

Nonlinear phenomena in the vocalizations of North Atlantic right whales (*Eubalaena glacialis*) and killer whales (*Orcinus orca*)

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Nonlinear phenomena or nonlinearities in animal vocalizations include features such as subharmonics, deterministic chaos, biphonation, and frequency jumps that until recently were generally ignored in acoustic analyses. Recent documentation of these phenomena in several species suggests that they may play a communicative role, though the exact function is still under investigation. Here, qualitative descriptions and quantitative analyses of nonlinearities in the vocalizations of killer whales (*Orcinus orca*) and North Atlantic right whales (*Eubalaena glacialis*) are provided. All four nonlinear features were present in both species, with at least one feature occurring in 92.4% of killer and 65.7% of right whale vocalizations analyzed. Occurrence of biphonation varied the most between species, being present in 89.0% of killer whale vocalizations and only 20.4% of right whale vocalizations. Because deterministic chaos is qualitatively and quantitatively different than random or Gaussian noise, a program (TISEAN[®]) designed specifically to identify deterministic chaos to confirm the presence of this nonlinearity was used. All segments tested in this software indicate that both species do indeed exhibit deterministic chaos. The results of this study provide confirmation that such features are common in the vocalizations of cetacean species and lay the groundwork for future studies. © 2007 Acoustical Society of America. [DOI: 10.1121/1.2756263]

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I. INTRODUCTION

Analyses of animal vocalizations have provided great insights into the communicative functions of many vocal signals, however, some features that may play a communicative role have been largely ignored (Tokuda *et al.*, 2002; Fitch *et al.*, 2002). One set of unexplored features, referred to as “nonlinear phenomena” or “nonlinearities” includes: subharmonics, frequency jumps, biphonation, and deterministic chaos. These complex features are produced by nonlinearities in the vocal production system, where rather simple neural commands to the system can result in highly complex and individually variable acoustic signals (Fitch *et al.*, 2002). Historically, vocalizations with these features have been either excluded from analyses (e.g. Hauser, 1993), ignored (e.g. Rendall *et al.*, 1996), or grouped together as “atonal” (e.g. Parks and Tyack, 2005) with analyses focusing primarily on harmonic signals. These phenomena have recently,

however, been documented in the vocal output of humans and other primates, birds, dogs, deer, and manatees (Mende *et al.*, 1990; Herzel *et al.*, 1995; Riede *et al.*, 1997; Wilden *et al.*, 1998; Fee *et al.*, 1998; Fletcher, 2000; Riede *et al.*, 2000; Fitch *et al.*, 2002; Facchini *et al.*, 2003; Robb, 2003; Neubauer *et al.*, 2004; Riede *et al.*, 2004; Mann *et al.*, 2006; Volodina *et al.*, 2006).

The presence of such phenomena in the vocalizations of several species suggests that these features may play an important communicative role. In some cases they may form the bulk of an individual’s vocalizations and/or of vocalizations of individuals within a certain age range (Fitch *et al.*, 2002). While this exact role is still under investigation, individual recognition, unpredictability, and/or indication of physical condition have been suggested as possible functions (Wilden *et al.*, 1998; Owren and Rendall, 2001; Fitch *et al.*, 2002; Mann *et al.*, 2006; Volodina *et al.*, 2006; Riede *et al.*, 2007). Before the testing of specific functions can begin, however, the occurrence and structure of these phenomena must be documented. Knowing the relative presence/prevalence of such features can indicate their level of importance and their structure may be indicative of their function.

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In this study, qualitative descriptions and quantitative analyses of nonlinear phenomena in the vocalizations of fish-eating, or “resident,” killer whales and North Atlantic right whales (hereafter referred to as right whales) are provided. These two mammals are representative of the two suborders of Cetacea (whales, dolphins and porpoises); killer whales belong to the suborder Odontoceti (the toothed whales) and right whales belong to the suborder Mysticeti (the baleen whales). Power spectral analyses and visual inspection of spectrograms were used to identify subharmonics, biphonation, frequency jumps, and deterministic chaos in the vocalizations of these species, but another method was applied to determine if segments we thought were chaotic were indeed chaotic, as chaos can resemble Gaussian noise. Deterministic chaos is generated by a nonlinear process and is therefore predictable once the underlying nonlinear dynamics are determined; Gaussian noise, however, is random and thus unpredictable. To determine the underlying dynamics of suspected chaotic segments found within these species vocalizations, the software package TISEAN® (Time Series Analysis; Hegger *et al.*, 1999; Kantz and Schreiber, 2004) was used, which reconstructs the attractor of the underlying dynamics of the signal in the phase space and gives a measure of the unpredictability of the system. The method of surrogate data was also applied to test the null hypothesis that the signals were stationary, linear, random Gaussian signals (Schreiber and Schmitz, 2000). In addition, behavioral functions of nonlinear phenomena and/or their underlying production mechanisms are explored as these two species differ in their social structure and sound production mechanisms.

II. METHODS

Acoustic data from right whales were collected on multiresensor digital acoustic recording tags (Johnson and Tyack, 2003; Nowacek *et al.*, 2004), which were attached noninvasively to animals in the Bay of Fundy, Canada in 2001, 2002, and 2005. Tags recorded sounds at sampling rates of $F_s = 16$ kHz (2001), $F_s = 32$ kHz (2002), and $F_s = 96$ kHz (2005) with a 12-bit resolution and received sounds from both the tagged whale and other whales in the area as well as ambient noise. Because high signal-to-noise ratio recordings are essential when investigating the occurrence of nonlinear phenomena, as significant background noise can confound the analyses, only vocalizations from the focal animal or from an animal vocalizing nearby the focal animal and those generally free of ambient noise were included in the analyses.

