

THE CALL REPERTOIRE OF HUMPBACK WHALES (*MEGAPTERA NOVAEANGLIAE*) ON
A NEWFOUNDLAND FORAGING GROUND (2015, 2016) WITH COMPARISON TO A
HAWAIIAN BREEDING GROUND (1981, 1982)

By

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Thesis Abstract

Understanding the vocal repertoire of a species can help researchers understand many aspects of its ecology. As acoustic communication is often the most effective form of communication in aquatic environments, many marine mammals rely on vocalizations for various aspects of their lives. Therefore, acoustic studies have become a crucial tool to answer many ecological questions about marine mammals and to inform conservation and management, particularly as marine mammals spend much of their lives underwater, making them difficult to study visually. Humpback whales (*Megaptera novaeangliae*) are a highly vocal species for which passive acoustics have been used to extensively study their song, and, to a lesser extent, their calls. Calls have been studied on a small number of foraging grounds and migration routes, but many regions are understudied, for example, northeast Newfoundland. Therefore, the goals of this thesis were to characterize the call repertoire of northeast Newfoundland humpback whales during July-August over two years (2015, 2016), and to identify whether five call types that have been previously described (i.e., swops, droplets, teepees, growls, whups) were present on both the Newfoundland foraging ground in 2015 and on a Hawaiian breeding ground from 1981-82. Twenty-two potential call types in four broad classes were qualitatively identified in the Newfoundland repertoire over the two years, with 12 of the call types qualitatively determined to be present in both years. The five previously described call types appear to be present in both Newfoundland years as well as in the Hawaiian recordings, though some differences in characteristics were present. These findings suggest that the Newfoundland humpback whales have an extensive and possibly stable repertoire as found in other regions. They also suggest that some of the humpback repertoire could be both fixed and innate, which

gives clues as to the function of some of the calls and points towards potential candidate calls for global passive acoustic monitoring efforts.

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General Introduction

Communication plays critical roles throughout the animal kingdom. Therefore, investigation of the communication system and repertoire of a population or species can help in answering many questions about their ecology (Bradbury and Vehrencamp 1998; Todt and Naguib 2000), such as how animals find mates (Gerhardt 1994; Seyfarth and Cheney 2003), avoid predators (e.g. alarm calls; Manser 2001; Sloan et al. 2005), compete for resources (Gerhardt 1994; Seyfarth and Cheney 2003; Baptista and Keister 2005), communicate internal state or behaviour (Marcoux et al. 2006), forage (e.g., manipulate or locate prey, coordinate foraging; Seyfarth and Cheney 2003; Stimpert et al. 2007; Parks et al. 2014), monitor social contexts (Reber et al. 2013), and communicate information about their environment (Marler 1961). Each communication system is made up of three general parts: production, usage and comprehension (Seyfarth and Cheney 2010). Most studies of communication begin with a study of the production aspect – the types of signals that are used. In vocal species, this involves a description of the vocal repertoire. Many species produce both graded/variable and discrete/stereotyped signals (Gautier and Gautier 1977; Marler and Tenaza 1977; Ford 1989; Corkeron and Van Parijs 2001) and, identifying signals as graded or discrete can help researchers understand the possible function of the calls, as each type is useful in different contexts and environments (Marler 1967, 1973; Gautier and Gautier 1977; Marler and Tenaza 1977; Wiley and Richards 1978; Waser 1982; Ford 1989; Krebs et al. 1993).

In addition to describing repertoires over the short-term, much can also be learned from examining the production of calls over the lifetime of an individual or over generational time. Over these longer time-scales, the drivers of vocal production and change can be examined (Waser 1982; Parks et al. 2007; Weilgart 2007; Luther and Baptista 2010). For example,

researchers can determine whether vocalizations are unlearned (i.e. innate) and whether the same vocalizations are used throughout the lifetime of an individual (i.e. stable) or over multiple generations with little or no change (i.e. fixed). For many species, determination of whether vocal production is innate is difficult, but various methods have successfully provided strong evidence for innate vocal behaviour in several taxa (e.g., hybrid gibbons, *Hylobates lar* and *H. pileatus*; Brockelman and Schilling 1984; vervet monkeys, *Chlorocebus pygerythrus*; Seyfarth and Cheney 1986; eastern phoebes, *Sayornis phoebe*; Kroodsma and Konishi 1991; fur seals, *Arctocephalus* spp.; Page et al. 2001; zebra finches, *Taeniopygia guttata*; Forstmeier et al. 2009). Innate calls may be honest indicators of individual characteristics (Forstmeier et al. 2009) or help in delineating closely associated groups of morphologically similar species (Page et al. 2001). Whether innate or learned, long-term stability of graded and stereotyped vocalizations has been found in many species such as killer whales (*Orcinus orca*; Ford 1989, 1991; Foote et al. 2008), harp seals (*Pagophilus groenlandicus*; Terhune 1994; Serrano and Terhune 2002), bearded seals (*Erignathus barbatus*; Risch et al. 2007) and bottlenose dolphins (*Tursiops truncatus*; Caldwell and Caldwell 1965; Sayigh et al. 1990). Stable call types may be important to maintain proper social interactions with conspecifics in stable or unstable associations (Ford 1991; Riesch et al. 2006; Rekdahl et al. 2013), especially for frequently occurring social interactions, such as mother-offspring contact (Dunlop et al. 2008; Dunlop 2017) and individual recognition (Caldwell and Caldwell 1965) and, thus, identifying stable call types can provide information about the social system of a species. Some stable call types exhibit variation in characteristics over time, or among different groups of the same species (Ford 1989; Terhune 1994; Deecke et al. 2000), presenting an opportunity to investigate factors causing that change.

Acoustic communication is often the most effective form of communication in the marine environment relative to other forms (e.g. visual; Urlick 1983; Tyack 2000; Dunlop et al. 2007). Therefore, many marine mammals rely on it for many aspects of their lives such as foraging (Madsen et al. 2002; Stimpert et al. 2007; Fournet et al. 2018b), reproduction (Tyack 1981; Croll et al. 2002; Oleson et al. 2007), and various social interactions (Caldwell and Caldwell 1965; Ford 1989; Janik and Slater 1998; Dunlop et al. 2008; Ford and Fisher 2008). Many marine mammals spend much of their lives underwater, making them difficult to study. However, the increased use of acoustic studies has allowed researchers to answer numerous questions relating to aspects of marine mammal ecology such as population structure and movement (Clapham and Mattila 1990; McDonald et al. 2006; Delarue et al. 2013; Stanistreet et al. 2013; Garland et al. 2015); habitat use (Davis et al. 2017; Kowarski et al. 2018); and responses to changing marine environments (Parks et al. 2007; Weilgart 2007). To answer these types of questions, an understanding of the types of acoustic signals a species uses and when and where it uses them is necessary (Van Parijs et al. 2009).

Study Species

Humpback whales (*Megaptera novaeangliae*) are a highly vocal, migratory species, that display variable ecological, social and vocal behaviour at different points during their annual cycle. Humpback whales also show strong site fidelity to foraging grounds (Baker et al. 1986, 2013; Clapham et al. 1993; Straley et al. 1993; Acevedo et al. 2014; Gabriele et al. 2017) and breeding grounds (Chittleborough 1965; Baker et al. 2013) with photo-identification and various genetic studies showing limited exchange within ocean basins, among ocean basins and across the equator (Payne and Payne 1985; Katona and Beard 1990; Baker et al. 1993, 1998, 2014;

Valsecchi et al. 1997; Acevedo et al. 2013; Schmitt et al. 2014). Due to this, there appear to be distinct feeding and breeding aggregations within each ocean basin, and the last common ancestor of humpback lineages among different ocean basins (North Pacific, North Atlantic and Southern oceans) was estimated to be 2-3 million years ago (Baker et al. 1993).

In most ocean basins, humpback whales exhibit breeding behaviours at low latitudes and feeding at higher latitudes (Dawbin 1966; Baker and Herman 1984a, 1984b; Clapham 1996); though breeding-associated behaviour, particularly song, has been reported on foraging grounds throughout much of the year (Mattila et al. 1987; Clark and Clapham 2004; Stimpert et al. 2012; Kowarski et al. 2019) and feeding is, on rare occasions, observed on breeding grounds (Baraff et al. 1991). The types of social interactions differ between breeding and foraging grounds. On the breeding grounds, competition between males, for access to females, is common and a number of studies have documented physically aggressive surface-active groups of male humpback whales (Tyack and Whitehead 1982; Baker and Herman 1984b, 1984a; Silber 1986a). Comparatively, similar aggressive behaviours on the foraging grounds are rare (Baker and Herman 1984b). Humpback whales tend to arrive on foraging grounds when their prey is abundant (Whitehead et al. 1980; Payne et al. 1986; Johnson 2018) and observations of individuals feeding in groups, cooperatively, or alone are common (Baker and Herman 1984b; D’Vincent et al. 1985; Fournet et al. 2018b).

Vocally, song, produced only by males (Payne and McVay 1971; Cerchio et al. 2001; Stimpert et al. 2012), has been mainly associated with the breeding grounds and is thought to play a role in breeding, however, whole or partial songs have been reported along migration routes and on foraging grounds (Mattila et al. 1987; Clark and Clapham 2004; Stimpert et al. 2012; Kowarski et al. 2019). The precise functions of song are still unclear, but may relate to

some aspect of reproductive behaviour, such as attracting or increasing access to females (Tyack 1981; Magnúsdóttir et al. 2014), synchronizing female estrus (Baker and Herman 1984a), and mediating social interactions among males (Darling and Berube 2001; Herman 2017; Cholewiak et al. 2018). Song always follows the same formula with units combining into phrases, then into themes (Payne and McVay 1971; Winn et al. 1981; McSweeney et al. 1989; Eriksen et al. 2005; Garland et al. 2011; Cholewiak et al. 2013; Magnúsdóttir et al. 2014). This conserved formula and some types of structural changes have been proposed to be innate in male humpbacks (Payne and Payne 1985; Cerchio et al. 2001). In contrast, it is hypothesized that changes in the content (i.e. order and types of units and phrases) of the song within and between breeding seasons is at least partially the result of cultural transmission and differs among regions (Winn et al. 1981; Payne and Payne 1985; McSweeney et al. 1989; Rendell and Whitehead 2001; Eriksen et al. 2005; Garland et al. 2011; Darling et al. 2014; Magnúsdóttir et al. 2014; Rekdahl et al. 2018).

Alternately, ‘calls’ are produced by males, females and calves (Winn et al. 1979; Mobley Jr et al. 1988; Dunlop et al. 2008; Zoidis et al. 2008) and are used in a variety of contexts. While some call types have been found to be the same as units used in songs (Dunlop et al. 2007; Rekdahl et al. 2013), they are typically un-patterned. Although these vocalizations have been referred to as non-song calls (Dunlop et al. 2008; Fournet et al. 2015) and social sounds/vocalizations (Silber 1986a; Dunlop et al. 2007, 2008), the simple term ‘call’ may be most appropriate (Fournet et al. 2018a) as some calls appear to function in roles other than social interactions (Stimpert et al. 2007; Fournet et al. 2018b). In addition, the term ‘call’ is in agreement with terminology used in a wide range of acoustic studies on other taxa (Catchpole 1982; Brockelman and Schilling 1984; Ey and Fischer 2009; Fournet et al. 2018a). Calls are produced during all parts of the annual cycle, including on breeding (Silber 1986a; Zoidis et al.

2008) and foraging grounds (Stimpert et al. 2011; Fournet et al. 2015, 2018c), as well as along migratory routes (Dunlop et al. 2007; Rekdahl et al. 2017), and many calls do not appear to change significantly over time (stable or fixed; Rekdahl et al. 2013; Fournet et al. 2018b). Humpback calls have been qualitatively described in a number of regions (e.g., Winn et al. 1979; Thompson et al. 1986; Chabot 1988), and quantitatively described on migration routes (Dunlop et al. 2007; Rekdahl et al. 2017) and foraging grounds (Cerchio and Dahlheim 2001; Stimpert et al. 2011; Fournet et al. 2015). As the number of regions with described repertoires has grown, comparison among years within regions as well as among regions has shown that some call types appear to be shared among contexts and regions (Dunlop et al. 2007; Rekdahl et al. 2013, 2017; Fournet et al. 2015, 2018c). These, and other studies, on humpback calls using passive acoustic monitoring (PAM) and animal-borne tags have also begun to identify possible functions of some call types, such as foraging (Cerchio and Dahlheim 2001; Stimpert et al. 2007; Fournet et al. 2018b), mother-offspring contact (Dunlop et al. 2008), and general contact or mediation of social interactions (Dunlop et al. 2008; Wild and Gabriele 2014; Fournet et al. 2018c). Thus far, comparisons have been among foraging grounds and some migration routes and have found that some of the same call types are shared between sympatric and allopatric regions (Fournet et al. 2018c) and some are stable over long time periods (Rekdahl et al. 2013; Fournet et al. 2018a), but a direct comparison between foraging and breeding grounds has not yet been conducted.

Study Sites

A large group of humpback whales returns annually to forage off the northeast coast of Newfoundland (Katona and Beard 1990). One previous description of the repertoire, to our knowledge, exists for this region (Chabot 1984, 1988), however, analytical differences preclude

comparison to this, and other, recent studies. Humpback whales arrive in the area when capelin (*Mallotus villosus*), their main prey during the summer (July-August), are abundant (Johnson 2018). It is estimated that over 1000 individuals pass through the area each year, with each individual whale staying resident for 1-21 days (Johnson 2018). Passive recordings were made in coastal Newfoundland during July-August 2015 and 2016 by placing the hydrophone near a cluster of four known, and persistently used, shallow-water (15-40m) capelin spawning sites (49.20N 54.20W; Penton and Davoren 2012). This location ensured recordings of humpback calls, as large, multi-species aggregations are observed in the vicinity shortly after capelin arrive to spawn each year (Davoren 2013). In addition, humpback whales have been observed foraging in the area during opportunistic encounters during photo-identification efforts (Johnson 2018). In contrast, the Hawaiian breeding ground represents a geographically, contextually and temporally separate region. Recordings in this region were made during 1981-82 using a dip hydrophone over the side of a boat (Silber 1986b, 1986a). Most of the groups recorded were made up of surface-active, aggressive males (Silber 1986b, 1986a).

Objectives

The overall objective of this thesis was to contribute to the growing number of regions with a described humpback whale call repertoire and, thereby, the global call catalogue. My first objective was to characterize and classify the repertoire of humpback whales on the northeast Newfoundland foraging ground (Chapter 1). To do this, I examined recordings from July-August 2015 and 2016 and used a combination of manual and statistical (i.e., classification and regression tree, random forest) classification to determine the number and types of calls and the variability between the two years. My second objective was to identify whether five previously

described call types (i.e., swops, droplets, teepees, growls, whups) were present in both the Newfoundland repertoire and the repertoire from a Hawaiian breeding ground (Chapter 2). To do this, I used the 2015 Newfoundland recordings from Chapter 1 and examined recordings made in Hawaii in 1981-82 (Silber 1986b, 1986a) and again used aural/visual and statistical classification to determine whether the five call types were present. This study provides insight into the call repertoire in a previously understudied region, further evidence for a portion of the humpback call repertoire being fixed and/or innate, clues as to the function of some of the calls, and aids in the identification of possible call types for use in passive acoustic monitoring efforts.

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Chapter One: The repertoire of foraging northeastern Newfoundland humpback whales over two years (2015, 2016)

Abstract

Characterization of the signal repertoire in a species represents an important first step in investigating many aspects of its ecology. Humpback whales (*Megaptera novaeangliae*) are a highly vocal species. While their song has been well studied, calls have only been described in a limited number of regions. The objective of this study was to characterize the call repertoire of humpback whales off the northeast coast of Newfoundland, where large numbers of humpbacks return annually, during the summer, to forage. The calls from two years of recordings (July-August 2015, 2016) were aurally/visually classified, and then validated using classification and regression tree (CART) and random forest (RF) analyses. From this, four broad classes were defined, containing 22 possible call types in the two years of recordings combined. Twelve call types appeared to be common to both years. Broad classes (i.e., high frequency, low frequency, pulsed, compound) had high classification success (CART & RF: 94%). Classification for call types was lower (CART & RF: 67%), with most call types misclassified as others within the same broad class, but the CART and RF classified calls into types regardless of year. Five of the call types common to both years were qualitatively similar to those described previously in the literature (i.e., droplets, swops, teepees, growls, whups) and found to be stable over three decades in Alaska. Our findings suggest that the Newfoundland humpback whale repertoire may share common call types with other regions and that some call types in the Newfoundland repertoire may be stable, as found in other areas.

