HUMPBACK WHALE SINGING BEHAVIOUR IN THE WESTERN NORTH ATLANTIC: FROM METHODS FOR ANALYSING PASSIVE ACOUSTIC MONITORING DATA TO UNDERSTANDING HUMPBACK WHALE SONG ONTOGENY

by

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I dedicate this to my husband Logan, who provided unending patience and support and never tired of a home filled with whale songs.

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ABSTRACT

Marine passive acoustic monitoring (PAM) is a valuable tool to assess the distribution, habitat use, and behaviour of marine mammals including the acoustically prolific humpback whale. With increasing amounts of data collected, the challenge of effectively mining PAM data for signals of interest and interpreting those signals is faced by researchers globally. I completed a literature review on the data analysis methods employed in PAM baleen whale studies (2000-2019) before exploring the dynamic and complex humpback repertoire, which is particularly challenging for PAM. The review revealed a spectrum of methodologies ranging from full manual data analysis by a human to fully automated techniques. I propose recommendations for future work to encourage the application of best practices that will result in more robust and comparable research.

Humpback whale vocalizations have been studied for years, but little is known of when, where, and how seasonal male singing begins in the fall and ends in the spring. Acoustic recordings of humpback whale vocalizations from Canada, the U.S.A, and the Caribbean in 2015-2017 were manually analysed. Humpback whales were present from Labrador to Massachusetts Bay during the fall and early winter. Song development occurred gradually over weeks with vocalizations transitioning from non-song calls to song fragments to full songs. Initially sporadic in occurrence, singing began in September, but was not regularly heard until late October, when full songs were common. I found evidence that the onset of regular singing occurs earlier at lower latitudes, longer photoperiods, and higher temperatures. The theme order in early season full songs was variable, until December when theme order became more consistent with what was observed the previous spring. Dominican Republic breeding ground songs recorded in January and March were crystalized in terms of theme order. Song duration increased gradually through the breeding season. Spring song cessation was only captured at a single site/season in Canada and compared to song development, it was abrupt with few song fragments. These late season songs had consistent theme orders. I propose that the patterns observed here may in part be driven by physiological processes like those of songbirds.

LIST OF ABBREVIATIONS USED

A Automated

ACC Accuracy

AMAR Autonomous Multichannel Acoustic Recorder

Ann. Annotations

AUC Area Under the Curve

CHLA Chlorophyll A

d Day

dB Decibel

DFO Department of Fisheries and Oceans

EDM Environmental Data Management

ESRF Environmental Sciences Research Fund

F F-value

FM Full Manual

FN False Negative

FNMOC Fleet Numerical Meteorology and Oceanography Center

FNR False Negative Rate

FP False Positive

FPR False Positive Rate

hr Hour

Hz Hertz

kHz Kilohertz

km Kilometer

kPa Kilopascal

m Meter

M&A Manual and Automated

MARU Marine Acoustic Recording Unit

MCC Matthew’s Correlation Coefficient

min Minute

N Sample Size

NA Not Applicable

NASA National Aeronautics and Space Administration

NEFSC Northeast Fisheries Science Center

NOAA National Oceanic and Atmospheric Administration

NS Non-song

p P-value

P Precision

PAM Passive Acoustic Monitoring

Pa Pascal

PM Partial Manual

r Correlation Coefficient

R Recall

ROC Receiver Operating Curve

s Seconds

S Song

SD Standard Deviation

SNR Signal-to-noise Ratio

SSP Sea Surface Pressure

SST Sea Surface Temperature

Stn Station

TN True Negative

TP True Positive

TPR True Positive Rate

Unc. Unclear

Voc. Vocalization

w Week

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CHAPTER 1 INTRODUCTION

This introduction provides an overview of the contexts of my thesis. My work has relevance in two distinct and significant areas of research: the passive acoustic monitoring (PAM) of marine animal vocalizations to map distributions and densities of marine organisms through space and time; and the nature and function of one of the most elaborate and extraordinary vocalizations in the animal kingdom, the song of the humpback whale (*Megaptera novaeangliae*).

Effective monitoring methods over large spatial and temporal scales is required to understand trends in occurrence, distribution, habitat use, density, and behaviour of many species. Such information is key in unravelling the behavioural ecology of wildlife and effectively implementing appropriate management measures in the face of ongoing or anticipated anthropogenic threats. PAM to survey acoustically active species was first applied to terrestrial animals, including bats (Gould 1975), frogs (Schmidt 1968), insects (Simmons et al. 2001), and birds (Thorpe 1961), and is now widely applied in the marine environment to study crustaceans (Au and Banks 1998), fish (Myrberg 1980), and marine mammals (Zimmer 2011). For cetaceans that spend much of their lives submerged and depend on acoustics for foraging, navigation, and communication, PAM provides an excellent monitoring method to replace or supplement traditional visual techniques (Zimmer 2011). Indeed, PAM is generally less negatively impacted by season and adverse weather conditions than visual surveys and can provide greater coverage (spatial and temporal) at reduced cost and effort (Wimmer et al. 2010). However, PAM comes with its own inherent set of challenges and limitations which have only been amplified as technology has allowed for the collection of immense amounts of acoustic data (where such large data sets are considered big data). Amongst other requirements, to effectively implement PAM, researchers must be able to both

1. utilize methods that allow large quantities of PAM data to be analysed in a reliable and cost-effective manner, and
2. have sufficient knowledge of the vocal behaviour of the animals being recorded.