Recordings of northern resident killer whales in Johnstone Strait, British Columbia, were made during August and September of 1998 and 1999 using a towed array of 16 hydrophones connected to multi-channel TASCAM® recorders, which digitally recorded sounds at a sampling rate of 48 kHz. Efforts were made to obtain vocalizations only from focal whales by keeping the focal animal to one side of the array at a distance of approximately 100 m (Miller and Tyack, 1998; Nousek *et al.*, 2006). Only vocalizations recorded from identified individuals and that were generally

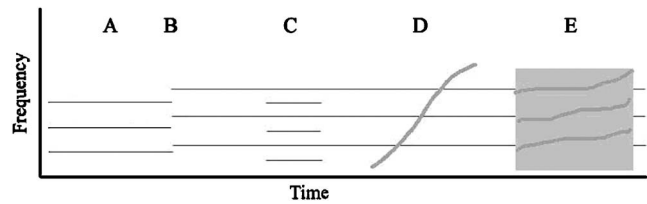


FIG. 1. Schematic narrowband spectrograms illustrating stable limit cycle (a), frequency jump (b), subharmonics (c), biphonation (d) and deterministic chaos (E) (modified after Fig. 1 from Riede *et al.*, 2004).

free from ambient noise were included in the analysis. Killer whales produce calls at diverse source pressure levels, and call types known to contain biphonation are produced at higher intensities than call types without biphonation (Miller, 2006). Since we used only the highest signal-to-noise ratio calls, call types without biphonation were generally excluded from our analyses. Thus, our sample cannot be considered fully representative of the killer whale repertoire.

Analyses of nonlinear features in calls followed previously applied methods (Mann *et al.*, 2006; Riede *et al.*, 2004; Wilden *et al.*, 1998). The vocalizations were analyzed using the fast Fourier transformation (FFT), with 1024 or 2048 points FFT order, hanning windows, and a 75% overlapping of the successive windows. Spectrograms were isolated and inspected for the presence of nonlinearities using Adobe Audition® on a PC-type computer. Each vocalization was judged to include or not include each of the four nonlinear types. While all vocalizations were of generally high signal-to-noise ratio and free from ambient noise, the possibility for questionable features in signals was still present as there are limitations on recording wild animals. Thus, when a feature was in question of being scored (e.g., chaotic segment or effect of recordings) the conservative option was always taken and the feature was not scored.

The basic structures of nonlinear phenomena are displayed in Fig. 1. In the simplest case, the synchronization of vocal folds lead to periodic, regular, self-sustained oscillations that result in a purely harmonic vocalization termed a *stable limit cycle* (Fig. 1(a), a fundamental frequency, F_o , with harmonics that are integer multiples of that frequency). Because the dynamics of the larynx as a whole are “nonlinear,” any and all sounds, including these harmonic signals, represent nonlinear phenomena (Riede *et al.*, 2004). For purposes of this study, however, we will contrast these harmonic, stable limit cycle signals with all other nonlinear signals.

A *frequency jump* represents a break in the F_o in which the vibration rate increases or decreases abruptly and discontinuously (Fig. 1(b)); it is qualitatively different from continuous, smooth modulation. Frequency jumps represent regime instability, i.e., the oscillation of the vocal folds may jump unpredictably (Wilden *et al.*, 1998; Riede *et al.*, 2004).

Subharmonics can occur when the natural vibratory frequencies of the two oscillators are different (Fig. 1(c); e.g., if there is more tension on one vocal fold than the other). This results in additional spectral components which appear as fractional integer values of an identifiable F_o (e.g., $F_o/2$, $F_o/3$, and so on) visible upon acoustic analysis. Energy ap-

appears on a spectrogram at evenly spaced intervals below the F_o and between adjacent harmonics (Fitch *et al.*, 2002).

Biphonation can be defined as two similar but unrelated, independent frequencies being produced simultaneously (Fig. 1(d)). On a spectrogram biphonation appears as two distinct, nonparallel autonomous fundamental frequencies (F_o and G_o) with no simple ratio relating them (e.g., 1/2 or 1/3). Biphonation can occur if the coupling between two oscillators is weak or if several oscillators are interacting (Brown and Cannito, 1995; Wilden *et al.*, 1998). Biphonation can also be found in the form of sidebands, which appear adjacent to harmonics and are associated with cyclic amplitude fluctuations in the time series waveform (Riede *et al.*, 2000; Riede *et al.*, 2004; Wilden *et al.*, 1998). Sidebands have previously been described in killer whale vocalizations, appearing off the high frequency component (Miller *et al.*, 2007).

Deterministic chaos refers to periods of nonrandom noise that are produced by desynchronized coupled oscillators (Fig. 1(e)). It is characterized by having energy across a relatively broad frequency band with some residual periodic energy related to the previous harmonic components. Deterministic chaos can often be interrupted by windows of stable limit phonation or subharmonic phonation (Neubauer *et al.*, 2004). After the initial inspection of spectrograms and power spectral analyses for deterministic chaos were completed, two segments from each species which we suspected were chaotic and which were representative across several calls of each species were cut from the original vocalizations and were analyzed in a similar manner as Facchini *et al.* (2003) and Mann *et al.* (2006) using the TISEAN[®] software package (Hegger *et al.*, 1999; Kantz and Schreiber, 2004).