Introduction

Studying the communication system of a species is a critical step in understanding many aspects of its ecology and behaviour (Bradbury and Vehrencamp 1998; Todt and Naguib 2000). In vocal species, investigating the vocal repertoire over short and long time-scales can help researchers gain insight into social structure (Payne and Payne 1985; Ford 1991; Riesch et al. 2006; Rekdahl et al. 2013), population and species boundaries (Oswald et al. 2003; Pearl and Fenton 2008), responses to environmental or other change (Luther and Baptista 2010; Proppe et al. 2012), and the mechanisms underlying vocal behaviour (Waser 1982; Payne and Payne 1985). Understanding the vocal communication of a species usually begins by describing the number and type of vocalizations used. Repertoire sizes vary within and among species, but many repertoires contain a mix of graded or variable calls (i.e., calls that vary in terms of one or more characteristics along a continuum, which may be due to factors such as individual variation or motivational state) and stereotyped or discrete calls (Gautier and Gautier 1977; Marler and Tenaza 1977; Ford 1989; Corkeron and Van Parijs 2001). Graded calls are commonly observed in closer range communication, where redundancy with other types of signals is possible (Marler 1967, 1973; Gautier and Gautier 1977; Marler and Tenaza 1977; Ford 1989; Krebs et al. 1993), while stereotyped calls are often used for longer-range communication (Marler 1973; Marler and Tenaza 1977; Wiley and Richards 1978; Waser 1982; Krebs et al. 1993). Some graded and stereotyped calls vary over time, while others are stable with little or no change in the call structure over decades (Caldwell and Caldwell 1965; Waser 1982; Deecke et al. 2000; Luther and Baptista 2010).

In the marine environment, acoustic communication is often the most effective, as acoustic signals can travel longer distances than other modalities, such as visual signals, and, thus, most

marine mammals appear to rely on it as the primary communication modality (Urlick 1983; Tyack 2000; Dunlop et al. 2007). Acoustic studies on marine mammals help to inform conservation and management as they have increased understanding of ecological aspects such as population structure and movement (Clapham and Mattila 1990; McDonald et al. 2006; Delarue et al. 2013; Stanistreet et al. 2013; Garland et al. 2015b); habitat use (Davis et al. 2017; Kowarski et al. 2018); and responses to changing marine environments (Parks et al. 2007; Weilgart 2007). Humpback whales (*Megaptera novaeangliae*) are a highly vocal cetacean. Song, is produced only by males and has been thoroughly investigated (Payne and McVay 1971; Cerchio et al. 2001; Stimpert et al. 2012; Cholewiak et al. 2013; Herman 2017). Alternately, ‘calls’ are produced by males, females and calves (Winn et al. 1979; Mobley Jr et al. 1988; Dunlop et al. 2008; Zoidis et al. 2008) and are used in a variety of contexts. While some call types have been found to be the same as units used in songs (Dunlop et al. 2007; Rekdahl et al. 2013), they are typically un-patterned. Although these vocalizations have been referred to as non-song calls (Dunlop et al. 2008; Fournet et al. 2015) and social sounds/vocalizations (Silber 1986; Dunlop et al. 2007, 2008), the simple term ‘call’ may be most appropriate (Fournet et al. 2018b) as some calls appear to function in roles other than social interactions (Stimpert et al. 2007; Fournet et al. 2018c). Humpback calls have been qualitatively described in a number of regions (e.g., Winn et al. 1979; Thompson et al. 1986; Chabot 1988), and quantitatively described on migration routes (Dunlop et al. 2007; Rekdahl et al. 2017) and foraging grounds (Cerchio and Dahlheim 2001; Stimpert et al. 2011; Fournet et al. 2015). Quantitative studies are becoming standardized in both number and types of acoustic variables as well as the statistical methods for comparing among regions. Specifically, classification and regression tree and random forest analyses are common (Rekdahl et al. 2013, 2017; Fournet et al. 2018d, 2018b), as

they are both minimally affected by outliers, non-normality, non-independent data, correlated variables, and sample size differences, all of which are common in humpback repertoire studies (Breiman et al. 1984; Breiman 2001; Armitage and Ober 2010). Studies have investigated whether call types are used over time with little or no change in characteristics (i.e. stable), revealing that a portion of the repertoires from two regions were stable across a period of 11 (Rekdahl et al. 2013) and 36 years (Fournet et al. 2018b).

Though studies on humpback call repertoires have increased, there are still many understudied regions. One such region is the northeast coast of Newfoundland, where a large group of humpback whales migrate annually to forage (Katona and Beard 1990). It is estimated that over 1000 individuals pass through the area each year, with each individual whale staying resident for 1-21 days (Johnson 2018). The objective of this study was to characterize and classify the call repertoire of humpback whales off the northeast coast of Newfoundland from recordings made during July-August, 2015 and 2016. Although one previous description of calls exists for this region (Chabot 1984, 1988), the lack of focus on calls and analytical differences preclude comparisons to this and other recent studies (e.g., Dunlop et al. 2007; Stimpert et al. 2011; Fournet et al. 2015; Rekdahl et al. 2017). Secondly, we qualitatively examined whether any call types were present in both years and we provide a description of a previously undescribed call type. Overall, this study will provide the first comprehensive description of the call repertoire of humpback whales on a Newfoundland foraging ground, thereby contributing to the growing global catalogue of these calls and aiding in the identification of potential calls for passive acoustic monitoring (PAM).

Methods

Data Collection

A Wildlife Acoustics SM2M marine recorder with standard hydrophone (recording bandwidth: 2Hz – 48kHz; sensitivity -165dB re: 1 V/ μ Pa; Wildlife Acoustics Inc. 2013) was deployed off the northeastern coast of Newfoundland to make continuous acoustic recordings (24 kHz sampling rate, 12 dB gain, 3 Hz high pass filter, 16 bit) from July-August, 2015 and 2016. The hydrophone was moored 2-3 m off the ocean floor at a central location (49.20N 54.20W) within a cluster of four persistently used shallow-water (15-40m) capelin (*Mallotus villosus*) spawning sites (Penton and Davoren 2012). Capelin appears to be the main prey type of humpback whales in coastal Newfoundland (Johnson 2018). This deployment site ensured acoustic recordings of humpback whale calls, as high-abundance, multi-species aggregations, including humpback whales, form shortly after capelin arrive at these sites to spawn (Davoren 2013). From each year, files were selected for analysis starting from the first day that humpback whales were observed < 5km from the hydrophone (July 15-22, 2015; July 29-August 8, 2016) during other shore- and boat-based work.

Aural and Visual Survey

Recordings were selection within each year based on humpback presence (July 15-22, 2015; July 29-August 8, 2016; Johnson 2018). Files were examined aurally and visually in *Raven Pro* 1.5 (2015) or 2.0 (2016; hereafter referred to as *Raven*; Cornell Laboratory of Ornithology; Bioacoustics Research Program 2014) using a Hann window, 8192 Discrete Fourier Transform, 2.93 Hz resolution, and 50% overlap. A selection box was placed around all calls with a clearly distinguishable start and end as close to the visible bounds of the call as possible. Any calls that overlapped with another call or non-biological sound were not selected. Approximately twelve

hours (2 files) of recordings were later removed from the 2015 set due to issues with the recordings. A similar issue was present in a portion of one additional file. In this file, calls in the affected portions of the file were examined, and we removed any call with higher frequency components near or in the affected portion as well as any calls that may have had components in the frequency range that appeared affected, based on similar calls in other files.

Classification

For most variable measurements, including signal-to-noise ratio (SNR), we used the Noise-Resistant Feature Set (NRFS) developed by Mellinger and Bradbury (2007) for the program *Osprey* and based on work by Fristrup and Watkins (1993), using the *Acoustat* package in MATLAB (version 9.2). The NRFS calculates the bounds of a smaller feature box within the manually created selection box from *Raven* (or any other sound viewing program) in which the loudest parts of the sound have the most impact on the variable measurements by ranking and summing the energy within the sound compared to the background noise (Mellinger and Bradbury 2007; Fournet et al. 2018b). Thus, variable measurements are more robust to differences in noise and equipment between recording sets as well as to differences in the selection boxes made in *Raven* (Mellinger and Bradbury 2007; Fournet et al. 2015, 2018b). Only calls with a SNR at least 15 dB above ambient noise were retained for analysis. In previous studies on humpback calls, a SNR cut-off of 10 dB above ambient has often been standard (Dunlop et al. 2007, 2008; Stimpert et al. 2011; Rekdahl et al. 2013; Fournet et al. 2015), but the Newfoundland recordings were of high enough quality to allow a higher threshold. Fifteen variables were measured on all calls with an SNR >15 dB (Table 1). Start and end frequency were measured manually in *Raven* by placing a point selection on the beginning and end of the

fundamental or lowest frequency component of each call (Fournet et al. 2018b). Bout was recorded manually, and was defined as the number of the same call type in sequence with relatively equal temporal separation (<2 s) between each instance, similar to the definitions used by Rekdahl et al. (2015) and Fournet et al. (2015). All frequency variables were log-transformed prior to analysis, as humpback whales are thought to perceive pitch on a logarithmic scale similar to other mammals (Chabot 1988; Dunlop et al. 2007; Fournet et al. 2015).

The calls above the SNR threshold were initially classified by one observer (ME). Aural and visual characteristics were used to first place all calls into four broad classes (i.e., low frequency, high frequency, pulsed, compound). Calls were classified as low frequency if the fundamental frequency was below ~ 0.4 kHz and as high frequency if the fundamental was above ~ 0.4 kHz. Calls classified into the pulsed class were those of short duration, generally less than 0.4 s, while compound contained two identifiable call types without audible temporal separation. Calls within each broad class were then iteratively separated into smaller groups until the calls within each grouping were subjectively considered to be of a single type (Fournet et al. 2015). Call types that were qualitatively deemed to be similar to previously described call types were given the same name. All other call types included in the analysis were given new names based on qualitative aural and visual characteristics (Fournet et al. 2015). Only call types that were present on two or more non-consecutive days were included in the analysis to avoid including call types that may only be produced by one or a few individuals or that may only represent more extreme individual variation of another call type (Fournet et al. 2015). Call types not fitting this criteria can be found in Appendix 1. All other call types were assigned a numerical gradation scale based on how confident the observer (ME) was in assigning calls to that call type as a proxy for the degree of stereotypy, whereby 5 indicated high confidence in classifying calls into

a particular type (i.e. high stereotypy of the call type) and 1 indicated low confidence (i.e. low stereotypy/high gradation).

Statistical Analysis

To quantitatively classify sound into groups, a supervised classification and regression tree (CART) and random forest (RF) were run for broad classes and then call types on the pooled 2015 and 2016 data using the *rpart* and *randomforest* packages in *R* (version 3.5.0), similar to a number of recent studies (Rekdahl et al. 2013, 2017; Fournet et al. 2018b, 2018d). Both tests were also run with and without year as a variable and a label to investigate the importance of year as a splitting variable. CART and RF are classification methods that have been found to have fairly high levels of agreement with manual classification in several humpback whale studies (Rekdahl et al. 2013, 2017; Fournet et al. 2018b, 2018d) as well as other taxa (e.g., Oswald et al. 2003; Garland et al. 2015a; Thiebault et al. 2019) and, thus, we used these methods to validate our human classifications and attempt to reduce classification subjectivity.

CART produces a single tree using the Gini index (“goodness of split” or measure of impurity), whereby all variables are taken into account and the one that results in the smallest splitting error is chosen as the most important and displayed at each node (Breiman et al. 1984; Berk 2008; Rekdahl et al. 2013, 2017; Fournet et al. 2018d). The minimum number of cases (i.e. calls) in each terminal node is defined (in this case 10) and the tree is fully grown and then pruned back. Pruning occurs until the tree has the smallest number of terminal nodes and the highest classification success rate or highest predictive accuracy (Breiman et al. 1984; Risch et al. 2007; Fournet et al. 2018d), meaning that the classification rate is not improved by further splits (Breiman et al. 1984). Both CART and RF use binary splits in a process of recursive

partitioning to get to terminal nodes that are as pure (containing mainly one grouping) as possible (Breiman et al. 1984; Strobl et al. 2009). While the underlying process is similar, RF is different from CART in that it grows many trees (in this case 1000) via bootstrapping (Keen et al. 2014). For each tree, a random sample of data, ~30% in this case, referred to as out-of-bag data (OOB data) is removed and the remaining data are used to grow the tree. The OOB data are then run down each tree to determine the misclassification rate (i.e. OOB error rate) for each call type, defined as the number of cases that were misclassified over all trees out of the total number of cases (Breiman 2001; Armitage and Ober 2010; Rekdahl et al. 2017; Fournet et al. 2018b). The OOB error is analogous to the misclassification rate in the CART, but is compiled over all the RF trees. Additionally, while the CART considers all variables during each split and chooses one as important, RF considers a random subset of the variables to grow each tree (Bao and Cui 2005; Rekdahl et al. 2017; Fournet et al. 2018b). The number of variables used to build each tree is determined by the number that minimizes the OOB error (three variables in this case). After all trees are grown, the variables are ranked in order of importance, which provides further information on the importance of each variable in discriminating between classifications (Breiman 2001; Liaw and Wiener 2002). As independence of data points was an issue in this data set, only qualitative comparison could be made among call classes and call types between years.

Lastly, the compound call type, the growl-moan, was described. For classification purposes, the two components of the growl-moan type compound call were treated as a single call, as they likely function together given the lack of audible temporal separation. For further description, however, a selection box was placed around each individual component (i.e., growl, moan), similar to the process used to measure ‘whups’ in Alaska (Wild and Gabriele 2014), and

all variables, except bout (Table 1), were measured on each component. Bout was not included in the analysis, as growl-moans and low moans were never found in bouts and growls rarely occurred in bouts. For this description, all growl-moans from both years were pooled together. The growl component was then qualitatively compared to the pooled 2015 and 2016 growls, and the moan component to the pooled low moans, to examine whether the components of the compound call appeared similar to their single unit call analogues.

Results

In total, 156 hours of recordings over seven recording days in 2015 and, 264 hours over 11 recordings days in 2016 were included in the final analysis. A total of 735 calls in 2015 and 1117 calls in 2016 were above the 15 dB SNR threshold and were classified. Many call types were identified in each year (2015: 28 call types; 2016: 30 call types), but only a portion of these were present on two or more non-consecutive days (2015: 18 call types, 708 calls; 2016: 16 call types, 854 calls). Of these, 12 call types were qualitatively deemed to be present in both years, while six call types appeared to be unique to 2015 and four appeared to be unique to 2016, resulting in 22 possible call types included in the analysis (Table 2). Audio clips and spectrograms of all call types described in this study are available at <https://eppm34.wixsite.com/marinebio>.

The broad class CART and RF with the pooled data from 2015 and 2016 both had 94% classification success (Table 3). The most important splitting variables were duration (1st split), start frequency and end frequency in the CART and duration, amplitude modulation, frequency modulation, end frequency and median frequency in the RF. The call type CART and RF both had 67% classification success (Table 4, Fig. 1). In the CART, duration (1st split), end frequency and lower frequency were important splitting variables (Fig. 1), while the five most important

variables in the RF, in order, were end frequency, upper frequency, duration, amplitude modulation and start frequency. The CART produced 28 terminal nodes from the 22 call types with growl-moans, whimpers, pews, oops, groaks, yips, pops, drums and honks not appearing in any terminal nodes (Fig. 1). When both tests were run with year included as a variable, the classification success increased to 70% for the CART and RF, with year appearing in the third level of splits on each side of the CART and as the 10th most important variable in the RF. When call types were labelled by year, calls in 2015 of a particular call type were classified as that same call type in 2016 and vice versa (e.g. 2015 whups were assigned as 2016 whups and 2016 whups as 2015), further illustrating that call types were not being classified by year (Table 4). When misclassified, call types were generally assigned to another type within their broad class, as indicated by the high agreement in the broad class CART and RF (Table 3, 4). For example, whups and growls (low frequency class) were misclassified as each other, several of the pulsed call types were incorrectly assigned as swops and several of the high frequency call types were assigned to another high frequency type. Growl-moans (compound class) were mainly misclassified as low moans (low frequency class), making them an exception to call types being misclassified within the same broad class. The RF showed the same call type misclassification trends as the CART. In general, the highest misclassification rates occurred for calls with the lowest confidence levels and those with low sample sizes (Table 2, 4).

The low frequency class contained seven call types (Fig. 2), with six found in both years; all low frequency call types were assigned a confidence level of three or five (Table 4). This was the most represented call class over both years (56% of calls), with the most common call types being growls (52% of low frequency; 29% of all calls) followed by whups (21% of low frequency; 12% of all calls). Compared to other call classes, low frequency calls had the lowest

average frequencies across all frequency measures (peak overall frequency range: 9-773 Hz; Table 2), had the lowest average entropy, and the highest average amplitude and frequency modulation rates and were the second longest duration on average, after compound calls (Table 2). In contrast, the least represented call class was compound calls across both years (1% of calls), which contained only one call type (growl-moan), found in both years and given a confidence level of 5 (Table 2, 4; Fig. 3). This call type is a combination of two low frequency call types (growl and low moan) and, thus, the characteristics were generally similar to the low frequency class. However, growl-moans were never found in bouts and were the longest duration call class and type on average relative to all others, with cases ranging from 0.94-5.80 s in length.

In contrast to the compound and low frequency call classes, the pulsed call class had the shortest average duration calls (range: 0.17 – 0.68 s) and was the second most represented class across both years (34% of calls; Table 2; Fig. 4). This class contained nine call types (Table 2), three of which comprised the majority of the class and were found in both years: swops (60% of pulsed; 20% of all calls), teepees (17% of pulsed; 6% of all calls) and droplets (9% of pulsed; 3% of all calls). Swops were assigned a confidence level of four, the highest level in this call class, with all other types assigned a one or three (Table 4). Pulsed calls were the most common call class to occur in bouts, had the highest average upsweep fraction, and had high entropy in both years relative to other call classes (Table 2). Finally, the high frequency call class comprised 9% of the total calls in both years and contained five call types, with two found in both years (Table 2). The two call types present in both years were assigned a confidence level of two and all other high frequency call types were assigned a one (Table 4). Calls in this class had the highest average frequency relative to all other classes (peak overall frequency range: 73-1673

Hz), high entropy (particularly in 2016) and fairly short duration, though slightly longer on average than pulsed calls (Table 2). None of the high frequency call types were very common in either year, but yawps (46% of high frequency; 4% of all calls) and oops (29% of high frequency; 2% of all calls) made up most of the cases (Table 2).