I explore the various methodologies applied to big data analysis before focusing the remainder of my thesis on describing the vocal behaviour of a species with a particularly dynamic acoustic repertoire, the humpback whale. The diversity of this repertoire over a wide range of spatial and temporal scales, provides particular challenges for PAM.

1.1 METHODS FOR BIG PAM DATA ANALYSIS

PAM has long been used to study cetaceans and an ever-increasing challenge is how to analyze large PAM data sets effectively and efficiently. With advancing technology, increasing amounts of marine PAM data are now collected over large scales of space and time, resulting in challenges commonly encountered across other big data sectors (e.g., social media, law, medicine, marketing). When considering marine PAM analysis methods for big data sets, it is important to first reflect on what techniques are commonly applied in other big data fields. One universal big data challenge is how to effectively (i.e., robustly, and quickly) analyze such vast quantities of digital information. Strategies typically encompass one or both of a) human manual analysis or b) automated analysis. Manual analysis is generally considered the preferred method. In PAM, acoustic data is manually reviewed via visual and aural examination of spectrograms of acoustic files. Analyst findings are considered ‘truth’ data as humans are less likely than automated techniques to misclassify signals or miss faint signals, in part because analysts can consider context (e.g., location, season, time of day, anthropogenic activities, presence of other species) when identifying acoustic signals. However, human analysts are subjective, can be inconsistent, and this method is considered unrealistic to apply to the entirety of big data sets (Lewis et al. 2013, Knight et al. 2017, Leroy et al. 2018b). In contrast, automated techniques can be efficiently applied to large amounts of data quickly (compared to human analysis) and have been used in the medical field (Sörensen et al. 2015) and when analyzing data from social media (Nguyen and Jung 2015, Dhaoui et al. 2017). In PAM, a plethora of algorithms have been created to automatically detect and classify the acoustic signals of whales and dolphins (Wimmer et al. 2010, Bittle and Duncan 2013), but automation is imperfect as detectors lack sensitivity to context and can suffer from the effects of masking (e.g., wind induced wave noise can mask signals), conflicting sound sources (e.g., from other species), and signal distortion during propagation (Lewis et al. 2013, Sivarajah et al. 2017).

A combination of manual and automated techniques to balance the efficiency of automation with the reliability of manual analysis is commonly implemented across sectors and allows for the evaluation of automatic detector performance. For example, in the medical field, manual results have been compared to automated results during analysis of carotid wall quantification (Saba et al. 2012) and cell counts (Johnson et al. 1996, Louis and Siegel 2011, Cadena-Herrera et al. 2015). In the software development field, coders restructuring large amounts of computer code have compared manual and automated methods (Negara et al. 2013). In the legal field, efforts to increase the efficiency of identifying relevant documents uses a combination of manual and automated techniques (Roitblat et al. 2010). Blended manual and automated methods may be ideal for social media analysis such as Twitter (Lewis et al. 2013) and have been used to analyze aerial data for disaster relief (Ofli et al. 2016). In both terrestrial and marine PAM, similar human-in-the-loop automation has been applied to supplement automation or evaluate automated detector performance (Wimmer et al. 2010, Kalan et al. 2015, Leroy et al. 2018b).

In summary, three overarching data analysis techniques are common across big data sectors (manual, automated, and a combination of the two) with a range of automated detector performance metrics, but which methods have been implemented for large marine PAM data sets in the past and, more importantly, what methods should be applied in the future? These questions are explored in Ch 2 where a literature review of baleen whale PAM data analysis methods is described.

1.2 UNDERSTANDING VOCAL REPERTOIRES FOR CETACEAN PAM

For any analysis method to be successful in PAM, an understanding of the vocalizations of the animals acoustically present in the data is required. A continuum of complexity and diversity occurs in cetacean vocal behaviour which inevitably impacts PAM analysis. For example, vocal repertoires can range from the relatively simple 1-3 vocalizations of sei whales (*Balaenoptera borealis*) (Tremblay et al. 2019), to the diverse 12 whistle classes of beluga whales (*Delphinapterus leucas*) (Belikov and Bel'kovich 2006). Some species produce acoustic signals unique and highly consistent in time-frequency characteristics, such as the 20 Hz song notes of the fin whale (*Balaenoptera physalus*), while others overlap closely with allospecifics, such as the whistles of many dolphin species (Ding et al. 1995). Simple, species-specific vocalizations are ideal for PAM analysis, while diverse vocalizations or those that are similar across species are more challenging (Wimmer et al. 2013). Further complications arise in species that alter their vocal behaviour across time, space, age, or sex, or, even more so, in species where the vocal behaviour is poorly understood. These challenges for PAM analysis are all presented by the vocal repertoire of the humpback whale.

1.3 HUMPBACK WHALES AND THEIR VOCALIZATIONS

A medium sized (15 m) mysticete whale found throughout much of the world's oceans, the humpback whale is famous for its uniquely large pectoral fins, surface-active behaviour (Kavanagh et al. 2017), complex foraging strategies (Hanser et al. 2009), large migrations (Dawbin 1966), and dynamic vocal repertoire (Payne and McVay 1971, Dunlop et al. 2008). Apart from the Arabian Sea whales, all humpback whale populations migrate annually from summer high-latitude foraging grounds to winter low-latitude breeding grounds to mate and give birth, although there is some evidence that at least some individuals delay or forego migration from feeding grounds (Brown et al. 1995, Pomilla et al. 2014, Magnúsdóttir and Lim 2019). During the winter breeding season, several behavioural changes have been observed that are thought to be related to mating, including an increase in male surface-active groups and the production of songs.