The method of surrogate data was used to test the null hypothesis that the signals were created by a stationary, linear, random Gaussian process (Hegger *et al.*, 1999; Schreiber and Schmitz, 2000; Kantz and Schreiber, 2004). This is a Monte Carlo technique which assesses the significance of the results by comparing the original time series data to appropriate realizations of the null hypothesis (Hegger *et al.*, 1999). Surrogates were made with the TISEAN[®] program *surrogates*, which generates constrained realizations of the original time series data; random Fourier transforms of the original data are created that have the same power spectrum and the same single time distribution as the observed data but that differ in phase (Hegger *et al.*, 1999). The TISEAN program *predict* was then used to compare the original time series data to the surrogates to assess the significance of the results. If the value computed for the original time series data was significantly different than the values computed for the surrogate data, $P \leq 0.05$, the null hypothesis was rejected and nonlinearity was detected (Theiler *et al.*, 1992).

The method of delays was used to reconstruct the attractor of the underlying dynamics in the phase space in the four segments which we suspected were chaotic (Hegger *et al.*, 1999). Here, vectors were formed in a new space, termed the embedding space, from time delayed values of the scalar measurements: $s_n = (s_{n-(m-1)\tau}, s_{n-(m-2)\tau}, \dots, s_n)$. The number m of elements is called the *embedding dimension* and the time τ is the *delay* (for a review see Kantz and Schreiber, 2004).

The TISEAN[®] *mutual* function was used to determine the appropriate time delay τ of each segment. This delay represents a measure of correlation existing between two consecutive components of m -dimensional vectors used in the trajectory reconstruction and its value is taken as the first minimum of the average mutual information function (Facchini *et al.*, 2003). The delay is then used in the analysis of the embedding dimension m , the minimum dimension at which a reconstructed attractor can be considered completely unfolded with no overlapping in the reconstructed trajectories (Facchini *et al.*, 2003; Kantz and Schreiber, 2004). The embedding dimensions were found using the method of false nearest neighbors with the TISEAN[®] program *false_nearest*. When an attractor is poorly reconstructed, a false neighbor can occur at a point of trajectory intersection. As the dimension increases, the attractor is unfolded at higher fidelity and the number of false neighbors decreases to zero. The first dimension with no overlapping points is the embedding dimension (Facchini *et al.*, 2003). The *false_nearest* function allows specification of a minimal temporal separation of valid neighbors.

The delay and embedding dimensions were used in the analysis of the Lyapunov exponents, which quantify the strength of chaos (Hegger *et al.*, 1999; Kantz and Schreiber, 2004). Chaotic systems display a sensitive dependence on the initial conditions of a trajectory. The Lyapunov exponents are a measure of the time it takes for the trajectories to diverge starting from infinitesimally close initial conditions and therefore give a coordinate-independent measure of the local stability properties of a trajectory (Facchini *et al.*, 2003; Kantz and Schreiber, 2004).

Since a trajectory evolves in an N -dimensional state space, there are N exponents that are arranged in the spectrum of Lyapunov exponents, which was generated by the TISEAN[®] *lyap_spec* function (Hegger *et al.*, 1999; Facchini *et al.*, 2003). A trajectory was considered chaotic if it had at least one positive exponent in the Lyapunov Spectrum since chaotic segments are identified as having a maximal Lyapunov exponent (MLE) between zero and infinity (noise has a MLE of infinity and a stable limit cycle has a MLE of zero; Kantz and Schreiber, 2004). The exact value of the MLE was found by taking the maximum linear regression of the curves generated by the TISEAN[®] *lyap_k* function in the region between 0 and 20 iterations (Hegger *et al.*, 1999; Facchini *et al.*, 2003; Kantz and Schreiber, 2004). The MLE is a measure of the unpredictability of the system and it gives a good characterization of the underlying dynamics (note: there is some uncertainty in the estimation of the MLE; Kantz and Schreiber, 2004).

To verify that TISEAN[®] was correctly identifying segments as deterministic chaos, we also tested a generated harmonic and a generated random signal to compare with our suspected chaotic segments. The harmonic segment resulted in zero positive exponents in the Lyapunov spectrum indicating that it was a stable limit cycle; the random noise signal had embedding dimensions that were greater than expected for a chaotic signal (>20). Thus, the program could correctly distinguish between chaotic, harmonic, and random segments.

TABLE I. Frequency of occurrence of nonlinear phenomena in the analyzed right whale (RW) and killer whale (KW) vocalizations: frequency jumps (FJ), subharmonics (SH), biphonation (BP), and deterministic chaos (DC).

	Total	Limit cycles only (%)	Total with at least one nonlinearity (%)	Total with more than one nonlinearity (%)	FJ (%)	SH (%)	BP (%)	DC (%)
RW	172	59 (34.3)	113 (65.7)	36 (20.9)	32 (18.6)	8 (4.7)	35 (20.4)	87 (50.6)
KW	173	13 (7.6)	160 (92.4)	98 (56.6)	42 (24.3)	11 (6.4)	154 (89.0)	68 (39.3)

Generated segments were utilized here because the TISEAN[®] software is sensitive to factors such as duration of segment, width of frequency band, and background noise.

