey, G., Bastian, M.L. & van Schaik, C. (2007). Animal innovation defined and operationalized. — Behav. Brain Sci. 30: 393-437.

Rand, S. & Ryan, M.J. (1981). The adaptive significance of a complex vocal repetoire in a neotropical frog. — Z. Tierpsychol. 57: 209-214.

Rankin, S., Oswald, J.N., Barlow, J. & Lammers, M.O. (2007). Patterned burst-pulse vocalizations of the northern right whale dolphin, *Lissodelphis borealis*. — J. Acoust. Soc. Am. 121: 1213-1218.

Richards, D.G., Wolz, J.P. & Herman, L.M. (1984). Vocal mimicry of computer-generated sounds and vocal labeling of objects by a bottlenosed dolphin, *Tursiops truncatus*. — J. Comp. Psychol. 98: 10-28.

Ridgway, S., Carder, D., Jeffries, M. & Todd, M. (2012). Spontaneous human speech mimicry by a cetacean. — Curr. Biol. 22: 860-861.

Sayigh, L.S., Quick, N., Hastie, G. & Tyack, P. (2013). Repeated call types in short-finned pilot whales, *Globicephala macrorhynchus*. — Mar. Mammal Sci. 29: 312-324.

Schulz, T.M., Whitehead, H., Gero, S. & Rendell, L. (2008). Overlapping and matching of codas in vocal interactions between sperm whales: insights into communication function. — Anim. Behav. 76: 1977-1988.

Sewall, K.B., Soham, J.A., Peters, S. & Nowicki, S. (2013). Potential trade-off between vocal ornamentation and spatial ability in a songbird. — Biol. Lett. 9: 20130344.

Stirling, I., Calvert, W. & Spencer, C. (1987). Evidence of stereotyped underwater vocalizations of male Atlantic walruses (*Odobenus rosmarus rosmarus*). — Can. J. Zool. 65: 2311-2321.

Strager, H. (1995). Pod-specific call repertoires and compound calls of killer whales, *Orcinus orca* Linnaeus, 1758, in the waters of northern Norway. — Can. J. Zool. 73: 1037-1047.

Taruski, A.G. (1979). The whistle repetoire of the North Atlantic pilot whale (*Globicephala melaena*) and its relationship to behaviour and the environment. — In: Behav. mar. anim., Vol. 3 (Winn, H.E. & Olla, B.L., eds). Plenum Press, New York, NY, p. 345-368.

Tyack, P.L. (1986). Whistle repertoires of two bottlenosed dolphins, *Tursiops truncatus*: mimicry of signature whistles? — Behav. Ecol. Sociobiol. 18: 251-257.

van Schaik, C.P. & Pradhan, G.R. (2003). A model for tool-use traditions in primates: implications for the coevolution of culture and cognition. — J. Hum. Evol. 44: 645-664.

Vergara, V. & Barrett-Lennard, L.G. (2008). Vocal development in a beluga calf (*Delphinapterus leucas*). — Aquat. Mamm. 34: 123-143.

Wagner, W.E. (1989). Graded aggressive signals in Blanchard's cricket frog: vocal responses to opponent proximity and size. — Anim. Behav. 38: 1025-1038.

Weilgart, L.S. & Whitehead, H. (1990). Vocalizations of the North Atlantic pilot whale (*Globicephala melas*) as related to behavioral contexts. — Behav. Ecol. Sociobiol. 26: 399-402.

Weinrich, M.T., Schilling, M.R. & Belt, C.R. (1992). Evidence for aquisition of a novel feeding behaviour: lobtail feeding in humpback whales, *Megaptera novaeangliae*. — Anim. Behav. 44: 1059-1072.

Whitehead, H., Rendell, L., Osborne, R.W. & Würsig, B. (2004). Culture and conservation of non-humans with reference to whales and dolphins: review and new directions. — Biol. Conserv. 120: 431-441.

Whitehead, H. & Weilgart, L.S. (1991). Patterns of visually observable behaviour and vocalizations in groups of female sperm whales. — Behaviour 118: 275-296.

Zwamborn, E.M.J. & Whitehead, H. (2017). Repeated call sequences and behavioural context in long-finned pilot whales off Cape Breton, Nova Scotia, Canada. — Bioacoustics 26: 169-183. DOI:10.1080/09524622.2016.1233457.