First described in the 1970's by Payne and McVay (1971), the humpback whale song has fascinated the public and scientists alike for decades. Produced only by males (Winn and

Winn 1978, Herman et al. 2013), songs are hierarchically structured, built of discrete sounds that range in frequency from 30 Hz to 7000 Hz (Cerchio et al. 2001). Notes in a pattern form phrases that, when repeated, create a theme. A series of unique themes creates a song that can be up to 30 min in duration. Songs are cyclical, repeating for hours on end in song bouts (Payne and McVay 1971, Payne et al. 1983, Au et al. 2006, Parsons et al. 2008, Cholewiak et al. 2013). While song is more predominant on tropical breeding grounds, it also occurs during migration and pre- and post- migration when the whales are still on their feeding grounds (Mattila et al. 1987, McSweeney et al. 1989, Magnúsdóttir et al. 2014, Kowarski et al. 2018).

All animals within a region sing nearly the same song, with some variability within and between individuals (Payne and Payne 1985, Mercado 2018, Schneider and Mercado III 2019). The song of a region evolves through time via social learning and songs can spread across regions (Garland et al. 2011). This cultural evolution of humpback whale song has been documented worldwide, including in Bermuda between 1957 and 1975 (Payne and Payne 1985), in Tonga through the 1990's (Helweg et al. 2005), in Hawaii and Mexico in 1991 (Cerchio et al. 2001), in the South Pacific from 1998-2008 (Garland et al. 2011), in eastern Australia (Allen et al. 2018), and in Iceland from 2008-2011 (Magnúsdóttir et al. 2015, Magnúsdóttir and Lim 2019). Song evolution can be gradual, with themes added, lost, or replaced through time, or songs can be entirely replaced within one to two seasons via a process of cultural diffusion where one region adopts the entire song of a neighbouring region. This has been termed a song revolution and occurs regularly in the South Pacific (Noad et al. 2000, Garland et al. 2017, Allen et al. 2018).

For decades, scientists have been perplexed by the song of the humpback whale. What is the purpose of complex male songs and what selective forces have produced both conformity within regions and plasticity through time, as well as the complexity itself? Given that it is produced only by males, primarily during the breeding season, it has reasonably been linked to mating strategies, but the exact process remains under debate. Singing in humpbacks whales may function to attract females (Winn and Winn 1978, Tyack 1981), stimulate female receptivity (Smith et al. 2008), or mediate male-male interactions (Darling and Bérubé 2001, Darling et al. 2006, Cholewiak et al. 2018), and many have proposed that it functions as a lekking system (e.g., Herman et al. 1980, Clapham 1996). Herman (2017) argues that song may have multiple functions and proposes that song initially evolved as an aggregating call.

In addition to songs, humpback whales produce non-song calls. These are produced by both sexes and all age groups throughout the year (Dunlop et al. 2008, Stimpert et al. 2011, Rekdahl et al. 2013). Many distinct types of non-song vocalizations have been described, ranging in frequency from 30 Hz to 2400 Hz (Dunlop et al. 2007). These vocalizations have been linked to social encounters, foraging techniques, and have been associated with mother-calf pairs (Silber 1986, Dunlop et al. 2007, Stimpert et al. 2007, Zoidis et al. 2008). Rekdahl et al. (2013) found that some non-song calls off eastern Australia were stable through time, while other calls were variable and could be incorporated into songs. In Alaska, some non-song calls were stable across decades (Fournet et al. 2018a).

One aspect of the humpback whale vocal repertoire that is insufficiently described is the period when singing begins in the fall and ends in the spring on high latitudes. While these two seasons have been reported in high latitude song data sets (Baker et al. 1985, Mattila et al. 1987, McSweeney et al. 1989, Clapham and Mattila 1990, Cato 1991, Helweg et al. 1998, Norris et al. 1999, Charif et al. 2001, Clark and Clapham 2004, Clark and Gagnon 2004, Dunlop et al. 2007, Noad and Cato 2007, Vu et al. 2012, Garland et al. 2013a, Stanistreet et al. 2013, Magnúsdóttir et al. 2014, Magnúsdóttir et al. 2015), there is little information reported on the specifics of how seasonal song onset and cessation occurs. Some authors have commented that early- and late- season songs lack the complexity of those heard later in the peak of the season (e.g., Stimpert et al. 2012, Rekdahl et al. 2013, Kowarski et al. 2017). For example, McSweeney et al. (1989) used the term "partial songs" to describe three fall recordings from Alaska and Mattila et al. (1987) described "song fragments" off Maine in the spring, but no definition of these behaviours was provided. Without understanding the timing and manner of humpback whale song onset, our ability to infer the mechanisms driving singing behaviour is limited. One species group where song has been studied in some depth is the oscine birds where, in comparison to humpback whales, a great deal of effort has been put into understanding song development. This avian research has provided a more comprehensive understanding of the social, environmental, and physiological factors that influence bird song, an important display for mating in many species (e.g., Smith et al. 1997, Meitzen et al. 2007).

1.4 WESTERN ATLANTIC HUMPBACK WHALES

Western North Atlantic humpback whales are believed to be a distinct population from those inhabiting the eastern Atlantic (Stevick et al. 2006). They migrate between high latitude feeding grounds and low latitude Caribbean breeding grounds, where they show preference for the Dominican Republic over the West Indies (Stevick et al. 2018). Humpback whales are known to sing in Iceland (Magnúsdóttir and Lim 2019), Canada (Kowarski et al. 2018), and the U.S.A. (Vu et al. 2012, Stanistreet et al. 2013) prior to migration to their Caribbean breeding grounds (Clapham and Mattila 1990, Palsbøll et al. 1997, Smith et al. 1999). However, the singing behaviour of this population is largely undescribed (Payne and Payne 1985, Magnúsdóttir and Lim 2019), particularly in the U.S.A and Canada, compared to the more well-studied humpback whales of areas like Hawaii, Alaska, and Australia.