III. RESULTS

Nonlinear phenomena were present in the vocalizations analyzed of both species, with 92.4% of the killer whale and 65.7% of the right whale vocalizations displaying at least one nonlinear feature and 56.6% and 20.9%, respectively, displaying more than one feature (Table I; Figs. 2 and 3). Additionally, all four types of nonlinear phenomena occurred in the vocalizations of both whales albeit at different rates. The most drastic difference between the two species was the appearance of biphonation. While biphonation was found in 20.4% of right whale vocalizations, it was found in 89.0% of killer whale vocalization. This difference can partially be explained because the killer whale calls we analyzed do not necessarily represent a random sample of the total repertoire (only call types *N1*, *N2*, *N3*, *N4*, *N5*, *N7*, *N8*, *N9*, *N12*, *N13*, *N32*, and *N33* were analyzed in this study).

Frequency jumps occurred in 24.3% of killer and 18.6% of right whale vocalizations analyzed. They could be found in both upward and downward directions and multiple frequency jumps could occur within a single vocalization. Additionally in killer whales frequency jumps could be found on either the F_o and/or G_o .

Subharmonics occurred at low rates in both species occurring in 6.4% of killer and 4.7% of right whale vocalizations analyzed and were only found in the $F_o/2$ pattern. While it appears to be common for subharmonics to be precursors to deterministic chaos in many species (e.g., Wilden *et al.*, 1998; Riede *et al.*, 2004) in the present study subharmonics were generally found alone. Subharmonics preceded deterministic chaos in only one killer whale vocalization and zero right whale vocalizations and succeeded chaos only once in both species.

Biphonation occurred in 89.0% of killer and 20.4% of right whale vocalizations analyzed. In both species, biphonation occurred either in the form of sidebands or unrelated nonparallel bands that occurred without evidence of linear combination (Wilden *et al.*, 1998; Riede *et al.*, 2004). In killer whales the unrelated nonparallel bands occurred in every *N1*, *N2*, *N4*, *N5*, *N9*, *N13*, *N32*, and *N33* call type analyzed ($N=147$) and were always initiated at the beginning of the signal, often following a characteristic introductory buzz. The unrelated nonparallel bands were also found in the *N7*

call type, but in only 40% of vocalizations of this call type analyzed ($N=20$). Here biphonation appeared as heightened energy in the introductory buzz that then swept up to overlap one of the harmonics of the low-frequency component. Biphonations in call type *N7* were not as intense as those found in call types *N1*, *N2*, *N4*, *N5*, *N9*, *N13*, *N32* and *N33*. Biphonation was not found in the *N3*, *N8* or *N12* vocalizations analyzed.

Sidebands occurred less frequently in killer whale vocalizations (63.0%; $N_{\text{kwsb}}=109$) than nonparallel bands and only occurred in call types displaying nonparallel bands (although not in every vocalization with nonparallel bands). No sidebands were present in the analyzed vocalizations of call types *N3*, *N7*, *N8*, *N12* or *N13*. Sidebands appeared primarily around the G_o (97.2% of N_{kwsb}), which most likely resulted from the harmonically sparse G_o being amplitude modulated by the harmonically rich F_o (Wilden *et al.*, 1998; Neubauer *et al.*, 2004; Miller *et al.*, 2007). Sidebands could also be found, however, around the F_o (19.3% of N_{kwsb}) or both the F_o and G_o (15.6% of N_{kwsb}).

In right whales biphonation occurred as unrelated nonparallel bands in 62.9% of total cases ($N_{\text{rwub}}=35$) and as sidebands in 37.1%. Every instance of biphonation as an unrelated parallel band occurred at the beginning of a signal and occurred in the form of a downsweep (Fig. 2(d)). Additionally 90.1% of these downsweep biphonations occurred simultaneously with deterministic chaos. Hence, it is possible that we have underestimated the percentage of vocalizations containing biphonation due to possible masking effects of chaos.

Deterministic chaos was present in both species and was the most frequently occurring nonlinearity in right whales (50.6%; $N_{\text{rwch}}=87$) and second most frequently occurring nonlinearity in killer whales (39.3%; $N_{\text{kwch}}=68$). In right whales chaos occurred most frequently at the initiation of the signal (78.2% of N_{rwch}) but it could also be found at the end of the signal or in multiple locations throughout the signal. In addition, one vocalization was entirely chaotic. In killer whales chaos also appeared most frequently at the initiation of a vocalization (89.7% of N_{kwch}), which generally followed an introductory buzz (Fig. 3(d)). The prevalence of chaos in this transition state may be the result of the sound production system mechanically transitioning from the stable limit cycle of the introductory buzz (which is lower in frequency) to the biphonic regime in killer whales or in both species the system transitioning from an inactive to an active state.