Compound calls

The growl-moan was the only compound call type that met all criteria for inclusion in both years. The moan portion of the compound call was qualitatively similar to the low moan with similar average variable values. The growl portion of the compound call was higher in frequency, longer duration and higher entropy on average than the individual growl call, but still appeared qualitatively similar (Table 5).

Discussion

The CART and RF for broad class had high classification success, validating the assignment of cases into the four broad call classes. For call type, classification success was lower, suggesting that some of the 22 call types fit well into discrete types, while others did not. Similar to previous studies, call types with lower sample sizes often had lower classification success (Garland et al. 2015a; Rekdahl et al. 2017). These call types often also had low confidence levels, indicating that they were less stereotyped and may represent more extreme variations of other call types (Rekdahl et al. 2013) or that metrics used may not adequately capture the characteristics that separate call types (Janik 1999). This trend reinforces the notion that humpback calls fall along a continuum (Chabot 1988; Dunlop et al. 2007; Stimpert et al. 2011; Fournet et al. 2015; Dunlop 2017). At least half of the possible call types (12 of 22)

appeared to be common to both years and were generally grouped into types regardless of year. These findings suggest that a portion of the Newfoundland repertoire may be stable across time, as found in other regions (Rekdahl et al. 2013; Fournet et al. 2018b). Some of the common call types, however, had differences between years in terms of one or more variables, as observed previously (Rekdahl et al. 2013, 2017; Fournet et al. 2018b), possibly due to a variety of factors, such as background noise conditions (Brumm and Slabbekoorn 2005; Dunlop et al. 2010; Fournet et al. 2018a, 2018b) or motivational/arousal state (Morton 1977; Dunlop 2017).

In previous repertoire studies, calls have been grouped into 11-46 types based on observer classification and a variety of quantitative methods (Dunlop et al. 2007; Rekdahl et al. 2013, 2017; Fournet et al. 2015). The variability in repertoire size among regions likely reflects some regional differences, but may also reflect differences in the amount of recording hours and classification methods (e.g., statistical analysis techniques, observer biases). For instance, human observers vary in their tendencies to lump and split call type categories and in their discrimination criteria, resulting in differences in the boundaries of a call type (Janik 1999). As most publications provide only one example of each call type, which are often the most stereotyped and best quality cases, it can be difficult to determine the criteria used by the observer to split call types and, thus, difficult to compare call types among publications (Stimpert et al. 2011; Fournet et al. 2015, 2018b). Nonetheless, five of the call types in the Newfoundland repertoire were qualitatively very similar to call types previously described, such that we gave them the same names (i.e., whups, growls, swops, droplets, teepees; Dunlop et al. 2007; Rekdahl et al. 2013, 2017; Fournet et al. 2015) and further comparison may reveal other common call types among regions.

In this study, the calls classified well into four broad classes with high agreement between

manual and statistical classification. In contrast, the 22 call types identified through manual classification were not as well supported by the results of the CART and RF. These findings are supported by other studies showing that many humpback whale calls seem to fall along a continuum (Chabot 1988; Dunlop et al. 2007; Stimpert et al. 2011; Fournet et al. 2015; Dunlop 2017). In our study, this was particularly apparent for high frequency call types as well as pulsed call types, though less so for previously described pulsed call types (i.e., swops, droplets, teepees; Fournet et al. 2015, 2018a, 2018c). Indeed, the previously undescribed high frequency and pulsed call types had poor classification success by the CART and RF (0-65%) and were assigned a confidence level of one or two (Table 4), indicating low confidence in the classification and high levels of gradation of call types within these call classes. Although poor classification success in the CART and RF could result from the measured variables not capturing variation apparent during aural and visual classification (Janik 1999), minimal variation in averaged variable values across these call types, and the low confidence levels of many of the call types (Table 2, 4), suggests that pulsed and high frequency calls may be better classified along a continuum, than into discrete groups, as done for other species (e.g. right whales, *Eubalaena glacialis*; Clark 1982). Graded vocal signals have been identified in the repertoires of many mammalian species (e.g., Old World monkeys, superfamily Cercopithecoidea; Gautier and Gautier 1977; great apes, family Hominidae; Marler and Tenaza 1977; right whales; Clark 1982; belugas, *Delphinapterus leucas*; Karlsen et al. 2002; Garland et al. 2015a) and are often used for shorter-distance communication (Marler and Tenaza 1977; Ford 1989; Krebs et al. 1993). Gradation may also reflect important information about an animal, such as the internal or motivational state of the producer (Morton 1977; Smith et al. 1982; Dunlop 2017), or individual variation related to age, sex and/or body mass (Gautier and Gautier 1977).

Future acoustic studies of humpback whales will be important to clarify the degree of gradation in their repertoire and tagging studies may help to identify whether certain variations are associated with particular contexts, motivational states; reflect individual differences; or result from other factors (e.g., vocal learning, controlled change of call characteristics; Tyack 1997).

In contrast to graded calls, some call types of humpback whales appear to be stereotyped and to fit into discrete call types based on aural/visual classification (Silber 1986; Chabot 1988; Ford 1989; Dunlop et al. 2007; Stimpert et al. 2011; Fournet et al. 2015; Dunlop 2017). Stereotyped acoustic signals are often used by mammals to maintain contact when out of visual range (Ford 1989), and have been described in primates (e.g., great apes; Marler and Tenaza 1977; *Cercocebus* spp. and *Papio* spp.; Waser 1982), killer whales (*Orcinus orca*; Ford 1989) and bottlenose dolphins (*Tursiops truncatus*; Caldwell and Caldwell 1965; Sayigh et al. 1990; Tyack 1997). Five of the 22 call types in this study were assigned high confidence levels based on confidence in manual classification (4 or 5), indicating stereotypy (Table 4). These five call types were also qualitatively similar to calls described in previous studies (i.e., whups, growls, swops, droplets, teepees; Dunlop et al. 2007; Rekdahl et al. 2013, 2017; Fournet et al. 2015, 2018c, 2018a). Given their stereotypy and that low frequencies generally travel further, the calls in the low frequency and compound class in this study would make good candidates for longer distance communication (Konishi 1970; Morton 1975; Wiley and Richards 1978; Brown 1982), which may also make them useful for PAM of humpback whales.

The classification of some of these more stereotyped calls, however, were still not well supported by the CART and RF, with only the growls and swops having high classification success in the CART and RF (>90%; Table 4), while whups, droplets and teepees had lower classification success (0-51%). This suggests again that many calls may fit better along a

continuum, rather than into discrete types. Indeed, teepees and droplets were generally misclassified as swops, suggesting that they could be graded variations of the same call type. The low classification success of the whups was likely a result of the variables not capturing the upsweep, which is the main distinguishing feature between a growl and a whup. Even call types that were more successfully classified still often ended up in more than one terminal node in the CART (Fig. 1), suggesting either that further separation is needed, that even the call types that appear more stereotyped may have certain graded characteristics, or that other adjustments to classification are needed.

Due to difficulties in comparing among publications, it could not be confirmed whether the remaining 17 potential call types are in fact novel in the literature and/or unique to Newfoundland. It is possible that at least some of these 17 call types could be related to some aspects of humpback whale ecology on their Newfoundland foraging grounds that are not present, or not yet identified, elsewhere. Indeed, some call types in other regions have been linked to foraging in general, or foraging on specific prey types. For instance, a feeding call has been associated with humpback whales feeding on herring (*Clupea harengus*) in Alaska (Cerchio and Dahlheim 2001; Fournet et al. 2018c). Although this call type was not present in the Newfoundland recordings, it was recently identified off of Nova Scotia, where humpback whales are associated with herring aggregations (Kowarski et al. 2019). In the Gulf of Maine, Stimpert et al. (2007) identified a call from tagged whales termed a ‘megapclick’ that appears to be associated with foraging on sand lance (*Ammodytes* spp.). The absence of these calls from our recordings, however, does not necessarily mean that they were not used in the area. During recording periods, humpback whales were associated with aggregations of capelin either spawning or traveling toward spawning sites (Johnson 2018). While moving towards spawning

sites, capelin form tight, ephemeral schools as they search for suitable spawning sites along the coast (Davoren et al. 2006). As this schooling behaviour is similar to herring schools (Jech and Stroman 2012), we might expect to hear the previously described feeding call off of spawning sites. In contrast, capelin form loose aggregations, or shoals, near the seabed at spawning sites and display little predator avoidance behaviour (Davoren et al. 2006). As the hydrophone was moored at an annually persistent capelin spawning site (Penton and Davoren 2012), any feeding calls in the region may have been produced out of range of the hydrophone. Given the limited anti-predator behaviour of prey at spawning sites, humpback whales may not use vocalizations to increase foraging efficiency during capelin spawning, but further work is needed to explore associations of call production with foraging behaviour. In particular, tagging studies may reveal whether some of the undescribed call types in Newfoundland are associated with foraging on capelin, or with particular foraging strategies.

One of the previously undescribed call types was the growl-moan, which seems to combine two other stereotyped call types (growls and low moans) and is relatively stereotyped itself. Growls are found in many regions and may function in contact or mediating social interactions (Dunlop et al. 2008; Wild and Gabriele 2014; Fournet et al. 2018b). Low moans are a novel call type, but based on their characteristics, may also play a role in contact, possibly over long distances (Konishi 1970; Morton 1975; Brown 1982). In species where the repertoire is constrained in terms of production, combining existing calls into compound calls may allow expansion of the repertoire (Seyfarth and Cheney 2010). Indeed, combining call types into novel compound calls has been observed in some frogs (e.g. Zhu et al. 2017), birds (e.g., Beer 1976; Hailman et al. 1985) and mammals (e.g., Robinson 1984; Corkeron and Van Parijs 2001) and has been hypothesized for some groups of killer whales (Strager 1995). Many marine mammals,

including humpback whales, do not appear to have constrained repertoires, but rather are able to add or substantially modify vocalizations over their lifetimes (e.g., dolphin signature whistles; Caldwell and Caldwell 1965; Sayigh et al. 1990; Tyack 1997, humpback whale song; Payne and Payne 1985; Eriksen et al. 2005), combining existing call types may still be a useful way to expand the repertoire. Humpback whales may have other methods of increasing the types of information they can convey. Call bouts, with variable numbers and types of calls, have been described in humpback whales, and could also serve to expand the repertoire (Silber 1986; Rekdahl et al. 2015). Overlap between units used in song and call types has also been found for humpback whales (Rekdahl et al. 2013). These ‘song-unit’ calls were not found to be stable, but matched units from song recorded in the same year or in previous years, seemingly changing in a similar time frame as the song content itself (Dunlop et al. 2007; Rekdahl et al. 2013). These ‘song-unit’ calls could be another way of expanding the repertoire on a temporary basis. The call types that appeared to be unique to one year in this study may represent song units for this group of humpback whales; however, recordings on the breeding grounds would be necessary for confirmation.

Long-term stability of a portion of call types within the repertoire has been found for humpback whales in two regions (Rekdahl et al. 2013; Fournet et al. 2018b), as well as in a number of other marine mammals, such as killer whales (Ford 1989, 1991; Foote et al. 2008), harp seals (*Pagophilus groenlandicus*; Terhune 1994; Serrano and Terhune 2002), bearded seals (*Erignathus barbatus*; Risch et al. 2007) and bottlenose dolphins (Caldwell and Caldwell 1965; Sayigh et al. 1990). On an Alaskan foraging ground, Fournet et al. (2018a) found that 12 of 16 described humpback whale call types were present in at least three decades between 1976 and 2012, including some of the same call types found during both years in Newfoundland. Over an

11 year period along a migration route off the east coast of Australia, 12 of 46 described call types of humpback whales were found to be stable and among the most commonly produced calls in the recordings (Rekdahl et al. 2013). Though we only had two years of data to compare, over half of the identified call types (12 of 22) appeared to be present in both years in Newfoundland, suggesting that the Newfoundland repertoire may follow similar stability trends as these other regions. As humpback whales are not known to form long-term stable groups (Whitehead 1983; Tyack 2000), call stability may be beneficial for communication between individuals that are not always associated (Rekdahl et al. 2013). Alternately, in the cases where stable associations are formed, call stability may also be useful in recognition (Ramp et al. 2010). Further recordings in the Newfoundland region will help to confirm which call types exhibit long-term stability.

Though the 12 common call types were deemed to be the same in terms of overall aural and visual characteristics, there were some differences in the average variable values (Rekdahl et al. 2013, 2017; Fournet et al. 2018b). Explanation for inter-annual differences in characteristics of call types may range from changes in noise conditions in the environment (Brumm and Slabbekoorn 2005; Fournet et al. 2018b) to differences in motivational state (Morton 1977; Dunlop 2017). Indeed, wind conditions differed between years, with 2015 being one of the windiest years in the past three decades in Newfoundland, resulting in increased noise from wave action relative to 2016 that could have impacted call characteristics. Inter-annual differences related to prey could also have played a role in call characteristic differences. Capelin did not spawn nearby the hydrophone during 2016 and peak biomass of capelin also was lower during 2016 (0.027 g/m²) relative to 2015 (0.126 g/m²; Calabria Carvalho 2018), indicating that predictably located high-density shoals of capelin were not available to humpback whales during

2016. Together with a higher number of humpback whales present in the area during 2016 relative to 2015 (Johnson 2018), this could have resulted in increased agitation of the whales (Morton 1977; Dunlop 2016, 2017). Without behavioural observations, however, it is difficult to identify why differences in call characteristics occurred between years.

In conclusion, we have provided the first contemporary, quantitative description of humpback whale call types on their Newfoundland foraging ground. More years of recordings from the Newfoundland area would help clarify call type boundaries and further describe the extent of the repertoire. In the first detailed, quantitative description of the humpback whale repertoire, Dunlop et al. (2007) recommended classification of humpback whale vocalizations into discrete call types, rather than broad classes. Although we found that a few call types are highly stereotyped and can be separated into well-defined, discrete types, many seem graded and may be better suited to a continuum-based classification (Ford 1989; Tyack 1997). Further study of humpback whale calls in this and other regions will help to determine whether classifying calls along a continuum versus distinct call types or broad classes, or some combination, captures more of the variation. Ultimately, determining what level of variation is biologically important and linking calls to contexts will be key in determining how best to delineate call types or establish call continua (Smith et al. 1982; Silber 1986; Tyack 1997; Dunlop et al. 2007; Rekdahl et al. 2013; Fournet et al. 2015). Although we described some of the call types in this chapter as novel in the literature and therefore possibly unique to Newfoundland foraging grounds, comparison among acoustic studies is limited by variable methods and inaccessible sound clips. Therefore, we reiterate the recommendation to standardize methods across similar studies, which is occurring more and more, and to provide sound clips and spectrograms of call types to allow comparison of aural and visual characteristics and variable measurements (Stimpert et al. 2011;

Fournet et al. 2015, 2018b).

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Tables and Figures

Table 1. Descriptions of the variables that were used in the CART, RF and pairwise call comparisons. Variables marked with a * were measured using the Noise-Resistance Feature Set (the same descriptions as for the program *Osprey* from Mellinger and Bradbury (2007)). The noise-resistant feature set placed a smaller feature box within the manually created selection box in *Raven* 1.5 and 2.0. Measurements of the call were made based on the contents of the feature box. Start frequency, end frequency and bout were determined manually in *Raven*. All frequency variables (i.e. with unit Hz) were log-transformed. Units are provided where applicable. Abbreviations are given for each variable that correspond to the other tables and figures.

Variable name	Unit	Abbreviation	Description
Lower frequency*	Hz	Lower	Lowest frequency of the call
Upper frequency*	Hz	Upper	Highest frequency of the call
Frequency range*	Hz	Range	Ratio of lower to upper frequency
Duration*	s	Dur	Length of the feature box
Bandwidth*	Hz	Band	Height of the feature box
Median frequency*	Hz	Median	The frequency at which 50% of the energy is to either side
Frequency of peak overall intensity*	Hz	Peak	The frequency with the greatest energy/amplitude in the feature box
Amplitude modulation rate*	Rate	Ampmod	Dominant rate of amplitude modulation
Frequency modulation rate*	Rate	Freqmod	Dominant rate of frequency modulation
Overall entropy*	Bits	Entropy	Measure of how evenly energy is distributed across the frequencies
Upsweep fraction*	%	Upsweep	Fraction of time that the median frequency in one time block is greater than the preceding time block
Bout		Bout	Number of the same call type in sequence in a discrete period of time
Start frequency	Hz	Start	Frequency at the beginning of the call measured on the fundamental frequency or lowest harmonic
End frequency	Hz	End	Frequency at the end of the call measured on the fundamental frequency or lowest harmonic
Frequency trend	Hz	Trend	Ratio of start to end frequency

Table 2. Mean (SE) for each broad class and call type with sample sizes for each year present. Call types in *italics* are those that were only present in one of the two years, all others were common to both years and $\diamond$ denotes call types with names used previously in the literature. Variable abbreviations correspond to those in Table 1.