1.5 THESIS OBJECTIVES

My thesis aims to explore big data analysis methods for baleen whale PAM (Ch2), before providing a description of the timing and location of humpback whale song onset and cessation and describing the manner in which seasonal song development occurs. I utilize long-term PAM data collected from Labrador, Canada to Massachusetts, U.S.A., to the Dominican Republic to understand song cessation in the spring, song development in the fall (Ch3, Ch4), and how songs recorded in high latitudes compare to those heard on the breeding grounds (Ch5). Throughout my thesis, findings are placed in the context of the breadth of available avian literature in an effort to understand observed trends and their implications about the drivers of humpback whale song behaviour. By exploring what is arguably the most diverse and dynamic periods of the humpback whale acoustic repertoire, and therefore a great challenge for PAM analysis, this thesis aims to provide insight that can be more broadly applied, not only to the field of humpback whale behavioural ecology, but also to the field of marine PAM.

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CHAPTER 2 A REVIEW OF BIG DATA ANALYSIS METHODS FOR BALEEN WHALE PASSIVE ACOUSTIC MONITORING

2.1 PUBLICATION STATUS

This chapter was published in Marine Mammal Science in November 2020 (Kowarski and Moors-Murphy 2020).

2.2 ABSTRACT

Many organizations collect large passive acoustic monitoring (PAM) data sets that need to be efficiently and reliably analyzed. To determine appropriate methods for effective analysis of big PAM data sets, I undertook a literature review of baleen whale PAM analysis methods. Methodologies from 166 studies (published between 2000-2019) were summarized, and a detailed review was performed on the 94 studies that recorded more than 1,000 hr of acoustic data (‘big data’). Analysis techniques for extracting baleen whale information from PAM data sets varied depending on the research observed. A spectrum of methodologies was used and ranged from manual analysis of all acoustic data by human experts to completely automated techniques with no manual validation. Based on this assessment, recommendations are provided to encourage robust research methods that are comparable across studies and sectors, achievable across research groups, and consistent with previous work. These include using automated techniques when possible to increase efficiency and repeatability, supplementing automation with manual review to calculate automated detector performance, and increasing consistency in terminology and presentation of results. This work can be used to facilitate discussion

for minimum standards and best practices to be implemented in the field of marine mammal PAM.

2.3 INTRODUCTION

Recent technological advances have resulted in the generation of vast quantities of data, mostly digital, known as ‘big data’. At a time when almost any information can be captured, stored, and shared digitally, big data has emerged in marketing, business, law, public administration, and science (Sivarajah et al. 2017). The potential benefits of big data are evident (Sivarajah et al. 2017), but the sheer volume of information creates hurdles in all aspects of big data management, including storage, integration, quality control, and visualization (Lee and Yoon 2017, Sivarajah et al. 2017). Here, I focus on the challenge of effectively analyzing big data sets (data mining) in passive acoustic monitoring (PAM).

PAM of wildlife is an increasing source of big data in the field of wildlife biology. Acoustically active species are surveyed using acoustic recorders to understand the occurrence, distribution, density, and behaviour of animals over space and time. First applied to terrestrial species including birds (Thorpe 1961, Evans and Rosenberg 2000, Slabbekoorn and Halfwerk 2009, Wimmer et al. 2013), apes (Lieberman 1968, Kalan et al. 2015), bats (Gould 1975, Johnson et al. 2002), and frogs (Schmidt 1968, Zelick et al. 1999), PAM technology is now utilized extensively in the marine realm (Stirling et al. 1983, Zimmer 2011, Mouy et al. 2018). Marine PAM allows for the collection of big data over space and time with minimal cost and effort when compared to boat- and aerial-based visual survey methods (Wimmer et al. 2010).

Marine acoustic signals of interest vary greatly from single distinct vocalizations like the North Atlantic right whale (*Eubalaena glacialis*) upcall (a contact call used by all individuals in the population throughout their range; Parks et al. 2011) to complex acoustic events such as the codas of the sperm whale (*Physeter macrocephalus*) (Weilgart and Whitehead 1997, Whitehead and Rendell 2004). Some signals are organized in a repeated manner and are considered songs such as the complex hierarchical songs of the humpback whale, *Megaptera novaeangliae* (Payne and McVay 1971) or the relatively simple songs of the fin whale, *Balaenoptera physalus* (Watkins 1981, Delarue 2008). Many baleen whale species produce songs and also produce social and/or feeding calls that are categorized as 'non-song' vocalizations.

Methods to efficiently and reliably analyze big data (in PAM and other fields) include manual (human) content analysis, automated (computational/algorithmic) content analysis, or a combination of the two. Manual techniques are typically considered the benchmark for analysis, but humans can be inconsistent, subjective, and their level of experience can impact results (Knight et al. 2017, Leroy et al. 2018b, Baumgartner et al. 2020). Manual analysis of complete data sets is also difficult or even unrealistic to apply due to the sheer quantity of big data (Lewis et al. 2013). The development of automated methods has greatly increased the efficiency of big data analysis. A range of automated detectors have been employed in PAM analysis, including matched filters, energy summation, image-processing, neural networks, wavelets, spectrogram correlation, and machine learning (Mellinger et al. 2007b, Dugan et al. 2010, Klinck et al. 2012a, Frouin-Mouy et al. 2017, Thomas et al. 2019). Some automated detectors are designed to identify discrete acoustic signals, while others detect the chorusing events of many singers by comparing the frequency band of interest to ambient to determine an index of occurrence. Automated techniques have yet to be perfected as they often lack the context-sensitivity of human analysts, rendering them insufficient for reliable information extraction without human oversight (Lewis et al. 2013, Sivarajah et al. 2017).