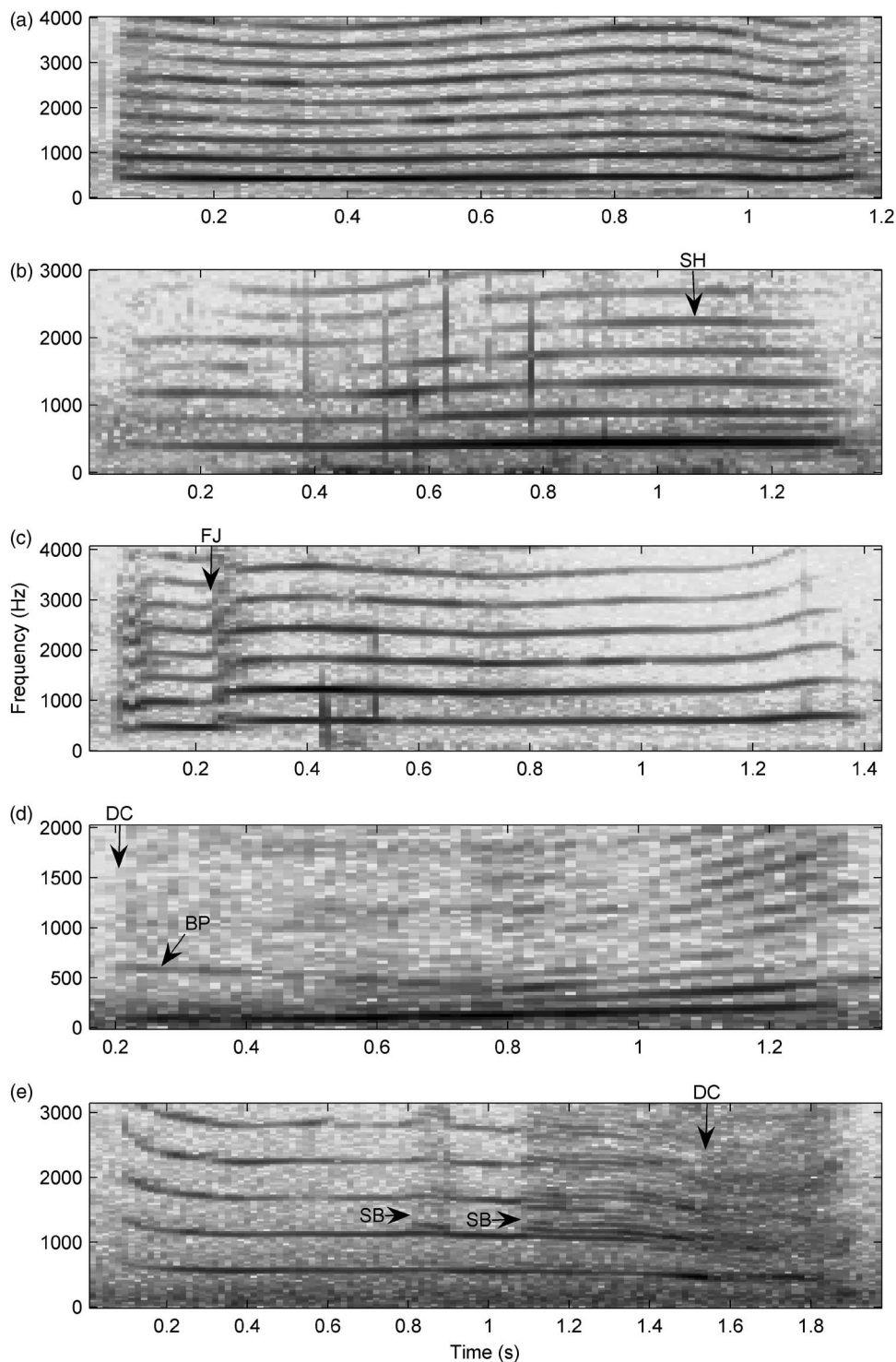


FIG. 2. Spectrograms of representative right whale vocalizations exhibiting nonlinear phenomena (note: spectrograms are zoomed in on for better resolution). (a) Stable limit cycle (SLC). (b) SLC then initiation of subharmonics (SH) indicated by arrow. (c) SLC then a frequency jump (FJ) to a higher frequency. (d) Deterministic chaos (DC, initiation indicated by arrow) with an embedded nonparallel biphonation (BP), then a transition to a SLC. (e) SLC then BP in the form of sidebands (SB) being produced twice, the second time transitioning into DC.

Of the four segments that we suspected were chaotic (two from each species) and of which we tested, only one (from a right whale, Fig. 4(a)) rejected the null hypothesis that the signal was a stationary, linear, random Gaussian signal ($P \leq 0.026$) after the method of surrogate data was applied. This may be due in part to excessive background noise in the other tested segments, which was often the result of the sound recording equipment and/or of the challenges of recording underwater sounds in the wild. In fact, [Hegger *et al.* \(1999\)](#) warned that as soon as more than a small or moderate amount of additive noise is present, scaling behavior

will be broken and predictability of the signal will be limited. Therefore, because of our lack of segments that were entirely free of ambient noise, the method of surrogate data may not have accurately predicted the significance of the results. In addition, it was difficult for us to find segments from our sample that were of long enough duration and/or that had a large enough bandwidth to test in the TISEAN® software package and therefore we were limited in the amount of segments we could test. We still analyzed the segments that did not reject the null hypothesis to gain a better understanding of their underlying dynamics. All four segments tested had a