Broad class Call type Year	n	Bout	Lower	Upper	Peak	Band	Median	Range	Trend	Start	End	Dur	Entropy	Ampmod	Freqmod	Upsweep
Low frequency 2015	238	1.18 (0.03)	46.63 (3.01)	300.97 (10.67)	106.22 (5.04)	254.34 (10.41)	114.84 (4.93)	0.17 (0.01)	0.85 (0.01)	78.94 (4.15)	90.04 (3.98)	0.68 (0.03)	15.50 (0.51)	1.70 (0.05)	1.75 (0.05)	49.74 (1.94)
	638	1.37 (0.06)	67.93 (1.66)	386.87 (12.92)	124.15 (3.11)	318.94 (12.48)	139.26 (3.15)	0.24 (0.01)	0.90 (0.01)	93.06 (2.24)	102.99 (2.25)	0.65 (0.01)	15.67 (0.46)	1.56 (0.03)	1.67 (0.04)	46.74 (1.09)
Growl $\diamond$ 2015	77	1.19 (0.05)	29.09 (1.38)	254.83 (22.30)	70.08 (2.81)	225.74 (22.50)	74.88 (3.29)	0.15 (0.01)	0.84 (0.02)	52.39 (1.80)	62.83 (1.96)	0.64 (0.02)	10.88 (0.60)	1.78 (0.06)	1.87 (0.07)	44.45 (2.92)
	380	1.30 (0.07)	52.80 (1.11)	324.96 (8.19)	107.03 (2.87)	272.16 (8.24)	121.63 (2.81)	0.19 (0.01)	0.87 (0.01)	71.60 (1.25)	82.74 (1.32)	0.67 (0.01)	14.75 (0.37)	1.70 (0.03)	1.84 (0.04)	46.14 (1.19)
Rumble 2015	8	1.13 (0.13)	30.76 (5.81)	322.63 (92.96)	112.79 (35.05)	291.87 (92.19)	111.11 (32.51)	0.13 (0.03)	0.90 (0.04)	68.04 (9.61)	74.50 (8.62)	0.61 (0.08)	18.48 (3.85)	1.88 (0.26)	1.88 (0.26)	45.12 (10.39)
	26	1.31 (0.13)	106.82 (18.85)	874.40 (172.25)	200.23 (35.46)	767.58 (159.36)	222.60 (36.26)	0.17 (0.02)	0.96 (0.02)	144.10 (23.65)	148.93 (23.61)	0.70 (0.07)	30.51 (5.88)	1.69 (0.13)	1.93 (0.16)	44.51 (5.95)
Dunno 2015	17	1.12 (0.08)	164.84 (11.84)	339.76 (38.63)	211.11 (14.68)	174.92 (41.41)	210.89 (12.21)	0.55 (0.05)	1.12 (0.09)	216.43 (18.21)	194.62 (12.35)	0.30 (0.01)	12.61 (1.33)	1.14 (0.34)	1.14 (0.34)	14.89 (7.97)
	2	1.50 (0.50)	180.18 (49.80)	257.81 (60.06)	219.73 (79.10)	77.64 (10.25)	224.49 (75.10)	0.69 (0.03)	1.31 (0.74)	215.78 (97.45)	180.97 (27.84)	0.26 (0.00)	11.08 (2.06)	0 (0)	0 (0)	79.00 (21.00)
Snore 2015	15	1.27 (0.12)	31.54 (5.52)	307.91 (59.04)	87.70 (12.77)	276.37 (55.85)	97.48 (11.72)	0.17 (0.04)	0.96 (0.06)	71.58 (10.60)	75.73 (10.50)	0.42 (0.03)	17.46 (2.85)	2.05 (0.25)	2.16 (0.26)	41.42 (9.29)
	25	2.84 (0.54)	80.68 (5.90)	356.78 (47.36)	116.95 (9.36)	276.09 (47.40)	135.38 (12.00)	0.32 (0.05)	0.96 (0.02)	98.90 (6.49)	102.43 (6.28)	0.39 (0.05)	13.53 (1.65)	1.74 (0.27)	1.81 (0.27)	59.00 (7.24)
Low moan 2015	18	1.00 (0)	115.72 (13.31)	490.72 (27.18)	282.71 (23.57)	375.00 (30.81)	300.96 (16.75)	0.25 (0.04)	0.92 (0.03)	200.68 (16.60)	225.41 (21.77)	1.63 (0.23)	18.77 (1.68)	1.06 (0.17)	1.07 (0.18)	51.37 (3.25)
	46	1.00 (0)	142.79 (7.22)	675.93 (56.16)	260.11 (10.24)	533.14 (58.23)	279.02 (8.34)	0.27 (0.03)	0.93 (0.02)	218.99 (8.93)	235.62 (7.28)	1.11 (0.08)	16.68 (1.62)	1.31 (0.11)	1.50 (0.12)	46.57 (3.52)
Whup $\diamond$ 2015	103	1.21 (0.05)	31.59 (1.47)	293.21 (8.79)	87.26 (3.93)	261.62 (8.78)	99.16 (3.87)	0.12 (0.01)	0.78 (0.02)	56.74 (2.24)	72.75 (2.10)	0.64 (0.04)	18.34 (0.75)	1.78 (0.07)	1.80 (0.08)	60.74 (2.76)
	80	1.13 (0.05)	53.54 (1.99)	493.03 (35.85)	97.41 (4.48)	439.49 (36.21)	124.93 (5.95)	0.15 (0.01)	0.86 (0.02)	75.73 (2.24)	90.86 (3.80)	0.66 (0.02)	22.32 (1.75)	1.83 (0.07)	1.91 (0.09)	53.76 (2.87)
Low hum 2016	79	1.75 (0.24)	92.03 (3.44)	261.21 (38.59)	129.28 (7.30)	169.18 (38.41)	128.79 (7.35)	0.54 (0.03)	1.01 (0.01)	118.75 (4.75)	118.51 (4.90)	0.31 (0.02)	8.70 (0.75)	0.69 (0.13)	0.64 (0.12)	38.64 (4.57)
Compound Growl-moan 2015	14	1.00 (0)	90.19 (14.67)	520.86 (26.17)	272.04 (32.43)	430.66 (27.29)	280.74 (18.02)	0.17 (0.03)	0.77 (0.06)	156.19 (23.50)	193.88 (17.40)	2.72 (0.45)	24.90 (2.61)	0.70 (0.10)	0.75 (0.15)	50.41 (4.28)
	3	1.00 (0)	113.77 (5.17)	891.11 (459.51)	238.28 (14.39)	777.34 (463.92)	274.02 (48.44)	0.23 (0.11)	0.87 (0.05)	210.96 (4.47)	242.56 (11.32)	2.02 (0.47)	22.08 (11.64)	0.56 (0.14)	1.28 (0.64)	57.11 (14.91)

Broad class Call type Year	n	Bout	Lower	Upper	Peak	Band	Median	Range	Trend	Start	End	Dur	Entropy	Ampmod	Freqmod	Upsweep
Pulsed 2015	385	2.18 (0.14)	133.22 (4.10)	711.88 (19.54)	236.69 (6.34)	578.66 (19.62)	259.92 (5.53)	0.23 (0.01)	0.71 (0.01)	173.10 (4.24)	280.20 (8.41)	0.25 (0.00)	38.32 (1.13)	0.34 (0.05)	0.34 (0.05)	84.04 (1.58)
	150	2.43 (0.23)	107.46 (4.22)	860.51 (52.94)	182.89 (6.28)	753.05 (53.08)	218.55 (10.24)	0.20 (0.01)	0.86 (0.02)	145.44 (5.09)	182.99 (7.33)	0.29 (0.01)	28.28 (1.44)	0.96 (0.11)	0.97 (0.11)	64.53 (3.35)
Droplet◇ 2015	39	1.56 (0.18)	279.11 (16.71)	727.35 (58.62)	371.24 (20.28)	448.24 (58.31)	379.26 (19.74)	0.44 (0.03)	0.58 (0.04)	292.61 (16.98)	555.20 (31.06)	0.24 (0.01)	37.33 (3.18)	0.08 (0.08)	0.08 (0.08)	87.41 (5.02)
	7	1.14 (0.14)	197.75 (37.10)	1014.30 (269.76)	282.09 (41.33)	816.55 (263.70)	312.55 (46.88)	0.25 (0.06)	0.84 (0.03)	239.29 (46.82)	281.25 (50.62)	0.26 (0.03)	23.12 (4.11)	0.33 (0.33)	0.33 (0.33)	66.86 (16.60)
Swop◇ 2015	278	2.21 (0.17)	121.86 (3.36)	746.05 (23.21)	233.65 (6.93)	624.19 (23.19)	258.08 (5.66)	0.20 (0.01)	0.68 (0.01)	161.99 (4.05)	266.13 (7.70)	0.26 (0.00)	40.35 (1.22)	0.39 (0.06)	0.39 (0.06)	87.75 (1.54)
	42	1.45 (0.18)	100.45 (6.94)	819.96 (71.89)	197.27 (13.42)	719.52 (72.86)	225.89 (11.24)	0.17 (0.02)	0.73 (0.04)	146.68 (9.54)	219.19 (15.80)	0.27 (0.01)	33.79 (2.86)	0.65 (0.18)	0.65 (0.18)	83.48 (4.80)
Teepee◇ 2015	34	3.00 (0.50)	74.10 (5.35)	470.73 (35.67)	145.71 (14.24)	396.63 (38.31)	166.64 (12.16)	0.20 (0.02)	0.94 (0.03)	120.41 (6.97)	132.87 (9.48)	0.25 (0.01)	19.86 (1.82)	0.26 (0.14)	0.26 (0.14)	71.89 (7.14)
	56	2.68 (0.21)	84.54 (4.88)	822.88 (70.37)	158.83 (9.77)	738.33 (71.02)	187.08 (9.24)	0.15 (0.01)	0.91 (0.03)	117.08 (5.77)	145.11 (10.55)	0.31 (0.01)	26.80 (1.86)	1.25 (0.19)	1.29 (0.19)	72.20 (4.94)
Groak 2015	10	1.00 (0)	93.75 (14.44)	747.36 (150.96)	158.20 (18.22)	653.61 (157.97)	194.67 (155.52)	0.18 (0.05)	0.91 (0.09)	156.00 (19.09)	204.80 (44.18)	1.63 (0.23)	18.77 (1.68)	1.06 (0.17)	1.07 (0.18)	51.37 (3.25)
Yip 2015	6	1.00 (0)	199.71 (25.50)	460.45 (49.36)	250.00 (19.34)	260.74 (67.93)	250.80 (19.47)	0.49 (0.11)	0.83 (0.09)	225.23 (24.55)	275.32 (21.02)	0.23 (0.03)	21.17 (3.83)	0.49 (0.49)	0.49 (0.49)	66.67 (21.08)
Pop 2015	9	1.00 (0)	163.90 (14.83)	704.92 (137.86)	268.88 (28.65)	541.02 (135.87)	316.14 (41.41)	0.28 (0.04)	0.91 (0.07)	255.31 (25.85)	280.92 (21.84)	0.25 (0.02)	43.46 (9.89)	0.33 (0.33)	0.33 (0.33)	75.05 (13.11)
Drum 2015	9	1.22 (0.22)	44.43 (9.06)	635.58 (174.86)	137.37 (46.87)	591.15 (169.55)	174.53 (48.20)	0.08 (0.01)	1.03 (0.25)	99.56 (8.01)	166.22 (56.14)	0.22 (0.01)	57.11 (19.38)	0 (0)	0 (0)	66.67 (16.67)
Honk 2016	29	2.21 (0.26)	140.78 (7.69)	1055.65 (169.52)	195.38 (8.53)	914.87 (170.59)	275.98 (42.74)	0.23 (0.03)	0.98 (0.03)	183.69 (9.18)	189.50 (9.16)	0.31 (0.01)	29.98 (4.39)	1.52 (0.26)	1.52 (0.26)	48.01 (7.39)
Chump 2016	16	5.06 (1.81)	106.20 (7.90)	677.67 (205.70)	163.33 (10.17)	571.47 (207.84)	164.26 (10.13)	0.38 (0.07)	0.81 (0.04)	127.53 (6.07)	165.80 (13.56)	0.21 (0.01)	18.18 (3.07)	0 (0)	0 (0)	16.89 (8.61)
High frequency 2015 2016	71	1.04 (0.02)	487.22 (17.91)	1361.58 (98.30)	631.49 (31.44)	874.37 (96.79)	631.78 (28.18)	0.49 (0.03)	0.97 (0.02)	584.02 (19.50)	616.20 (21.43)	0.29 (0.01)	31.44 (3.79)	1.08 (0.17)	1.08 (0.17)	53.65 (5.04)
	63	1.06 (0.03)	588.19 (24.93)	2117.72 (134.71)	744.00 (35.80)	1529.53 (134.28)	829.56 (42.96)	0.36 (0.03)	1.02 (0.04)	684.27 (28.11)	694.53 (30.44)	0.40 (0.03)	51.25 (6.25)	1.49 (0.15)	1.49 (0.16)	34.07 (3.96)
Yawp 2015 2016	39	1.08 (0.04)	484.56 (26.24)	1673.26 (130.81)	679.24 (51.24)	1188.70 (129.62)	679.30 (44.65)	0.37 (0.04)	0.96 (0.03)	607.46 (27.61)	651.27 (30.74)	0.30 (0.01)	37.77 (5.95)	1.00 (0.22)	1.00 (0.22)	47.92 (6.54)
	23	1.09 (0.06)	554.67 (30.50)	2406.61 (259.74)	707.71 (62.87)	1851.94 (257.44)	769.05 (70.08)	0.30 (0.04)	1.02 (0.04)	669.35 (44.26)	673.63 (55.72)	0.32 (0.02)	51.93 (9.83)	1.36 (0.28)	1.36 (0.28)	24.68 (6.53)
Oop 2015 2016	13	1.00 (0)	486.89 (42.65)	605.88 (47.76)	527.57 (43.23)	118.99 (27.44)	527.77 (42.99)	0.81 (0.04)	0.97 (0.03)	524.85 (44.56)	538.11 (41.11)	0.24 (0.01)	13.29 (1.83)	0 (0)	0 (0)	64.42 (12.17)
	26	1.08 (0.05)	693.55 (39.18)	1801.87 (201.07)	774.90 (44.44)	1108.32 (189.19)	857.42 (66.09)	0.50 (0.05)	0.99 (0.02)	762.72 (45.03)	770.90 (43.60)	0.34 (0.02)	43.10 (10.82)	1.32 (0.25)	1.32 (0.25)	40.31 (6.53)

Broad class Call type Year	n	Bout	Lower	Upper	Peak	Band	Median	Range	Trend	Start	End	Dur	Entropy	Ampmod	Freqmod	Upsweep
<i>Whimper</i> 2015	15	1.00 (0)	497.95 (34.89)	1008.69 (176.30)	591.21 (44.23)	510.74 (164.57)	586.21 (42.74)	0.62 (0.06)	0.93 (0.05)	557.28 (37.03)	615.27 (46.37)	0.32 (0.02)	21.31 (4.13)	2.11 (0.34)	2.11 (0.34)	73.54 (9.17)
<i>Pew</i> 2015	4	1.00 (0)	473.88 (51.50)	2102.05 (205.53)	654.79 (72.66)	1628.17 (165.10)	677.42 (66.80)	0.23 (0.02)	1.22 (0.12)	648.00 (75.82)	528.00 (23.55)	0.30 (0.02)	66.79 (14.23)	1.46 (0.85)	1.46 (0.85)	0 (0)
<i>Fluctuating moan</i> 2016	14	1.00 (0)	447.61 (45.02)	2229.70 (178.18)	746.23 (95.75)	1782.09 (177.48)	877.25 (98.03)	0.22 (0.03)	1.08 (0.15)	563.11 (47.27)	587.02 (51.90)	0.64 (0.08)	65.29 (11.27)	2.01 (0.20)	2.00 (0.21)	37.89 (6.89)

Table 3. Broad class CART confusion matrix for pooled 2015 and 2016 showing the number of cases correctly assigned to each observer classified call class in bold. CART classification success percentage is presented along with the RF classification success for comparison. The CART and RF had an overall classification success of 94%.

Broad class	n	Compound	High Frequency	Low frequency	Pulsed	CART classification success %	RF classification success %
Compound	17	8	0	9	0	47	18
High Frequency	134	0	124	0	10	93	92
Low Frequency	876	4	0	829	43	95	95
Pulsed	535	0	7	19	509	95	95

Table 4. CART confusion matrix for all 2015 and 2016 call types, showing the number of cases correctly assigned to each observer classified call type in bold along the diagonal. Confidence level (1-5 scale) is given for each call type, with 5 indicating high confidence in assignment of cases to that type and 1 indicating low confidence. The percentage agreement with observer assignments in the CART and RF are given in the last column; note that the confusion matrix for the RF differed from the CART, but the trends remained the same. An * next to the CART agreement highlights call types with no agreement with observer classifications in the CART. The CART and RF had 67% overall classification success. Blank cells represent zeroes in the matrix.