Lewis et al. (2013) argued that the most efficient and reliable method to analyze big data combines manual and automated methods. This common "human-in-the-loop" automation involves some manual analysis to validate or supplement automation, allowing performance of the automated method to be evaluated by comparing the outcome of the two methods. Performance metrics include accuracy, sensitivity, specificity, receiver operating curve (ROC) characteristics, precision (P), recall (R), f-measure or F-score (F), the number of positive predictions, the number of false positives, and false negatives (Sokolova and Lapalme 2009, Knight et al. 2017). The evaluation metrics utilized depend on the nature of the data and the question at hand, with multiple measures often used (Sokolova and Lapalme 2009). Emerging and experienced researchers must determine the appropriate methods to employ for effective analysis of big PAM data sets.

The present study undertakes a literature review on the reported methods of analysis in baleen whale PAM studies. Other marine animals, such as odontocetes, seals, and fish, were excluded from the review to keep the literature reviewed to a manageable size. First, I describe how the amount of PAM data varies by platform (e.g., surface or near-surface buoys, over-the-side hydrophones, bottom-mounted recorders). Then, I explore how big PAM data analysis methods vary (in terms of when manual, automated, and combined techniques are employed) depending on how many species are targeted and the research question of interest. I consider the metrics used to describe automated signal detector performance and the terminology applied to methods. This work aims to summarize past efforts for baleen whale PAM analyses and present recommendations for ways forward to standardize how results of PAM studies are reported to encourage application of robust, comparable, and reliable methodologies.

2.4 METHODS

I used Web of Science, EndNote, and Covidence to perform a systematic literature search for peer-reviewed publications on baleen whale PAM. Detailed methods on the literature search (including keywords used) and subsequent screening are provided in APPENDIX A. This literature review was based on a keyword search; therefore, some relevant studies may have been missed because they did not include keywords such as ‘acoustic’ in their title, abstract, or keywords. The initial search resulted in 1,557 studies. Through title, abstract, and full text screening, the review was ultimately reduced to 166 studies on the topic of baleen whale PAM that were published in the years 2000 - 2019, presented original research (were not review or overview articles), did not implement real-time or near real-time analysis or aim to localize animals, and were not entirely based on describing automated detectors (see APPENDIX A TABLE A-1). Real-time and localization studies were excluded to keep the review to a manageable size, as these topics have specific methodological requirements and the literature on these topics is large.

Data from the 166 studies (see APPENDIX A TABLE A-2) were collected in two stages. In stage one, the overall data analysis method, data volume (in hours recorded), and the data collection platform (e.g., bottom mounted, over-the-side, tag) were recorded for each article (see APPENDIX A TABLE A-3). The overall data analysis method was categorized as full manual (no automated detector, manually reviewed all acoustic data collected), partial manual (no automated detector, manually reviewed a subset of the acoustic data collected), automated (employed one or more automatic detectors, did not manually review any data), or manual and automated (employed some combination of automated and manual analysis). In the second stage of the literature review, questions specific to big data were investigated, where I defined 'big data' as studies with 1,000 hr or more of acoustic data. Big data articles were subjected to a methodology-based review that considered how much data were manually analyzed, how many baleen whale species were targeted, how data for manual analysis were selected, and what metrics were used to report automated detector performance (see APPENDIX A TABLE A-3). Each study's main research question was categorized as one of the following: occurrence (the spatial, temporal, and/or diel presence of vocalizations); characterization (the description of vocalization characteristics that can vary from frequency-time characteristics of discrete non-song vocalizations to characterizing changing patterns over time and space of songs); a combination of occurrence and characterization; or, other (e.g., anthropogenic impacts).

Data extracted from the literature reviewed (in stage one and two) were summarized by data volume (seven categories ranged from 0–10 to 100,000–860,000 hr), number of species targeted (studies targeting 1–2 species or studies targeting all baleen whale species possibly acoustically present in the PAM data set), and the overarching research question (as defined above) to determine commonalities and differences in data analysis methods across studies. Similarities and differences among studies were examined to determine if there are general best practices commonly used and to develop recommendations for future studies. Some variables, such as data volume and percent of data manually analyzed, were not always explicitly provided and were calculated or estimated based on available information where possible.

2.5 RESULTS

The systematic literature review resulted in 166 articles (from 110 different first authors) on the topic of PAM and baleen whales. Detailed tabular data by study can be found in APPENDIX A. With increasing data volume included in a study, I observed a shift in both the data collection platform and the data analysis method. Studies with relatively small amounts of acoustic data were associated with varied data collection platforms, including tags directly attached to animals (Videsen et al. 2017), drifting buoys (Širović et al. 2006), and even snorkelers (Zoidis et al. 2008) (Figure 2.1). In contrast, studies using big data predominantly collected data from autonomous bottom, or near-bottom, mounted systems (Soldevilla et al. 2014, e.g., Burnham and Duffus 2019, Wright et al. 2019) (Figure 2.1). With increasing data volume, the predominant data analysis method switched from full manual analysis to a combination of manual and automated analysis (Figure 2.2).