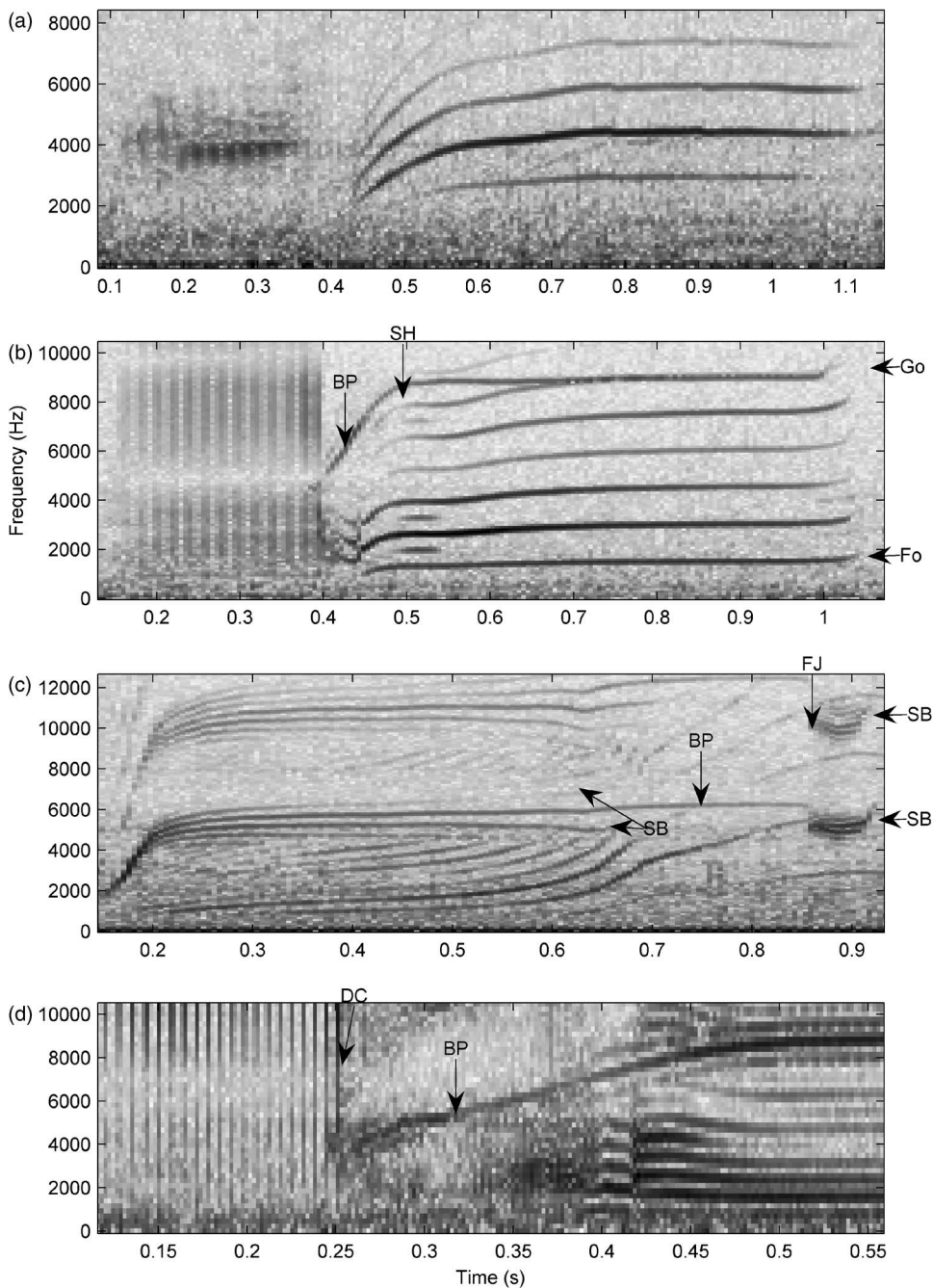


FIG. 3. Spectrograms of representative killer whale vocalizations exhibiting nonlinear phenomena (note: spectrograms are zoomed in on for better resolution). (a) Stable limit cycle (SLC) following the characteristic introductory buzz. (b) Introductory buzz then biphonation (BP) in the form of a nonparallel band and subharmonics (SH); G_o is the high frequency component, F_o is the low frequency component. (c) Nonparallel BP with sidebands (SB) appearing around the G_o and a frequency jump (FJ) to a lower frequency with SB's being produced at a new lower rate. (d) Introductory buzz followed by deterministic chaos (DC, initiation indicated by arrow) and then a transition into a nonparallel BP and a SLC.

positive Lyapunov exponent in the Lyapunov spectrum, indicating they were chaotic signals and not Gaussian noise (Fig. 4(e)). In addition, the embedding dimensions ranged from 5 to 6, whereas the embedding dimension of purely random noise is very high, e.g., 10^2 , 10^3 (Table II, Fig. 4(c)).

This sensitivity of the TISEAN® software may have caused us to overestimate the occurrence of chaos to a degree because we could not test segments that were of particular interest (e.g., segments in which biphonation and potential chaos occurred simultaneously). In such cases we argue these cases are likely to be chaotic as they were similar spectrographically to segments which were run in the TISEAN® software and which had Lyapunov spectra consistent with them being in fact chaotic. The likely chaotic segments not

run in TISEAN® were band limited and had bandwidths similar to the harmonic sections of the signals, but the energy was spread across the band instead of being in discrete frequencies.