Call type	n	Growl	Rumble	Dunno	Snore	Low moan	Whup	Low hum	Growl-moan	Droplet	Swop	Teepee	Groak	Yip	Pop	Drum	Honk	Chump	Yawp	Oop	Whimper	Pew	Fluctuating moan	Confidence level	CART/RF Classification success (%)
Growl	457	413			2	7	28	1			1	5												5	90/91
Rumble	33	18	4		1	1	6				2	1							1					3	12/6
Dunno	19			9		1	1	1			7													3	47/63
Snore	40	8			6	2	4	15			3	2												3	15/20
Low moan	64		1			59	4																	5	92/92
Whup	183	82			6	3	85				3	1						3						5	46/51
Low hum	79	10				2	1	59			3	4												3	75/68
Growl-moan	17		1			15	1		0															5	0*/24
Droplet	46						1			15	28								2					3	33/41
Swop	320	1	4	1	2	5	2			1	297	4						2		1				4	93/91
Teepee	90	5			2	1	1	10			42	29												3	32/44
Groak	10										6	4	0											1	0*/10
Yip	6										6			0										1	0*/0
Pop	9										9				0									1	0*/0
Drum	9										6	2				0		1						1	0*/0
Honk	29		3			1	1	2			20	2					0							1	0*/45
Chump	16				1			3			7							5						1	31/50
Yawp	62									2	4								39	15			2	2	63/65
Oop	39					1				3	2								8	25				2	64/51
Whimper	15			1		1				3									3	7	0			1	0*/13
Pew	4																		4			0		1	0*/0
Fluctuating moan	14	0	1																1	4			8	1	57/57

Table 5. Mean (SE) of variables measured on compound call components with those of individual call analogues (call types and components were combined for both years for this comparison). Variable abbreviations correspond to those in Table 1.

Call type	Lower	Upper	Peak	Band	Median	Range	Trend	Start	End	Dur	Entropy	Ampmod	Freqmod	Upsweep
Growl (compound)	84.53 (10.45)	563.45 (93.38)	224.21 (24.86)	478.92 (91.95)	239.02 (13.64)	0.18 (0.02)	0.85 (0.04)	155.64 (16.11)	178.05 (13.67)	0.99 (0.16)	29.90 (3.62)	1.54 (0.27)	1.44 (0.23)	46.35 (5.46)
Growl	48.81 (1.04)	313.15 (7.86)	100.80 (2.52)	264.34 (7.86)	113.75 (2.53)	0.18 (0.01)	0.86 (0.01)	68.36 (1.13)	79.39 (1.20)	0.67 (0.01)	14.10 (0.33)	1.71 (0.02)	1.84 (0.03)	45.86 (1.11)
Moan (compound)	123.99 (10.23)	589.47 (72.00)	258.85 (28.84)	465.48 (74.17)	286.37 (18.57)	0.24 (0.03)	0.95 (0.08)	199.32 (13.87)	221.88 (19.60)	1.89 (0.41)	21.90 (2.75)	1.10 (0.14)	1.21 (0.17)	56.19 (4.50)
Low moan	135.18 (6.53)	623.84 (42.45)	266.46 (9.88)	488.66 (43.51)	285.19 (7.65)	0.26 (0.02)	0.92 (0.02)	213.84 (7.93)	232.75 (7.97)	1.26 (0.09)	17.27 (1.26)	1.24 (0.09)	1.38 (0.10)	47.92 (2.69)

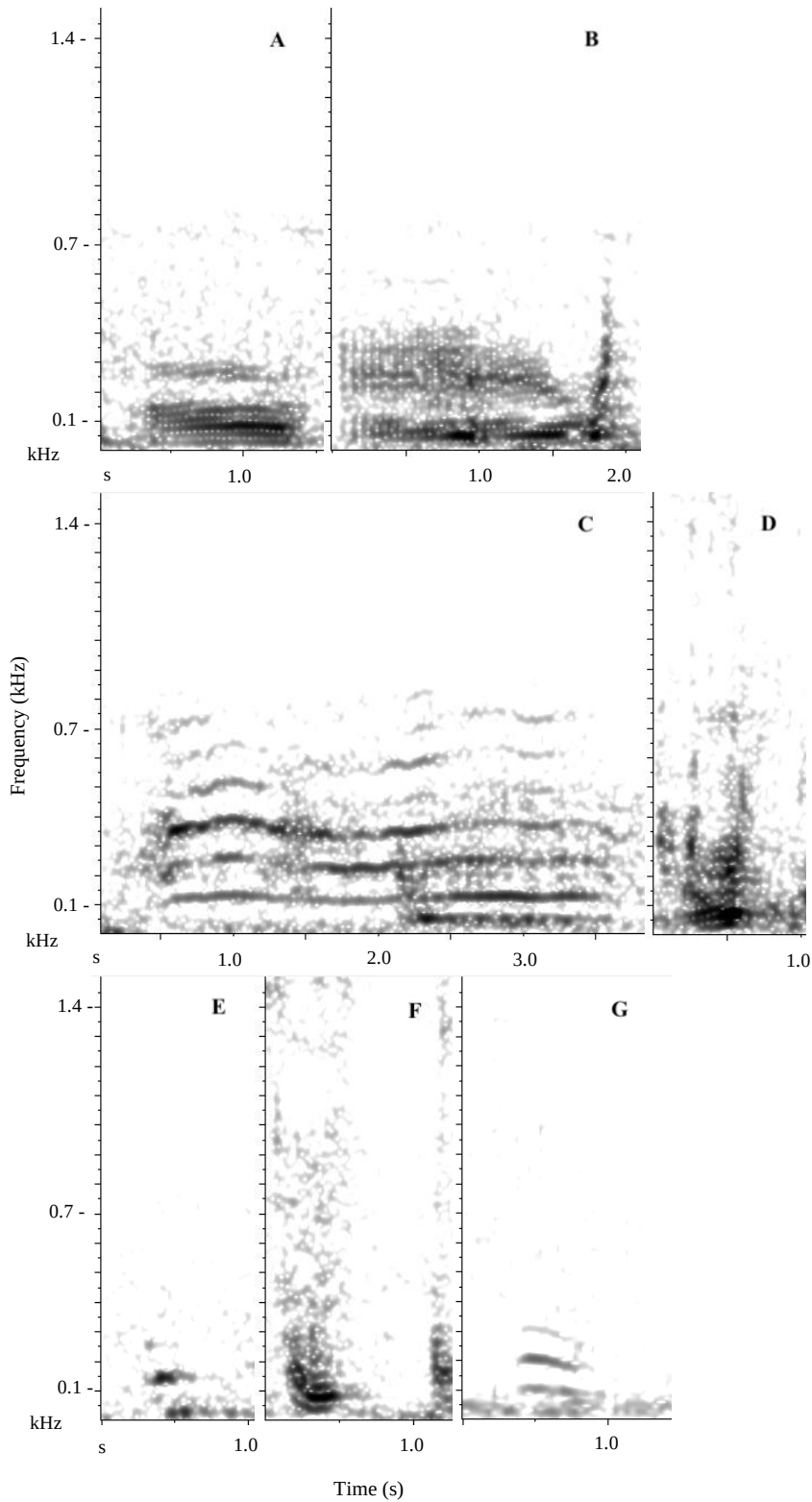


Figure 2. Spectrograms of the call types assigned to the low frequency class through manual classification from *Raven Pro* (Hann window, 8192 Discrete Fourier Transform, 2.93 Hz resolution, and 50% overlap): (A) growl, (B) whup, (C) low moan, (D) rumble, (E) dunno, (F) snore, (G) low hum.

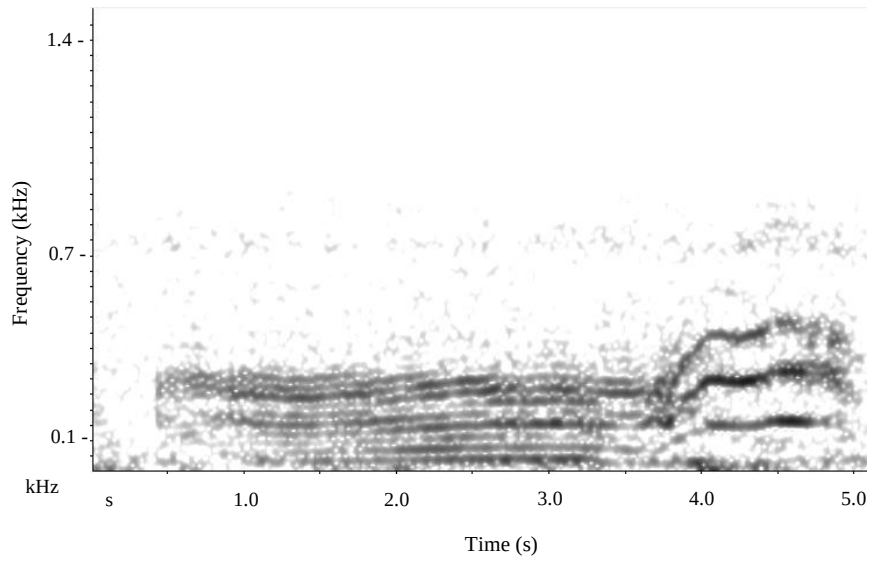


Figure 3. Spectrogram example of the only compound class call type from *Raven Pro* (Hann window, 8192 Discrete Fourier Transform, 2.93 Hz resolution, and 50% overlap), the growl-moan.

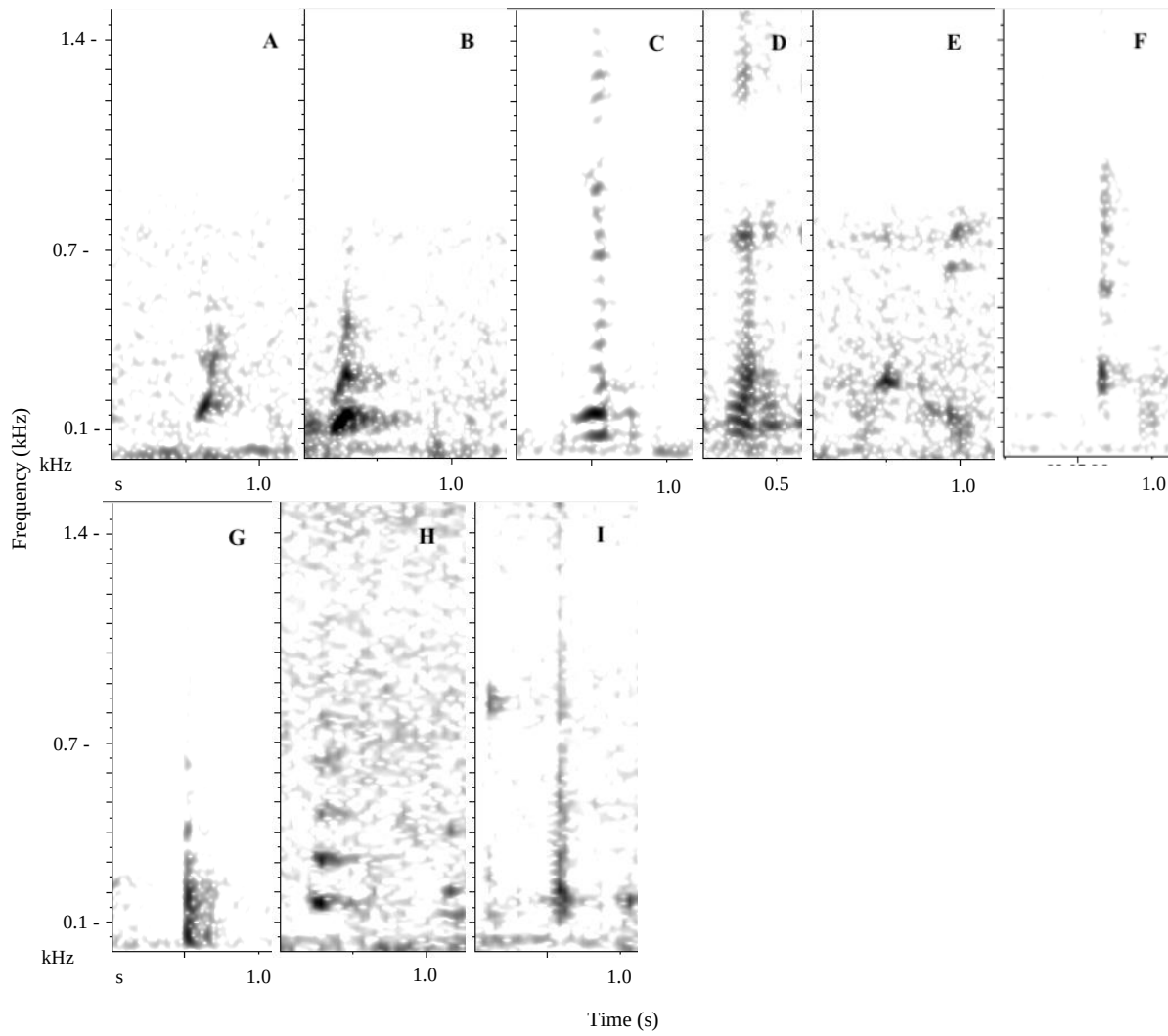


Figure 4. Spectrograms of the call types assigned to the pulsed class through manual classification from *Raven Pro* (Hann window, 8192 Discrete Fourier Transform, 2.93 Hz resolution, and 50% overlap): (A) droplet, (B) swop, (C) teepee, (D) groak, (E) yip, (F) pop, (G) drum, (H) honk, (I) chump.

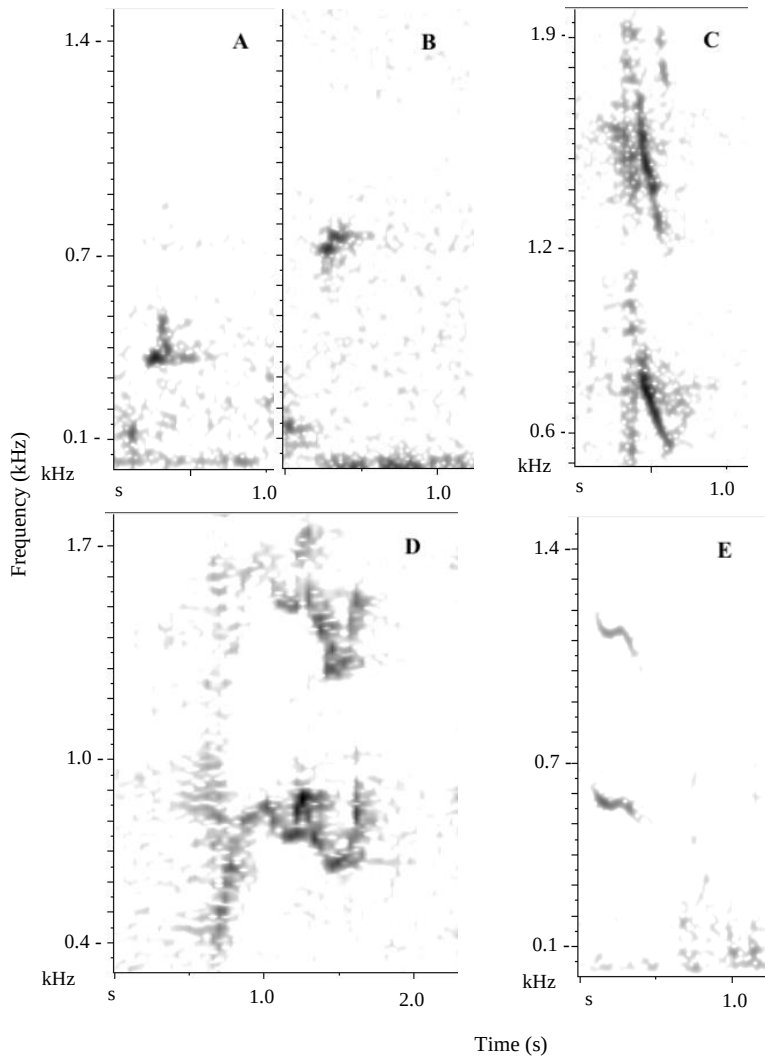


Figure 5. Spectrograms of the call types assigned to the high frequency class through manual classification from *Raven Pro* (Hann window, 8192 Discrete Fourier Transform, 2.93 Hz resolution, and 50% overlap): (A) yawp, (B) oop, (C) pew, (D) fluctuating moan, (E) whimper.

Appendix 1. Mean (SE) for call types that did not meet the inclusion criteria. Calls with an * appeared to be present in both 2015 and 2016 and those marked with a τ are similar to call types previously described in the literature and so were given the same name. Variable abbreviations correspond to those in Table 1.