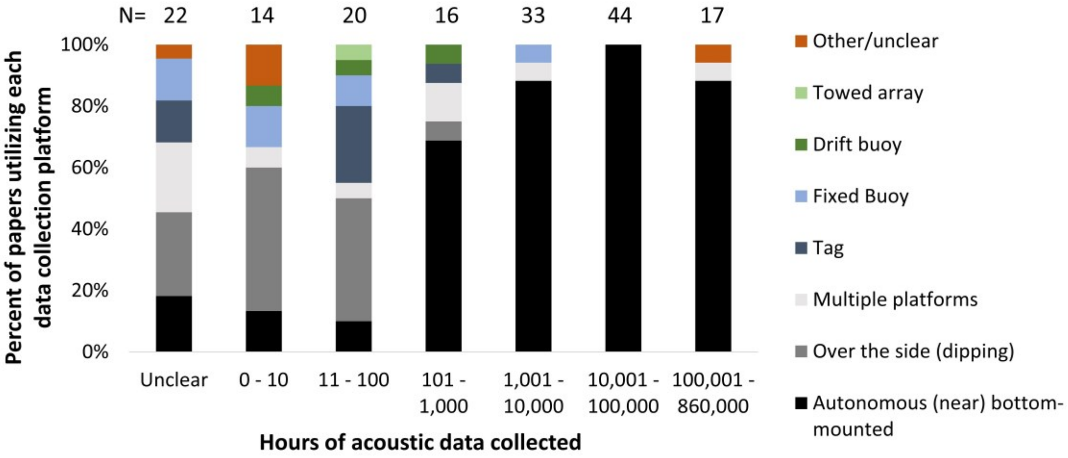

Figure 2.1. Percent of baleen whale PAM papers (N=166) utilizing each data collection platform for different data volumes (hours of acoustic data collected). Some papers had insufficient information to confidently determine data volume (unclear).

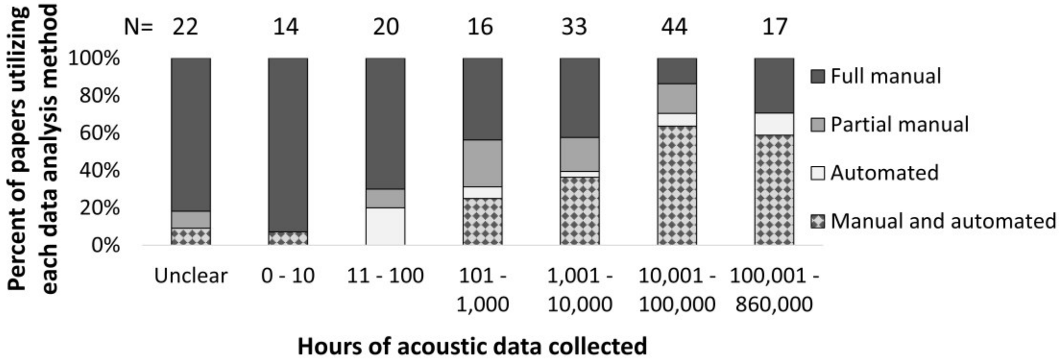

Figure 2.2. Percent of baleen whale PAM papers (N=166) utilizing each data analysis method for different data volumes (hours of acoustic data collected). Some papers had insufficient information to confidently determine data volume (unclear).

2.5.1 Big PAM data

The following results are restricted to articles with 1,000 hr or more of data (94 articles) and are considered big PAM data. Studies of big PAM data sets for baleen whales covered a range of species and research questions. The majority (71 out of 94 papers) targeted blue (*Balaenoptera musculus*), humpback, fin, or right whales with proportionally fewer studies (24%) on bowhead (*Balaena mysticetus*), Bryde's (*Balaenoptera brydei*), gray (*Eschrichtius robustus*), or minke whales (*Balaenoptera acutorostrata, Balaenoptera bonaerensis*; Figure 2.3). Most research questions focused on vocalization characterization (16 articles), occurrence (46 articles), or a combination of the two (16 articles) and the frequency of questions varied across target species (Figures 2.3 and 2.4). Studies on humpback whales were more focused on vocalization characterization than studies on blue, right, and fin whales, which more commonly described occurrence (Figure 2.3). Six studies investigated less common research questions and were considered 'other' (Figure 2.3). These studies investigated the impacts of anthropogenic activities on baleen whale acoustics (Castellote et al. 2012b, Melcon et al. 2012, Risch et al. 2012, Cerchio et al. 2014), the acoustic response of baleen whales to predation (Burnham and Duffus 2019), and baleen whale density (Marques et al. 2011). Studies with 'other' research questions were too varied to observe patterns and draw meaningful conclusions or recommendations; therefore, they will not be described further, limiting the total number of papers described below to 88 of the 94 big PAM data studies.