IV. DISCUSSION

The presence of nonlinear phenomena in the analyzed vocalizations of both right and killer whales suggests that these features are important and could play an integral role in the communication of these species. Fitch *et al.* (2002) hypothesized that these features function to increase auditory impact on listeners by providing cues as to signaler fitness, mate quality, and overall health and may assist in communicating individual identification, animal size, and urgency. It

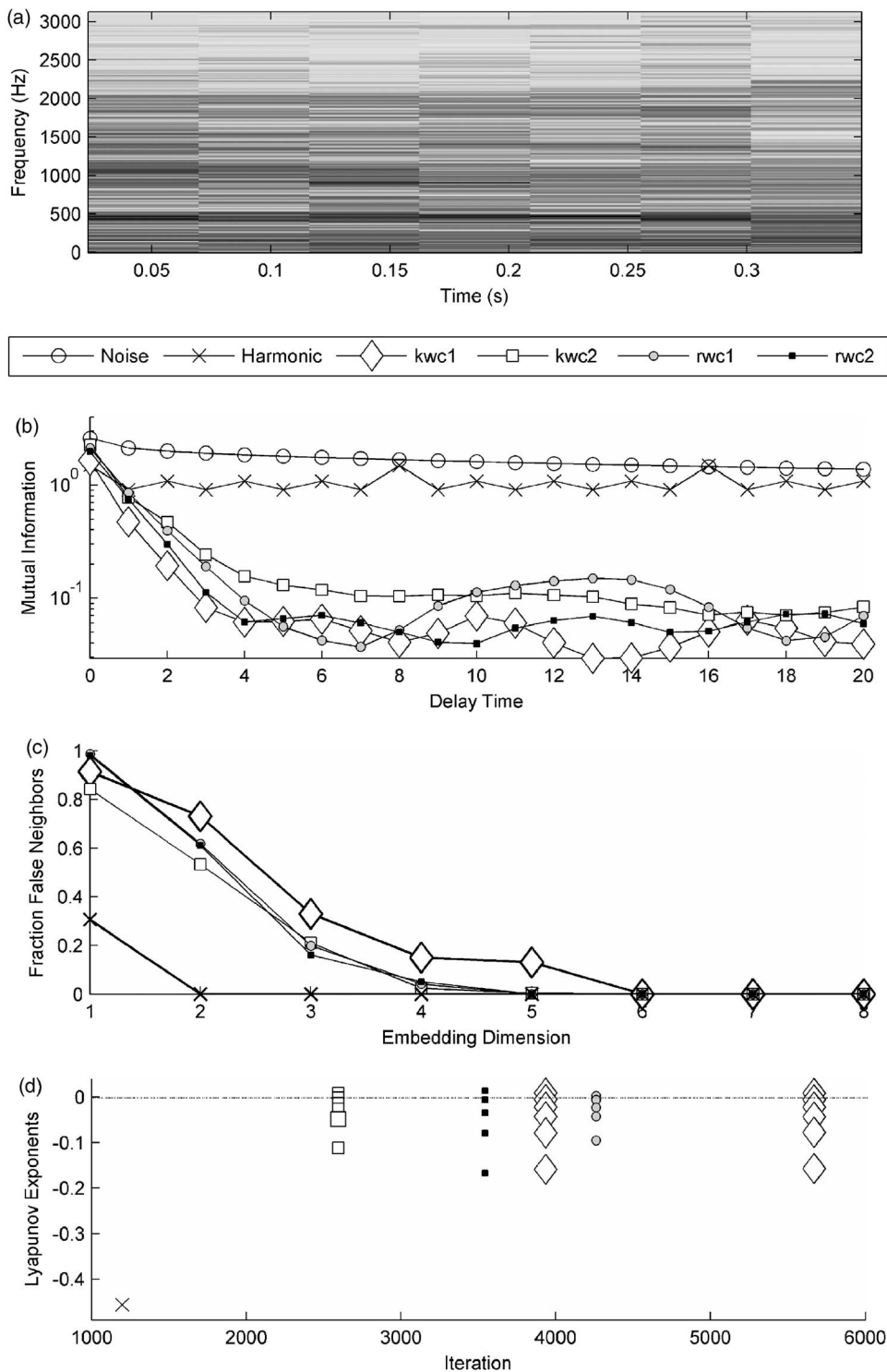


FIG. 4. Deterministic chaos analysis using the TISEAN[®] software program. (a) Spectrogram of a segment analyzed by the TISEAN[®] software program (rwc2 in Table II). This segment was cut from the vocalization seen in Fig. 2(e) at approximately 0:01.532 s and was the only segment which rejected the null hypothesis that the signal was a stationary, linear, random Gaussian signal. (b) Mutual information analysis to determine the appropriate time delay of each signal tested; taken as the first minimum (the noise segment was not further analyzed because its first minimum was >20). Note: mutual information scale is logarithmic to better display results. Legend labels follow Table II. (c) False nearest neighbor analysis to determine the appropriate embedding dimensions; taken as point where the number of false neighbors decreases to zero. (d) The spectrum of Lyapunov exponents. All signals suspected of being chaotic exhibited one positive exponent indicating they are indeed non-Gaussian signals. Note: kwc1 had results at two iterations while all other segments had results at only one iteration; an iteration is a repetition process used by TISEAN[®]. Also, the exponent for the harmonic signal is the maximum exponent found; an additional exponent was found at -1.13.

should be noted that the rates of nonlinear phenomena within the high signal-to-noise ratio vocalizations analyzed here cannot be considered typical of the species because the sound recording system may obtain a sample which is biased in some way in relation to nonlinear properties of signals (e.g., killer whale calls containing biphonation are produced at higher intensities than calls that do not contain biphonation; Miller, 2006). Also, rates of nonlinear signal production may be sensitive to the behavioral state of the caller, and our samples cannot be assumed to be representative. Thus, the rates discussed here only apply to our sample.