Call type	n	Bout	Lower	Upper	Peak	Band	Median	Range	Trend	Start	End	Dur	Entropy	Ampmod	Freqmod	Upsweep
compound2	1	1	19.04	247.56	79.10	228.52	78.23	0.08	0.54	67.30	124.20	3.16	12.73	0.32	0.95	40.47
compound3	1	1	19.04	221.19	26.37	202.15	27.67	0.09	1.00	25.90	25.90	0.60	6.41	1.67	1.67	18.86
descending moan τ	4	1 (0)	124.51 (48.73)	566.16 (70.04)	296.63 (15.97)	441.65 (48.52)	293.13 (15.35)	0.21 (0.06)	0.95 (0.09)	179.15 (36.22)	192.10 (40.71)	1.09 (0.19)	17.00 (2.55)	0.99 (0.14)	1.83 (0.43)	60.67 (6.53)
descending shriek τ	2	1 (0)	578.61 (14.65)	3389.65 (1387.21)	1411.11 (194.82)	2811.04 (1372.56)	1169.19 (158.72)	0.20 (0.08)	1.17 (0.10)	780.00 (172.00)	656.00 (88.00)	0.34 (0.09)	81.66 (29.90)	1.17 (1.17)	1.17 (1.17)	33.39 (26.46)
downsweep	2	1 (0)	276.86 (32.23)	587.40 (49.80)	394.04 (21.97)	310.55 (82.03)	382.81 (10.56)	0.48 (0.10)	2.11 (0.26)	635.10 (3.90)	306.60 (40.10)	0.64 (0.13)	17.81 (5.12)	1.63 (0.33)	1.63 (0.33)	0 (0)
Groan* τ	7	2.14 (0.51)	57.97 (13.02)	280.20 (24.15)	79.94 (12.46)	222.24(21.81)	92.40 (13.23)	0.20 (0.04)	0.89 (0.03)	70.53 (11.55)	77.77 (11.35)	0.74 (0.23)	11.00 (1.59)	1.91 (0.33)	1.91 (0.33)	41.27 (13.20)
hf10	3	1 (0)	857.91 (264.67)	4617.68 (1780.03)	1001.95 (243.51)	3759.77 (1516.49)	1287.46 (494.97)	0.20 (0.02)	1.02 (0.01)	978.54 (265.34)	963.30 (262.58)	0.37 (0.03)	60.64 (27.94)	2.73 (0.20)	2.73 (0.20)	39.40 (30.75)
hf3	8	1 (0)	423.71 (50.15)	1760.74 (276.00)	867.19 (95.29)	1337.04 (293.93)	863.99 (73.60)	0.29 (0.07)	1.23 (0.26)	584.15 (67.17)	537.77 (64.06)	0.39 (0.03)	56.14 (9.85)	2.66 (0.44)	2.17 (0.34)	67.96 (8.91)
hf7	3	1.27 (0.12)	950.42 (30.24)	2964.62 (296.89)	1406.25 (65.07)	2014.20 (290.55)	1441.98 (54.50)	0.42 (0.04)	1.54 (0.05)	1477.73 (40.68)	979.80 (30.18)	0.97 (0.07)	65.93 (10.36)	1.29 (0.10)	1.23 (0.08)	23.45 (3.55)
hf8	1	1.50 (0.20)	652.40 (78.39)	4508.06 (325.11)	1277.71 (199.94)	3855.65 (335.52)	1360.96 (155.38)	0.16 (0.03)	0.98 (0.05)	936.55 (100.11)	1007.60 (128.29)	0.41 (0.06)	121.07 (16.74)	1.93 (0.30)	1.87 (0.29)	74.80 (7.47)
lf1*	6	3.16 (0.32)	59.01 (4.78)	470.91 (77.31)	121.87 (10.14)	411.91 (77.76)	134.79 (10.50)	0.24 (0.03)	1.06 (0.04)	93.42 (4.72)	96.52 (6.74)	0.64 (0.04)	14.34 (1.54)	1.88 (0.11)	1.85 (0.11)	41.71 (3.73)
m1	1	1	171.39	221.19	190.43	49.80	194.37	0.77	1.12	214.70	191.40	0.34	6.67	2.93	2.93	36.54
m2	7	1 (0)	121.58 (14.69)	714.63 (164.15)	216.38 (25.04)	593.05 (174.30)	281.52 (47.69)	0.22 (0.04)	0.77 (0.09)	168.85 (12.32)	232.84 (25.17)	0.90 (0.13)	16.62 (2.43)	1.82 (0.35)	1.38 (0.17)	48.49 (5.27)
m3	5	1.20 (0.20)	284.47 (45.96)	975.29 (193.25)	404.30 (57.98)	690.82 (198.21)	401.55 (57.52)	0.35 (0.10)	0.93 (0.06)	363.94 (67.21)	378.84 (58.61)	1.13 (0.14)	22.66 (3.21)	0.96 (0.14)	0.96 (0.14)	33.48 (12.20)
m4	2	1 (0)	361.82 (55.66)	3076.17 (2588.38)	437.99 (42.48)	2714.36 (2644.04)	946.71 (469.52)	0.45 (0.40)	0.90 (0)	412.36 (22.05)	457.56 (23.15)	3.67 (2.47)	168.89 (162.59)	0.50 (0.34)	0.50 (0.34)	54.75 (5.51)
modulated moan τ	2	1 (0)	74.71 (8.79)	2589.84 (2005.37)	437.99 (86.43)	2515.14 (1996.58)	619.34 (97.19)	0.07 (0.05)	0.78 (0.07)	111.90 (1.90)	144.40 (16.00)	1.19 (0.43)	61.97 (29.49)	0.96 (0.34)	0.96 (0.34)	66.14 (29.62)
p10	6	2.83 (0.31)	84.47 (20.26)	677.73 (129.85)	172.36 (21.31)	593.26 (145.58)	172.81 (15.22)	0.21 (0.09)	1.00 (0.01)	148.95 (10.87)	149.89 (11.38)	0.23 (0.02)	21.37 (2.97)	0 (0)	0 (0)	55.19 (20.57)
p6	1	1.20 (0.13)	83.20 (9.12)	543.46 (81.77)	150.59 (23.51)	460.25 (78.97)	170.84 (21.02)	0.19 (0.04)	0.85 (0.08)	141.83 (22.47)	176.66 (28.32)	0.29 (0.01)	23.69 (3.84)	1.17 (0.48)	1.17 (0.48)	51.50 (14.18)
p8	6	4.41 (0.33)	142.50 (7.12)	1415.45 (81.45)	227.28 (11.63)	1272.95 (79.68)	288.90 (16.76)	0.13 (0.01)	0.90 (0.02)	195.35 (8.08)	222.04 (10.19)	0.29 (0.01)	42.54 (3.98)	0.88 (0.16)	0.88 (0.16)	57.06 (4.97)
p9	4	4 (0)	128.91 (16.59)	987.30 (35.97)	228.52 (3.97)	858.40 (36.24)	233.30 (3.52)	0.13 (0.02)	1.73 (0.17)	297.77 (19.12)	174.73 (8.64)	0.23 (0.02)	27.05 (2.11)	0 (0)	0 (0)	4.28 (2.28)
upsweep	1	1	48.34	1835.45	123.05	1787.11	190.68	0.03	0.12	80.00	664.00	0.51	39.49	3.91	1.95	100.00

Chapter Two: Humpback whale call use across time, space and context: A comparison between a North Atlantic foraging ground during 2015 and a North Pacific breeding ground during 1981-1982

Abstract

Study of the repertoires of allopatric groups of the same species can yield a great deal of information on the drivers of signal adaptation and evolution. Humpback whales (*Megaptera novaeangliae*) are a cosmopolitan baleen whale with three geographically isolated lineages in the three main ocean basins (North Pacific, North Atlantic and Southern oceans). The last common ancestor of these lineages was estimated to be 2-3 million years ago. Five call types have been previously identified on allopatric foraging grounds in two ocean basins, and found to be stable over three decades in one of these regions, suggesting that they are both innate (i.e. unlearned) and possibly fixed (i.e. no or minimal change in call structure over generations), but it is unclear whether they are also produced on the breeding grounds, which represents a different ecological context. Thus, the objective of this study was to identify whether these five call types were present in recordings from humpback whales on a Newfoundland foraging ground in 2015 and a Hawaiian breeding ground in 1981-82. Humpback calls were identified in recordings from both areas and first manually classified using aural and visual characteristics and then validated with classification and regression tree and random forest analyses. The five call types appear to be present in both areas based on manual classification, with some differences in characteristics possibly resulting from differences in recording methods, background noise or motivational state. These results, coupled with those from studies showing that these five call types are stable across decades and regions, suggests that they are likely innate and fixed in the humpback

repertoire, and that they may be used by all individuals throughout their annual cycle. The features of these calls also suggest that they serve a function in social interactions, such as mother-offspring contact, and that they would be a good starting point for passive acoustic monitoring of humpback whales globally.

Introduction

Many studies have investigated the roles that genetics and learning play in the types of signals used by acoustically communicating animals (Seyfarth and Cheney 2010). The number and type of acoustic signals are often under strong genetic control, with many species having a fairly constrained vocal repertoire (Seyfarth and Cheney 2010). In some cases, some or all of this repertoire is unlearned (i.e. innate) and does not change throughout the life-span of an individual or sometimes over generations. (i.e. stable or fixed; Caldwell and Caldwell 1965; Waser 1982; Seyfarth and Cheney 2010). Indeed, evidence for innate vocal behaviour has been found for a number of species, whereby acoustic features of infant and adult calls are similar (e.g. vervet monkey alarm calls, *Chlorocebus pygerythrus*; Seyfarth and Cheney 1986), calls are similar to kin even without contact (e.g. distance calls of female zebra finches, *Taeniopygia guttata*; Forstmeier et al. 2009), acoustic features of hybrids are intermediate to both parent species (e.g., gibbons, hybrids of *Hylobates lar* and *H. pileatus*; Brockelman and Schilling 1984; fur seals, *Arctocephalus* spp.; Page et al. 2001), and calls of deafened individuals are similar to non-deafened counterparts (e.g. eastern phoebes, *Sayornis phoebe*; Kroodsma and Konishi 1991). Vocal repertoires of a number of species appear to be stable over the lifetime of individuals and possibly fixed across generations, such as killer whales (*Orcinus orca*; Ford 1989, 1991; Foote et al. 2008), harp seals (*Pagophilus groenlandicus*; Terhune 1994; Serrano and Terhune 2002),

bearded seals (*Erignathus barbatus*; Risch et al. 2007) and bottlenose dolphins (*Tursiops truncatus*; Caldwell and Caldwell 1965; Sayigh et al. 1990). Call types that are stable may be important to maintain proper social interactions with conspecifics in stable or unstable associations (Ford 1991; Riesch et al. 2006; Rekdahl et al. 2013) especially for frequently occurring social interactions, such as mother-offspring contact (Dunlop et al. 2008; Dunlop 2017) and individual recognition (Caldwell and Caldwell 1965). Therefore, identifying stable call types may be helpful in understanding a species' social structure, the function of calls types, and provide opportunities to examine vocal responses to short or long-term environmental change (Parks et al. 2007; Weilgart 2007; Luther and Baptista 2010).

Humpback whales (*Megaptera novaeangliae*) are a highly vocal and migratory species that display variable ecological, social and vocal behaviour throughout their annual migratory cycle. They exhibit site fidelity to foraging grounds (Baker et al. 1986, 2013; Clapham et al. 1993; Straley et al. 1993; Acevedo et al. 2014; Gabriele et al. 2017) and breeding grounds (Chittleborough 1965; Baker et al. 2013) with limited exchange of individuals within ocean basins and rare exchange among ocean basins (Payne and Payne 1985; Katona and Beard 1990; Baker et al. 1993, 1998, 2014; Valsecchi et al. 1997; Acevedo et al. 2013; Schmitt et al. 2014). In general, humpback whales breed at low latitudes and feed at higher latitudes (Dawbin 1966; Baker and Herman 1984a, 1984b; Clapham 1996), although, feeding has been observed on breeding grounds (Baraff et al. 1991). Social interactions and vocal behaviour differ between foraging and breeding grounds. On the breeding grounds, physically aggressive surface-active groups of male humpback whales are commonly observed (Tyack and Whitehead 1982; Baker and Herman 1984b, 1984a; Silber 1986a). Song, produced only by males (Payne and McVay 1971; Cerchio et al. 2001; Stimpert et al. 2012), is mainly associated with breeding, but has been

reported on foraging grounds (Mattila et al. 1987; Clark and Clapham 2004; Stimpert et al. 2012). On foraging grounds, aggressive behaviours appear to be rare (Baker and Herman 1984b) and individuals are instead observed feeding in groups cooperatively or individually (Baker and Herman 1984b; D’Vincent et al. 1985; Fournet et al. 2018c), possibly because whale aggregations are associated with abundant prey (Whitehead et al. 1980; Payne et al. 1986; Johnson 2018). In contrast to song, the other main vocalization type of humpback whales, referred to as non-song calls (Dunlop et al. 2008; Fournet et al. 2015), social sounds/vocalizations (Silber 1986a; Dunlop et al. 2007, 2008), or ‘calls’ (Fournet et al. 2018b), occur on all parts of the range, are produced by all demographics (Winn et al. 1979; Mobley Jr et al. 1988; Dunlop et al. 2008; Zoidis et al. 2008), and some call types do not appear to change significantly over time (stable; Rekdahl et al. 2013; Fournet et al. 2018b).

Some call types are shared among contexts and regions (Dunlop et al. 2007; Rekdahl et al. 2013; Fournet et al. 2015; Rekdahl et al. 2017; Fournet et al. 2018d). Indeed, five call types (i.e., droplets, swops, teepees, growls, whups) were present on foraging grounds in both the North Atlantic and North Pacific (Fournet et al. 2018c). As the last common ancestor of humpback lineages within different ocean basins (North Pacific, North Atlantic and Southern oceans) is estimated to be 2-3 million years ago (Baker et al. 1993), the presence of these call types in the two ocean basins suggests that they may be innate (Fournet et al. 2018d). These five call types were also stable across 36 years on a southeast Alaskan foraging ground (Fournet et al. 2018b), as were other call types on an Australian migration route over 11 years (Rekdahl et al. 2013), suggesting that some call types may be fixed. It is unclear, however, whether these call types are produced on breeding grounds, which represent a different ecological context. Therefore, the objective of this study was to identify whether the five call types are present on a

Hawaiian breeding ground during 1981 and 1982 (Silber 1986a, 1986b), and the coastal Newfoundland foraging ground during 2015. The presence of these five call types in both regions and contexts across this temporal range provides further clues as to whether they may be innate and/or fixed in the repertoire and may help to identify their functions.

Methods

Data Collection

Passive acoustic recordings were made in coastal Newfoundland (NL) during July-August 2015 using a moored hydrophone and boat-based recordings were made in Hawaii (HI) during January-April 1981 and February-April 1982 using a portable hydrophone over the side of a boat when whales were within ~200 m or less (Silber 1986b, 1986a; see Table 1 for details). During recordings in HI, concurrent behavioural observations were made of the focal animals (Silber 1986b, 1986a). In NL, concurrent behavioural data were not collected, but anecdotal observations were made during photo-identification studies (Johnson 2018).

Aural-Visual Survey and Classification

The recordings from both regions were examined aurally and visually in *Raven Pro* 1.5 (NL) or 2.0 (HI; hereafter referred to as *Raven*; Cornell Laboratory of Ornithology; Bioacoustics Research Program 2014) using a Hann window, 8192 (NL) and 32768 (HI) Discrete Fourier Transform, 2.93 Hz resolution, and 50% overlap for the five call types. For most variable measurements, including signal-to-noise ratio (SNR), we used the Noise-Resistant Feature Set (NRFS) developed by Mellinger and Bradbury (2007) for the program *Osprey* and based on work by Fristrup and Watkins (1993), using the *Acoustat* package in MATLAB (version 9.2).

The NRFS calculates the bounds of a smaller feature box, in this case, within the manually created selection box from *Raven* in which the loudest parts of the sound have the most impact on the measurements by ranking and summing the energy within the sound compared to the background noise (Mellinger and Bradbury 2007; Fournet et al. 2018b). Thus, measurements are more robust to differences in noise and equipment between recording sets as well as to differences in the selection boxes made in *Raven Pro* (Mellinger and Bradbury 2007; Fournet et al. 2015, 2018b). Only calls with a SNR at least 15 dB above ambient noise were retained for analysis. In previous studies on humpback calls, a SNR cut-off of 10 dB above ambient has been standard (Dunlop et al. 2007, 2008; Stimpert et al. 2011; Rekdahl et al. 2013; Fournet et al. 2015), but due to recording differences between the two regions, we chose only the highest quality calls. Fifteen variables were measured on all calls with an SNR >15 dB (Table 2). Additionally, start and end frequency were measured manually in *Raven* by placing a point selection on the beginning and end of the fundamental or lowest frequency component of each call (Fournet et al. 2018b). Bout was recorded manually, and was defined as the number of the same call type in sequence with relatively equal temporal separation (<2 s) between each instance, similar to the definitions used by Rekdahl et al. (2015) and Fournet et al. (2015). All frequency variables were log-transformed prior to analysis, as humpback whales are thought to perceive pitch on a logarithmic scale similar to other mammals (Chabot 1988; Dunlop et al. 2007; Fournet et al. 2015). Summary statistics for the call types from each region are provided as mean $\pm$ SE for qualitative comparison. The NL calls above the SNR threshold were classified to describe the call repertoire by one observer (ME; see Chapter 1) and classifications were validated by a second observer (MF) to confirm agreement. In contrast, the HI calls were classified into one of the five call types only, with other calls left unclassified.