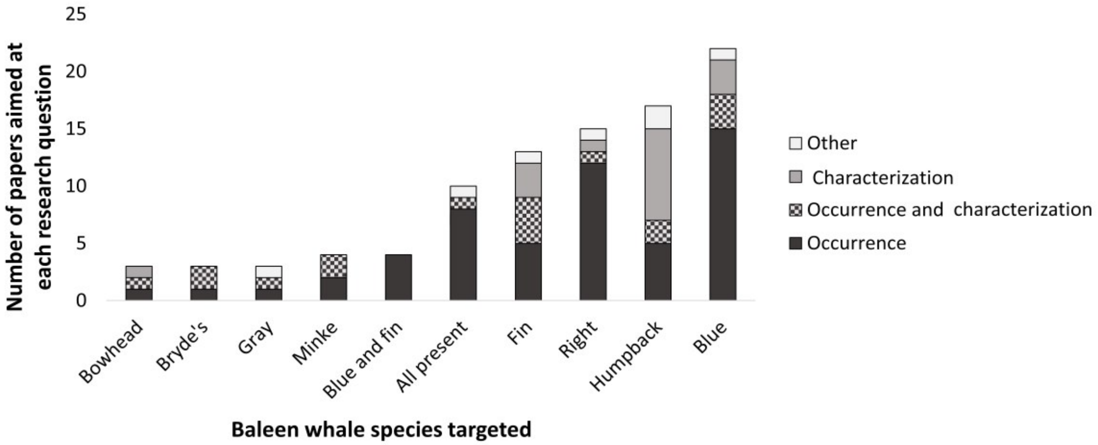

Figure 2.3. Distribution big PAM data (1000+ hr) baleen whale papers (N=94) by each research question and species targeted where 'all present' indicates that all acoustically active species in the acoustic data were targeted.

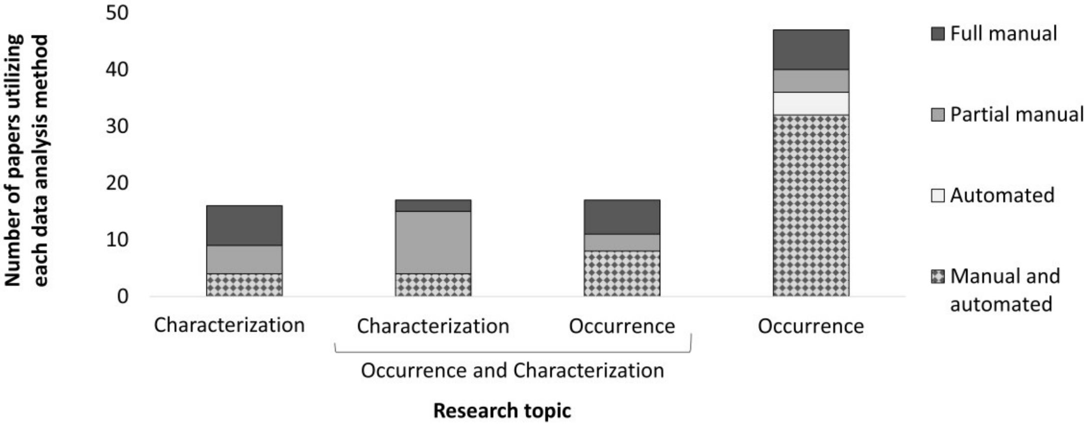

Figure 2.4. Number of big PAM data baleen whale papers that used each data analysis technique for research For Peer Review questions involving characterization, occurrence, or both (N=88). Papers investigating both occurrence and characterization were duplicated to show how each question was addressed separately within the same study.

2.5.1.1 STUDIES TARGETING 1–2 BALEEN WHALE SPECIES

Of the 88 articles that investigated characterization and/or occurrence, 75 targeted 1 species, 4 targeted 2 species (fin and blue whales), and 9 targeted all baleen whale species acoustically present in the acoustic recordings (Figure 2.3). In this section I consider studies targeting 1 or 2 species (N=79) and how data analysis methods varied across different research questions (see APPENDIX A Tables A-5 to A-11). Studies were separated based on number of species because those looking at all species will face challenges (e.g., many different vocalization types requiring analysis of a potentially broader frequency range, more automated detectors, greater breadth of human expertise) beyond those faced by studies focused on 1 or 2 species.

2.5.1.1.1 **Characterization studies**

Studies focused solely on characterization of vocalizations encompassed 19% (15/79) of the big PAM data papers reviewed that targeted 1 or 2 species (Figure 2.4). Ten of the papers focused on aspects of baleen whale song, including how songs vary in space, time, between populations, and in different behavioural contexts, while the remaining papers described characteristics of non-song vocalizations. Analysis methods included full manual analysis, partial manual analysis, and a combination of automated and manual analysis with specific analysis protocols varying across studies and the percent of data manually reviewed ranging from 3% to 100% (see APPENDIX A TABLE A-5). The most common methodology for characterizing song was the full manual analysis of all acoustic data (see APPENDIX A TABLE A-5). Most of these studies had data sets less than 2,000 hr in size (Miksis-Olds et al. 2008a, Johnson et al. 2015, Cholewiak et al. 2018, Mercado 2018, Miksis-Olds et al. 2018) though one study spanned 10 years and still seemed to have employed full manual review (Garland et al. 2015). Partial manual analysis was the most commonly employed methodology for the characterization of non-song vocalizations with protocols for selecting data varying across studies. For example, Fournet et al. (2018b) selected 60 hr of data randomly while Jacobs et al. (2019) reviewed 4 of every 24 hr (see APPENDIX A TABLE A-5).

2.5.1.1.2 **Occurrence studies**

Understanding the occurrence of a vocal species was the most common research question for big PAM data set analysis, encompassing 59% (47/79) of the papers reviewed that targeted 1 or 2 species (see APPENDIX A Tables A-6 and A-8). The temporal breadth of occurrence studies ranged from 64 days to 10 years, with the majority (35/47) ranging from 1–4 years. All four analysis methods were used to determine occurrence: full manual (7 papers), partial manual (4 papers), fully automated (4 papers), and manual and automated (32 papers; Figure 4).