Subharmonics and frequency jumps have been found in relatively low rates in the vocalization of several species, including manatees (*Trichechus spp.*) and common chimpanzees (*Pan troglodytes*) (Mann *et al.*, 2006; Riede *et al.*, 2004). In the present study, comparable low rates were found in the analyzed vocalizations of both species. While these rates cannot necessarily be considered representative of each species' vocal repertoire, subharmonics and frequency jumps did not appear to dominate any of the call types analyzed in either species. Thus, it is possible that these features, while not prevalent, may in fact play some communicative role.

TABLE II. Analysis of four signals exhibiting deterministic chaos and the generated harmonic and random signals.

Segment analyzed	Delay time	Embedding dimension	Maximal Lyapunov exponent	Number of points sampled	Sampling rate (Hz)	Sample length
kwc1	4	6	0.093	5694	48,000	0:00.118
kwc2	8	6	0.079	2636	48,000	0:00.054
rwc1	7	5	0.089	4192	11,025	0:00.380
rwc2	4	5	0.135	3563	10,800	0:00.329
Harmonic	1	2	-0.013	1200	1200	0:01.000
Noise	>20	12,323	48,000	0:00.256

The increased prevalence of biphonation in killer whales reported here is partly due to the fact that calls known to contain biphonation are produced at more intense levels (Miller, 2006) and are therefore more commonly received at high signal-to-noise ratios required for this study. Biphonation may be less common in less intense calls not included in the sample of calls analyzed here. Still, the mechanism by which biphonation is produced may be different in killer whales compared with right whales and other mammals due to differences in the sound production mechanism of this species.

The cetacean sound production system differs from that of other mammals as they lack vocal cords typical of non-cetacean species, and the precise mechanisms even differ between odontocetes (killer whales) and mysticetes (right whales). In odontocetes, the exact location of sound production and generation occurs in tissues located above the superior bony nares, termed the monkey lips/dorsal bursae (MLDB) or phonic lips (Cranford, 2000; Cranford, 1997). Excluding sperm whales (*Physeteridae*), all odontocetes have a bilateral though asymmetrical skull configuration, in that they have two MLDB complexes, one associated with each of the two nasal passages, with the right side generally larger than the left (Cranford and Amundin, 2004). These two complexes (left and right) act as two signal generators as both pairs of phonic lips, and possibly multiple locations along each of them, can produce sound (Cranford, 2000). In addition, it is possible that these sounds can be produced independently or simultaneously providing the opportunity of multiple sounds being produced at the same time (Cranford, 2000). While this has only been documented in sonar signals, it is likely that the same is true for nonsonar signals, such as the vocalizations being examined in this study (Cranford, 2000; Cranford and Amundin, 2004). Thus the source of biphonation in killer whales and other odontocetes may be the result of air being pushed across these two sets of phonic lips, though other mechanisms are also possible (Cranford, 2000). If this is the case, then biphonation in killer whales, in the form of nonparallel bands, may be viewed as a linear and not a nonlinear phenomenon as the two independent frequency contours are being produced by separate and independent sound production mechanisms. However, sidebands were commonly observed in association with the biphonations of killer whale calls, and never in calls without biphonation. Therefore, even though the production of two independent frequency contours may itself not be a nonlinear phenomenon, the mechanism by which biphonation sounds

are produced by killer whales appears to commonly include a nonlinear interaction between the two independent contours (Miller *et al.*, 2007).

Little is known about the sound production system of mysticetes, but it is known that they lack such structures as phonic lips and instead have a larynx with vocal folds which may vibrate under the passage of airflow (Reidenberg and Laitman, 1988, 1992; Matthews *et al.*, 1999). This lack of phonic lips may partially explain the comparably lower rates of biphonation found in the right whale repertoire in this study. Biphonation in right whales may then result from weak couplings between other oscillators located within the larynx, such as in humans (Wilden *et al.*, 1998) and other species lacking such structures (e.g., common chimpanzees (*Pan troglodytes*) (Riede *et al.*, 2004), but our current lack of understanding of their sound production system precludes further conclusion or discussion. Any further anatomical understandings of sound production mechanisms in right whales or other mysticetes would provide useful insights.

While deterministic chaos occurs in both species, in killer whales it was primarily found as part of an otherwise harmonically rich signal (except call-type *N3* where it could be found throughout the signal; $N_{N3}=3$). In right whales, however, chaos could be found throughout signals and in greater duration. It has been hypothesized that deterministic chaos may be used as an unpredictable signal thereby making them harder to habituate to and ignore (Fitch *et al.*, 2002). It may be possible that these species are using chaos in this way, however, in killer whales it seems more likely that chaos is generally a by-product of the sound production system transitioning from a stationary to active state.

Though few studies have reported the presence of nonlinearities, their prevalence in both right and killer whales indicates that they may play an integral role in the vocal communication of these species, and possibly across all the cetacea. The lack of correlating detailed behavioral information in this study and the lack of information on the individual whales that produced each vocalization (particularly for the right whales), however, did not allow us to address any of the proposed functional hypotheses but their prevalence indicates that they are likely more than an artifact of production and may serve communicative function(s). In future studies, collecting concurrent behavioral data would greatly increase our understanding of nonlinearities in these and perhaps other species and would bring us closer to addressing many of the functional hypotheses. Here we have provided qualitative descriptions and quantitative analyses of

nonlinearities in the vocal repertoire of North Atlantic right whales and killer whales in hopes of providing more insight into the potential functions and underlying mechanisms of these phenomena.

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