Statistical Analysis

A supervised classification and regression tree (CART) and random forest (RF) were run with all calls from both regions together, using the *rpart* and *randomforest* packages in *R* (version 3.5.0). Both the CART and RF were run with and without region as a variable to determine if region was an important splitting variable. Additionally, the CART and RF were run with and without region labels attached to each call type to further examine whether calls were primarily separated by type or by region. CART and RF are classification methods that are becoming standard in studies of call repertoires of humpback whales (Rekdahl et al. 2013, 2017; Fournet et al. 2018b, 2018d) and other taxa (Garland et al. 2015; Thiebault et al. 2019) as both methods are minimally affected by outliers, non-normality, non-independent data, correlated variables, and sample size differences, which are all common in these studies (Breiman et al. 1984; Breiman 2001; Armitage and Ober 2010). Both methods also have fairly high levels of agreement with manual classification in several studies on humpback whales (e.g., Rekdahl et al. 2017; Fournet et al. 2018a, 2018b) as well as other marine mammals (e.g., Oswald et al. 2003; Garland et al. 2015). As in Chapter 1, the CART produced a single tree using the Gini index (“goodness of split” or measure of impurity), whereby all variables were taken into account and the variable that resulted in the smallest splitting error was chosen as the most important and displayed at each node (Breiman et al. 1984; Berk 2008; Rekdahl et al. 2013, 2017; Fournet et al. 2018d). The minimum number of cases (i.e. calls) in each terminal node was defined as 10 and the tree was fully grown and then pruned back until the tree had the smallest number of terminal nodes and the highest classification success rate (Breiman et al. 1984; Risch et al. 2007; Fournet et al. 2018d). In contrast, the RF grew 1000 trees via bootstrapping (Keen et al. 2014), whereby a

random sample of 30% of the data (i.e. OOB data) was removed and the remaining data were used to grow the tree. The misclassification rate (i.e. OOB error rate) for each call type was defined as the number of cases that were misclassified over all the trees out of the total number of cases (Breiman 2001; Armitage and Ober 2010; Rekdahl et al. 2017; Fournet et al. 2018b). The RF also considered a random subset of three variables to grow each tree, which minimized the OOB error (Bao and Cui 2005; Rekdahl et al. 2017; Fournet et al. 2018b). After all trees were grown, the variables were ranked in order of importance (Breiman 2001; Liaw and Wiener 2002).

Results

All five call types were qualitatively identified in both the NL and HI datasets, with a total of 531 calls across the five types in NL and 136 in HI being above the SNR threshold. Swops comprised the largest proportion of calls in both regions (45% HI, 52% NL), while whups were the second most represented call type in NL (19%), but the second least represented in HI (11%) after growls (10%). The proportion of teepees also varied between regions (6% NL, 22% HI), while droplets represented a similar proportion in both regions (12% HI, 7% NL).

Although CART and RF are robust to sample size differences (Breiman et al. 1984; Breiman 2001; Armitage and Ober 2010), both were run with a random subsample (40%) of the NL dataset. CART and RF output did not differ from those with the full NL dataset and, thus, the subsampled results are not presented. The CART without region included as a variable had an 84% classification success (Table 3), with twenty terminal nodes created from the five calls types, with all five call types occurring in multiple terminal nodes (Fig. 1). The RF without region included had 80% classification success and the five most important variables in order of

importance were end frequency, lower frequency, duration, median frequency and entropy.

When region was included as a variable, the five most important variables in the RF were the same, and region was never an important splitting variable in the CART. Though region was not an important variable in either the CART or RF, when region labels were added to call types in the CART and RF, the call types seemed to primarily separate by region (Table 3). When misclassified, NL growls were most commonly assigned as NL whups and vice versa and a portion of whups from both regions were also assigned as swops (Table 3). Droplets and teepees from both regions were most commonly misclassified as NL swops, and a small portion of swops were misclassified as all other call types (Table 3). HI growls and teepees had higher classification success than their NL counterparts, while the other three HI call types had lower classification success (Table 3). With all cases from both regions, droplets had the lowest CART classification success, teepees had the lowest RF classification success and teepees had the largest difference between the overall CART and RF classification success (Table 3).

Some general trends were apparent from the averaged variables (Table 4). In particular, swops and teepees in HI occurred more often in bouts and frequently in longer bouts than in NL (Table 4). The calls in HI were higher frequency on average across nearly all frequency measures and had wider average bandwidths than in NL (Table 4, Fig. 2). Lastly, the average entropy of calls in HI was higher than in NL for all types except droplets (Table 4). Qualitatively, many of the calls in HI had less clear structure and definition on the spectrograms than those in NL (Fig. 2).

Discussion

While the overall classification successes of the CART and RF were high, each call type had lower classification success and was found in numerous terminal nodes. Additionally, call types seemed to classify by region. These findings do not fully support the presence of these same five call types in both regions. Based on qualitative classification, however, we propose that at least some of the five call types are present in both regions with differences in measured call characteristics possibly resulting from varying environmental and recording conditions. The identification of the same call types across multiple ocean basins and contexts (i.e., foraging, migration and possibly breeding) over a long period, suggests that these calls are innate and common to all humpbacks (Fournet et al. 2018d). Indeed, these five call types have been previously recorded and described in four other regions: Southeast Alaska, USA (foraging; Fournet et al. 2015, 2018a, 2018b), Massachusetts Bay, USA (foraging; Fournet et al. 2018b), Southeast Queensland, Australia (migration; Dunlop et al. 2007; Rekdahl et al. 2013), Angola, Africa (migration; Rekdahl et al. 2017). Genetic control may actually be a driver of multiple aspects of humpback vocal behaviour as the song formula also appears to be innate (Payne and Payne 1985; Cerchio et al. 2001); however, learning plays an important role in humpback song content and other behaviours (Payne and Payne 1985; Weinrich et al. 1992; Rendell and Whitehead 2001; Eriksen et al. 2005; Garland et al. 2011). Recordings of humpback calf vocalizations and comparisons with adult calls could provide further evidence regarding innate humpback vocal behaviour, as in other species (e.g., gibbons, hybrids of *Hylobates lar* and *H. pileatus*; Brockelman and Schilling 1984; vervet monkeys, *Chlorocebus pygerythrus*; Seyfarth and Cheney 1986; fur seals, *Arctocephalus* spp.; Page et al. 2001).

The lack of support by the CART and RF for the manually classified call types may have resulted from a number of factors. First, the variables used may not adequately capture the

variation among the call types observed by a human (Janik 1999). This is likely the case for whups and growls, as they vary only by an upsweep at the end of the whup that is not present in the growl. Several studies have noted that some, or all, humpback calls appear to fall along a continuum (Chabot 1988; Dunlop et al. 2007; Stimpert et al. 2011; Fournet et al. 2015; Dunlop 2017). Given this observation, it is possible that some of these five call types do not fit into discrete types or that some of the categories are not biologically relevant (Smith et al. 1982; Silber 1986a; Tyack 1997; Dunlop et al. 2007; Rekdahl et al. 2013; Fournet et al. 2015). Swops, droplets and teepees are all short duration, pulsed type calls with many similarities in their characteristics. Droplets and teepees were commonly misclassified as swops, indicating that the three may fit better in a continuum-based classification (Ford 1989; Tyack 1997). As each call type also ended up in more than one terminal node in the CART (Fig. 1), a continuum-based system may be preferable or further division of the call types may be needed.

Long-term stability of some, or all, of the five call types in both Alaska (foraging grounds, 1976-2012; Fournet et al. 2018b) and Australia (migratory route, 1997-2008; Rekdahl et al. 2013), as well as possibly between the 1980's in HI and 2015 in NL (this study), indicates that they are likely fixed in the humpback call repertoire (Fournet et al. 2018d, 2018b). Given that some of the same individuals that forage in Alaska likely also breed in Hawaii (Baker et al. 1986), the likely presence of these calls in the 1980's in Hawaii is not surprising, but their presence on both a foraging and a breeding ground would indicate that they are used in multiple ecological contexts. Long-term stability of call types is common among marine mammals with evidence found for killer whales (Ford 1989, 1991; Foote et al. 2008), harp seals (Terhune 1994; Serrano and Terhune 2002), bearded seals (Risch et al. 2007) and bottlenose dolphins (Caldwell and Caldwell 1965; Sayigh et al. 1990). In killer whales, stable calls are suggested to serve a

contact function and in bottlenose dolphins the most studied stable calls are used for individual identification (Caldwell and Caldwell 1965; Ford 1989; Janik and Slater 1998), suggesting that stable calls in humpback whales may serve similar purposes (Wild and Gabriele 2014). Long-term studies on call stability in more regions over multiple generations will provide further insight into whether the humpback call repertoire is fixed.

Though the overall structure of the calls qualitatively indicates that the same five call types are used in both regions, differences in some characteristics were present, as found in previous studies (Rekdahl et al. 2013; Fournet et al. 2018b, 2018d). Indeed, some of these differences were large (Table 4), although they were not as obvious in the aural and visual analysis of the spectrograms during manual classification (Fig. 2). Differences could be due to a number of factors in isolation or combination. First, differences in call characteristics could be related to divergence in genetics (Valsecchi et al. 1997) during the long time period since contact between the whales from these two regions (Baker et al. 1993). Second, recordings were only made in HI while whales were within ~200 m of the boat and hydrophone (Silber 1986a), while recordings of calls in NL were made while whales were likely at more variable distances from the hydrophone. The proximity of the whales to the hydrophone likely resulted in varying propagation effects on the recorded calls, such as the hydrophone detecting more of the high frequency components of calls from closer whales in HI (Konishi 1970; Morton 1975; Wiley and Richards 1978; Bradbury and Vehrencamp 1998, 2012). Third, background noise conditions over the short- or long-term may have contributed to differences in the call type characteristics. In HI, humpback song was present on many recordings, and often overlapped the calls, while abiotic factors (e.g., wind, waves) were the main source of background noise in NL. Humpback whales appear to increase the source level of their calls (Fournet et al. 2018a), or switch to surface-

generated sounds from vocal sounds in increased noise (Dunlop et al. 2010). Other marine mammals respond to noise by reducing call rate and increasing minimum frequency (e.g. right whales; *Eubalaena glacialis*; Parks et al. 2007) or adjusting frequency modulation (e.g. Indo-pacific bottlenose dolphins; *Tursiops aduncus*; Morisaka et al. 2004). HI calls in this study were generally higher frequency and had wider bandwidths on average than NL calls (Table 4), which could be strategies to deal with background noise. However, an examination of the source levels would be required to confirm this. Finally, these differences could be related to the motivational state of the whales (Morton 1977). Many of the HI recordings were from surface-active, aggressive males (Silber 1986a), which is expected on breeding grounds, as competition and aggression between males is often observed (Tyack and Whitehead 1982; Baker and Herman 1984b, 1984a; Silber 1986a). In contrast, aggressive behaviours were not observed among foraging whales in NL during opportunistic encounters during photo-identification (Johnson 2018). Additionally, the humpback whales within the vicinity of the hydrophone arrive in the area only when capelin (*Mallotus villosus*), their main prey in the area, are abundant (Johnson 2018), possibly further reducing the likelihood of competitive interactions. As there appears to be motivational information in humpback whale calls (Dunlop 2016, 2017), this may explain some of the differences observed between the calls in this study; however, the behaviour of NL whales needs to be quantified to further examine this. To identify which factor, or combinations of factors, is responsible for the differences in characteristics, further comparison among more allopatric and sympatric regions will be required.

In conclusion, we have provided the first comparison of humpback call type presence on allopatric foraging and breeding grounds with decadal separation. Though not supported by the CART and RF, we propose that the same five call types that have been identified in other regions

are present in both Newfoundland and Hawaii, with variation in characteristics resulting for a number of reasons. This finding adds to the evidence that these call types may be fixed and innate. These findings also provide insight into the function of these calls, whereby some have previously been proposed to serve a contact function (Dunlop et al. 2008; Wild and Gabriele 2014; Fournet et al. 2018d). Indeed, whups and growls may be used for longer distance social interaction and contact as they are relatively discrete and low frequency (Konishi 1970; Morton 1975; Wiley and Richards 1978; Brown 1982; Dunlop et al. 2008), while swops, droplets and teepees may be used when whales are in closer proximity as they are more graded and higher frequency (Marler and Tenaza 1977; Ford 1989; Krebs et al. 1993; Dunlop et al. 2008; Fournet 2014). It is likely that all five calls types are useful for mediation of various social interactions within the generally unstable social relationships of humpback whales (Whitehead 1983; Tyack 2000; Rekdahl et al. 2013). More behavioural observations during the recordings and the use of animal-borne tags will be necessary to gain further insight into the function of these calls.

Adding to suggestions in previous studies, we conclude that any of these five call types, but particularly whups and growls, may make ideal calls for PAM of humpback whales around the globe, with the potential for building automated detectors for this purpose (Stimpert et al. 2011; Rekdahl et al. 2017; Fournet et al. 2018d). Indeed, the stability, stereotypy and widespread use of whups and growls among regions, decades and ecological contexts suggests that they could at least provide reliable indicators of humpback presence in an area, if not also some indication of the number of individuals, with further study on call production. While this, and other studies (Dunlop et al. 2007; Fournet et al. 2015, 2018d; Rekdahl et al. 2017), provide evidence that these call types are used by most, if not all, humpback whale groups, identification in additional

regions, particularly breeding grounds and migration routes, as well as additional recordings from both Newfoundland and Hawaii to confirm their presence, would be valuable.

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Tables and Figures

Table 1. Description of recording equipment, settings and contexts for each study area.

Location	Context	Recording Year	Recording Equipment and Collection Method	Sampling rate
West Maui, Hawaii (~20.89 N 156.59 W) (Silber 1986a, 1986b)	Breeding ground	1981, 1982	Nakamichi 550 portable cassette recorder with Gould CH-17U, Aquadyne AQ-17 or sonobuoy hydrophones Barcus Berry preamplifier 16 bit Dip hydrophone off of boat – 10-16 m depth, recordings made when whales were within 200 m of boat	96 kHz
Northeast Newfoundland (49.20N 54.20W)	Foraging ground	2015	<i>Wildlife Acoustics</i> SM2M marine recorder with standard hydrophone 12 dB gain, 3 Hz high pass filter, 16 bit Bottom mounted hydrophone - ~30m depth, passive, continuous recording	24 kHz

Table 2. Descriptions of the variables that were used in the CART, RF and pairwise call comparisons. Variables marked with a * were measured using the *Acoustat* noise-resistance feature set (the same descriptions as for the program *Osprey* from Mellinger and Bradbury (2007)). The noise-resistant feature set places a smaller feature box within the manually created selection box (made in *Raven*). Measurements of the call are made based on the contents of the feature box. Start frequency, end frequency and bout were determined manually in *Raven*. All frequency variables (i.e. with unit Hz) were log-transformed. Units are provided where applicable. Abbreviations are given for each variable that correspond to the other tables and figures.

Variable name	Unit	Abbreviation	Description
Lower frequency*	Hz	Lower	Lowest frequency of the call
Upper frequency*	Hz	Upper	Highest frequency of the call
Frequency range*	Hz	Range	Ratio of lower to upper frequency
Duration*	s	Dur	Length of the feature box
Bandwidth*	Hz	Band	Height of the feature box
Median frequency*	Hz	Median	The frequency at which 50% of the energy is to either side
Frequency of peak overall intensity*	Hz	Peak	The frequency with the greatest energy/amplitude in the feature box
Amplitude modulation rate*		Ampmod	Dominant rate of amplitude modulation
Frequency modulation rate*		Freqmod	Dominant rate of frequency modulation
Overall entropy*		Entropy	Measure of how evenly energy is distributed across the frequencies
Upsweep fraction*	%	Upsweep	Fraction of time that the median frequency in one time block is greater than the preceding time block
Bout		Bout	Number of the same call type in sequence in a discrete period of time
Start frequency	Hz	Start	Frequency at the beginning of the call measured on the fundamental frequency or lowest harmonic
End frequency	Hz	End	Frequency at the end of the call measured on the fundamental frequency or lowest harmonic
Frequency trend	Hz	Trend	Ratio of start to end frequency

Table 3. CART confusion matrix with sample size for each call type with separate regions, showing the number of cases correctly assigned to each observer classified call type in bold along the diagonal. Percent classification success in the CART is given for each call type in each region with the classification success for the RF provided for comparison. Total n for each call type (number in both regions combined) is also indicated and the CART and RF classification success rates per call type (not separated by region) are presented in the last column. The CART had an overall classification success of 84% and the RF 80%. Blank cells represent zeroes in the matrix.

Call type	Total n	n	Droplet HI	Droplet NL	Growl HI	Growl NL	Swop HI	Swop NL	Teepee HI	Teepee NL	Whup HI	Whup NL	CART/RF classification success per region (%)	CART/RF classification success regions combined (%)
Droplet HI	55	16	6				2	8					38/44	60/58
Droplet NL		39	1	23				15					59/56	
Growl HI	91	14			14								100/71	78/67
Growl NL		77				66		1				10	86/64	
Swop HI	339	61	5		1		34	16	5				56/52	94/96
Swop NL		278	4	3	2	1	7	252	1	3		5	91/92	
Teepee HI	64	30						11	17	2			57/53	65/47
Teepee NL		34				4		20		6		4	18/35	
Whup HI	118	15			7			6			0	2	0/40	79/76
Whup NL		103			2	20		5				76	74/77	

Table 4. Mean (SE) for each call type from both regions (Newfoundland – NL, Hawaii – HI) with sample sizes. Variable abbreviations correspond to those in Table 2.

Call Type Region	n	Bout	Lower	Upper	Peak	Band	Median	Range	Trend	Start	End	Dur	Entropy	Ampmod	Freqmod	Upsweep
Growl NL	77	1.19 (0.05)	29.09 (1.38)	254.83 (22.30)	70.08 (2.81)	225.74 (22.50)	74.88 (3.29)	0.15 (0.01)	0.84 (0.02)	52.39 (1.80)	62.83 (1.96)	0.64 (0.02)	10.88 (0.60)	1.78 (0.06)	1.87 (0.07)	44.45 (2.92)
	14	1.14 (0.10)	107.56 (17.56)	2135.11 (357.72)	793.95 (282.96)	2027.55 (343.65)	1000.92 (250.74)	0.06 (0.01)	0.90 (0.03)	196.97 (15.40)	220.29 (16.50)	1.05 (0.11)	119.00 (28.13)	1.28 (0.19)	1.43 (0.19)	38.09 (4.85)
Whup NL	103	1.21 (0.05)	31.59 (1.47)	293.21 (8.79)	87.26 (3.93)	261.62 (8.78)	99.16 (3.87)	0.12 (0.01)	0.78 (0.02)	56.74 (2.24)	72.75 (2.10)	0.64 (0.04)	18.34 (0.75)	1.78 (0.07)	1.80 (0.08)	60.74 (2.76)
	15	1.53 (0.19)	58.50 (7.23)	1372.56 (291.08)	320.90 (99.73)	1314.06 (288.88)	410.34 (94.10)	0.08 (0.02)	0.69 (0.07)	103.07 (7.72)	175.76 (29.36)	0.53 (0.05)	85.39 (19.81)	1.82 (0.19)	1.97 (0.21)	58.17 (8.71)
Droplet NL	39	1.56 (0.18)	279.11 (16.71)	727.35 (58.62)	371.24 (20.28)	448.24 (58.31)	379.26 (19.74)	0.44 (0.03)	0.58 (0.04)	292.61 (16.98)	555.20 (31.06)	0.24 (0.01)	37.33 (3.18)	0.08 (0.08)	0.08 (0.08)	87.41 (5.02)
	16	1.81 (0.40)	210.94 (24.94)	674.93 (128.91)	278.50 (24.58)	463.99 (126.37)	297.09 (22.24)	0.39 (0.05)	0.58 (0.04)	224.92 (22.88)	381.48 (22.05)	0.29 (0.02)	27.23 (5.03)	0.95 (0.32)	0.95 (0.32)	96.27 (3.73)
Swop NL	278	2.21 (0.17)	121.86 (3.36)	746.05 (23.21)	233.65 (6.93)	624.19 (23.19)	258.08 (5.66)	0.20 (0.01)	0.68 (0.01)	161.99 (4.05)	266.13 (7.70)	0.26 (0.00)	40.35 (1.22)	0.39 (0.06)	0.39 (0.06)	87.75 (1.54)
	61	5.05 (0.87)	180.03 (7.31)	1547.24 (134.12)	355.64 (33.23)	1367.20 (133.65)	408.86 (39.80)	0.17 (0.01)	0.72 (0.02)	216.02 (7.72)	323.20 (16.59)	0.26 (0.01)	58.65 (7.27)	0.33 (0.12)	0.33 (0.12)	51.83 (5.78)
Teepee NL	34	3.00 (0.50)	74.10 (5.35)	470.73 (35.67)	145.71 (14.24)	396.63 (38.31)	166.64 (12.16)	0.20 (0.02)	0.94 (0.03)	120.41 (6.97)	132.87 (9.48)	0.25 (0.01)	19.86 (1.82)	0.26 (0.14)	0.26 (0.14)	71.89 (7.14)
	30	6.73 (0.87)	142.29 (7.99)	2024.19 (275.00)	505.76 (103.50)	1899.90 (271.54)	849.16 (126.20)	0.17 (0.03)	0.60 (0.04)	162.48 (8.41)	285.91 (12.38)	0.30 (0.01)	87.45 (14.32)	1.51 (0.26)	1.51 (0.26)	77.41 (6.43)

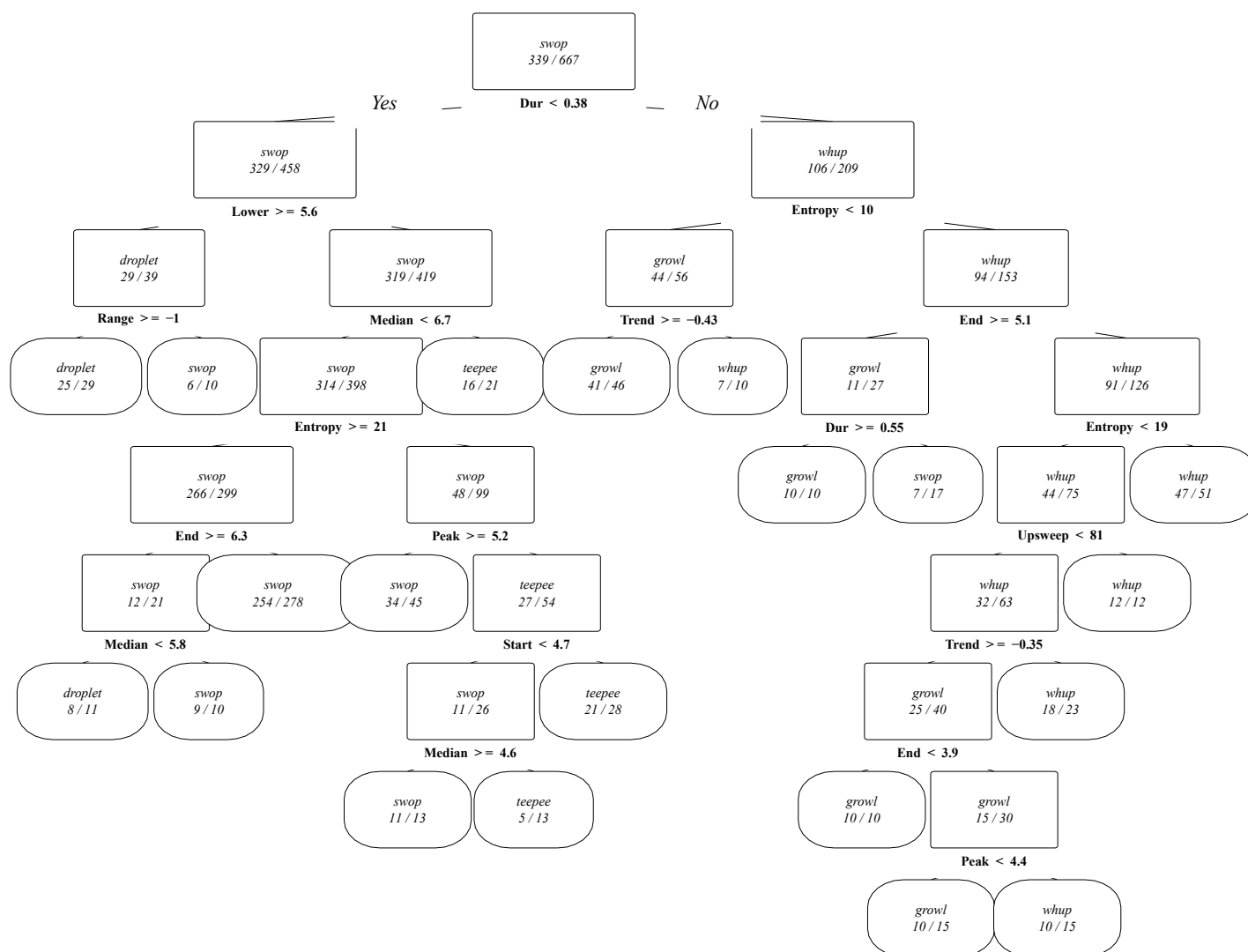


Figure 1. Call type CART with all call types from both regions combined without region included as a variable or label, showing the main splitting variable at each node (bold) and the value at which the split was made. The call type name in each box (node) represents the call type making up the majority of the cases in that node and the number of that call type out of the total cases in the node is given below the name. Terminal nodes are indicated by rounded node boxes. Variable abbreviations correspond to those in Table 2.

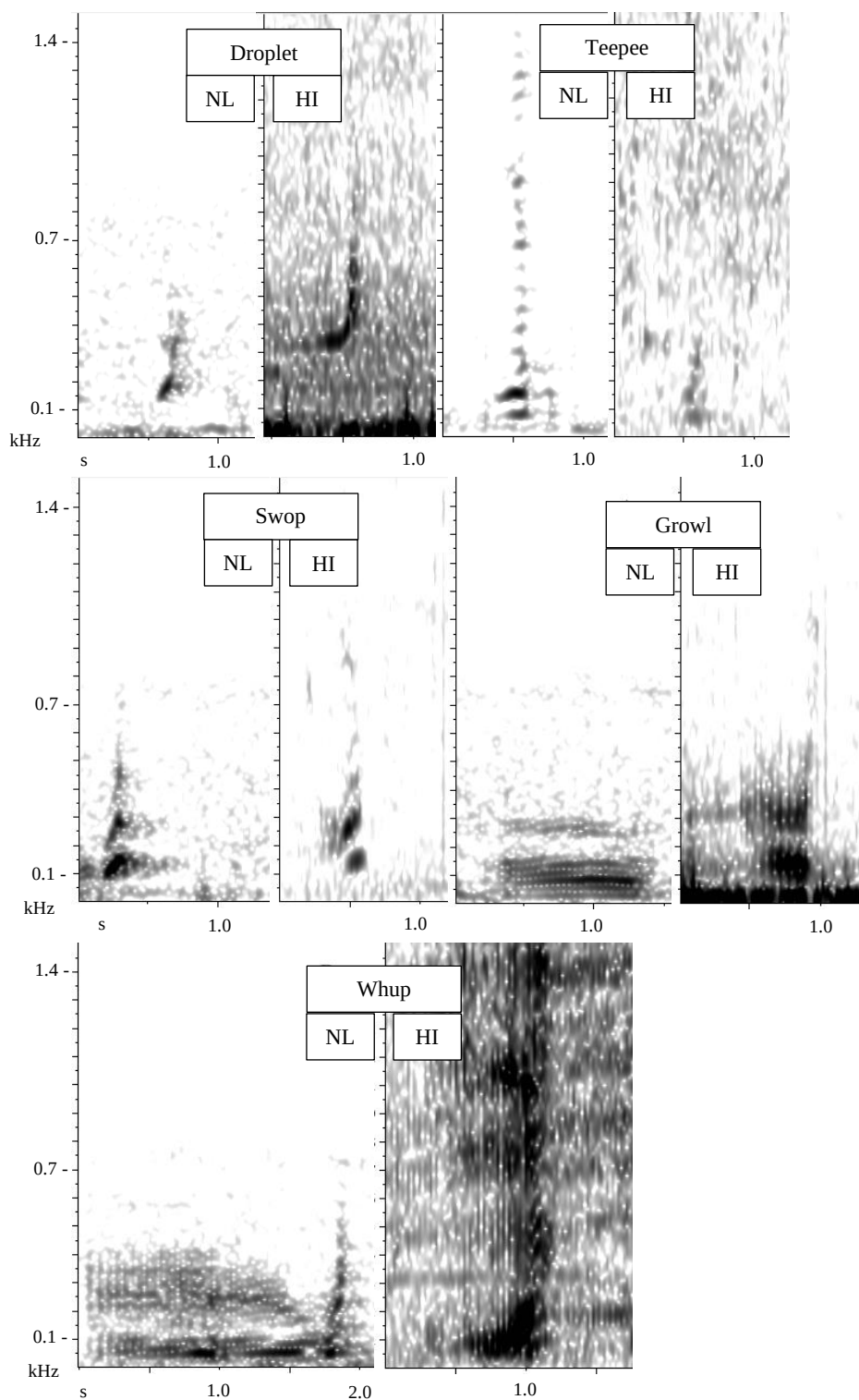


Figure 2. Spectrograms examples of each of the five call types from *Raven Pro* (Hann window; 8192 (NL), 32768 (HI) Discrete Fourier Transform; 2.93 Hz resolution; and 50% overlap) from each region, NL = Newfoundland during 2015, HI = Hawaii during 1981-1982.

General Conclusion

An understanding of the types of vocalizations produced by a population or species can be extremely valuable in answering questions about many aspects of their ecology and for investigating conservation and management strategies, particularly for vocal marine species that are difficult to study using other methods (e.g. visually). In this thesis, we found that humpback whales on their Newfoundland foraging ground produce an array of calls that classified well both manually and statistically into four broad classes (i.e., low frequency, high frequency, pulsed, compound) in the years 2015 and 2016. Some of the calls were very stereotyped, fitting well into discrete types, while others were more graded and may fit better along a continuum. We also propose, based on qualitative classification, that five call types (i.e., swops, droplets, teepees, growls, whups) that have been previously described in the literature (Fournet et al. 2015, 2018b, 2018a) were present on both the Newfoundland foraging ground during 2015 and 2016 and on the Hawaiian breeding ground during 1981-1982. The common call types between the two Newfoundland years and the five in Newfoundland and Hawaii did exhibit differences in characteristics and the possible reasons for these differences warrant further investigation. In particular, identifying whether differences are related primarily to motivational state seems like an important avenue of future research (Morton 1977; Dunlop 2017). Despite differences in characteristics, the possible presence of these five call types in both Newfoundland and Hawaii adds to evidence that these call types are likely innate and fixed in the humpback repertoire (Fournet et al. 2018b, 2018a). To further investigate whether some humpback calls are innate, recordings of humpback calves would be useful. Zoidis et al. (2008) was the first to confirm that calves produce vocalizations and further study of their calls and comparisons to adult calls could provide evidence for the innate hypothesis. Likely being innate and fixed, suggests that these

calls could be used for global passive acoustic monitoring (PAM) of humpback whales to better inform conservation and management decisions (Dunlop et al. 2008; Stimpert et al. 2011; Wild and Gabriele 2014; Rekdahl et al. 2017; Fournet et al. 2018b).

These five call types within the humpback whale repertoire appear to be present in four to six regions in three ocean basins (Dunlop et al. 2007; Rekdahl et al. 2013, 2017; Fournet et al. 2015, 2018a, 2018b; this study). In some of these regions, the contexts in which the calls are used have been examined and suggest that they serve a social function, such as maintaining contact between a mother and calf or members of a group (Dunlop et al. 2008; Fournet 2014; Wild and Gabriele 2014; Fournet et al. 2018b), providing further support that these call types are a good starting point for PAM. In particular, whups and growls are relatively stereotyped, widely used and are likely used for longer-distance communication between whales (Konishi 1970; Morton 1975; Wiley and Richards 1978; Brown 1982), making them ideal candidates for PAM. Similarly, PAM of right whales using the stereotyped “up call” has been found to be a tool to try to mitigate deaths from ship strikes (Van Parijs et al. 2009) and monitoring of humpback song production shows promise as an indicator of migration routes (Clapham and Mattila 1990). PAM for whups and growls could be used for real-time monitoring throughout the range of humpback whales, similar to right whales (Van Parijs et al. 2009). Additionally, whups and growls may be used to examine movement patterns as well as habitat characteristics and preferences for certain habitat features around the globe, for all demographics, to inform conservation and management. While repertoire studies, thus far, would suggest that at least some calls of humpback whales could be universal, to most effectively use PAM to monitor and manage humpback whales around the globe, recordings from more regions, particularly breeding grounds and migration

routes, but also feeding grounds from more allopatric regions, will be necessary (Van Parijs et al. 2009).

To classify the calls, we used primarily manual classification with two statistical methods for validation. Manual classification alone can be subjective, but, statistical methods aid in reducing that subjectivity. The statistical methods used in this study, classification and regression tree and random forest, are becoming standard in studies of humpback whale repertoires, as well as other species (e.g., Oswald et al. 2003; Garland et al. 2015a; Thiebault et al. 2019), as they are robust to the common features of typical acoustic datasets, such as non-normality and variable sample sizes (Breiman et al. 1984; Breiman 2001; Armitage and Ober 2010). Even with standardization and the use of robust methods, however, classification of calls within one study, and comparison among studies, is difficult. This difficulty arises from many, if not all, humpback whale calls falling along a continuum, as noted in many studies (Chabot 1988; Dunlop et al. 2007; Stimpert et al. 2011; Fournet et al. 2015; Dunlop 2017). In this thesis, the classification success of the same manually assigned call type differed between Chapter 1 and 2, suggesting that there is still work to be done on making classification consistent and meaningful. Determining whether it is appropriate or not to classify calls into discrete types/classes could be informed by collecting more information on the contexts in which calls are used (Smith et al. 1982; Silber 1986; Tyack 1997; Dunlop et al. 2007; Rekdahl et al. 2013; Fournet et al. 2015), and this will be an important avenue of future research. Regardless, determining the types of calls produced and whether they are discrete or graded in this study and others (Dunlop et al. 2007; Fournet et al. 2015; Rekdahl et al. 2017) has helped to gain a better understanding of whether the humpback repertoire is innate and fixed and gives clues as to the calls' functions.

In conclusion, this study provides a quantitative description of the repertoire of humpback whales on their foraging grounds in coastal Newfoundland, a previously understudied area, and adds to the growing knowledge of the humpback whale repertoire globally. More years of recordings would be helpful to further describe the repertoire. For Newfoundland, this study serves as a starting point to begin investigating the function of these calls, such as whether any call types are related to foraging strategies generally, or in relation to capelin (*Mallotus villosus*) specifically. Future studies using a combination of behavioural observations and portable hydrophones, as well as animal-borne tags, could address these questions directly, similar to previous studies (e.g., Stimpert et al. 2007; Friedlaender et al. 2009; Parks et al. 2014; Dunlop 2016, 2017).

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