Manual analysis methods to determine species occurrence varied greatly across studies both for full manual and partial manual techniques (APPENDIX A TABLE A-6). For partial manual analysis studies, both the amount reviewed (10% to 44% of data) and manner in which reviewed data were selected (randomly versus systematically) varied (APPENDIX A TABLE A-6). Similarly, full manual studies differed in how data were reviewed, with some authors interested in finding presence over some timeframe (e.g., manually reviewed every day until a vocalization was observed to determine daily presence), while others determined the occurrence of every individual vocalization (APPENDIX A TABLE A-6).

All studies that solely used automated techniques to determine species occurrence targeted fin and/or blue whales (Matsuo et al. 2013, Leroy et al. 2016, Gavrilov et al. 2018, Leroy et al. 2018a). For 3 out of 4 of the studies, automated detector performance was either not calculated or not reported. Gavrilov et al. (2018) reported both missed and false detection rates that had been previously calculated in earlier publications.

A combination of manual and automated analysis was the most common methodology applied to determine species occurrence (Figure 2.4). Factors that were inconsistent across studies included: how much data were manually analyzed, how files for manual analysis were selected, if automated detector performance was determined, and how automated detector performance was determined. These studies were broadly categorized into those that manually reviewed every automated detection and those that did not (APPENDIX A TABLE A-7). Only two studies could not be categorized, as they applied different analysis techniques to different portions of their data sets (Kerosky et al. 2012, Buchan et al. 2015).

Most manual and automated occurrence studies (21/32) completed some form of manual review of every automated detection or automated detection event (e.g., days with detections). Nine studies applied automated detectors and then manually checked all automated detections and removed false positives, but never determined how often their detector missed vocalizations (Stafford et al. 2004, Stafford et al. 2005, Mellinger et al. 2007a, Širović et al. 2009, Stafford et al. 2011, Morano et al. 2012a, Whitt et al. 2013, Risch et al. 2014a, Salisbury et al. 2016). In addition to manually checking all detections and removing false positives, seven studies analyzed a subset of data without automated detections to determine the missed detection rate of their automated detector (Lammers et al. 2011, Mussoline et al. 2012, Balcazar et al. 2015, Hodge et al. 2015, Tripovich et al. 2015, Davis et al. 2017, Buchan et al. 2018). The amount of data reviewed and data selection protocol to determine missed detection rate varied greatly across these studies, with <1% to 33% of data reviewed that were selected randomly, based on ambient sound levels, or selected systematically (e.g., every third day; APPENDIX A TABLE A-7).

Some studies that reviewed every automated detection undertook manual analysis independent of the automated detection results and did not use the analysis to determine detector performance. In addition to checking every detection, Bort et al. (2015) carried out a systematic partial manual analysis (reviewed every third day). Munger et al. (2008) carried out full manual analysis via long-term spectral averages where successive fast Fourier transforms are averaged into long-term spectrograms for review.

Ten occurrence studies that utilized both automated and manual techniques did so without checking every automated detection (see references in APPENDIX A TABLE A-7). Instead, they applied automated detectors and subsequently completed variable amounts of manual data review (<1 to 7% or unclear to reader) to determine automated detector performance, optimize automated detectors, or create ROC curves (APPENDIX A Table B-3). The subset of acoustic data for manual review were randomly selected, spread over time, spread over locations, spread over number of detections, or not specified, depending on the study (APPENDIX A TABLE A-7).

The presentation of baleen whale occurrence results in big PAM data varied across studies, with results generally presented as one of two measures: number of vocalizations/detections or presence (APPENDIX A TABLE A-8). Half of studies (23/47) presented results as number of vocalizations or number of automated detections over some duration (e.g., number of automated detections per week; APPENDIX A

Table B-4). In contrast, 18/47 studies presented results as presence within a timeframe, commonly over some larger timeframe (e.g., number of days with presence per week (Davis et al. 2017) (APPENDIX A TABLE A-8). Risch et al. (2014a), Morano et al. (2012a), and Wright et al. (2018) presented results using both measures. A few studies presented results using completely different measures such as a daily index (Simon et al. 2010, Nieukirk et al. 2012, Leroy et al. 2018a). The most common descriptors of occurrence were number of vocalizations (or automated detections) per month (9 studies) or per day (6 studies) and number of hours (or percent of hours) with presence per day (4 studies) or per month (3 studies; APPENDIX A TABLE A-8).

Diel patterns were explored in 14 of the 47 occurrence papers with an additional two papers that commented on diel patterns in the occurrence and characterization papers. Most diel studies incorporated all days where vocalizations occurred while some limited diel analysis to a portion of the data (e.g., only months where the vocalizations were most common; APPENDIX A TABLE A-9). The number of light regimes in a 24-hr day to explore diel patterns varied across studies with the most common being 3 light regimes (light, dark, and twilight; 4 studies) or 4 light regimes (light, dark, dusk, dawn; 3 studies; APPENDIX A TABLE A-9). Light regimes were most frequently defined using nautical twilight determined by angle of the sun (11/15 studies; APPENDIX A TABLE A-9). The most common unit to compare vocalizations across light regimes was hourly mean adjusted number of vocalizations (or presence of vocalizations) per hr (7/15 studies; APPENDIX A TABLE A-9).

2.5.1.1.3 **Combined occurrence and characterization studies**

A number of studies (22%; 17/79) explored the acoustic occurrence of baleen whale species and characterized some aspect(s) of the recorded vocalizations (Figure 2.4). While the overarching aim of the research was often focused on either occurrence or characterization, both questions were addressed throughout each study. The characterization aspect of these studies largely targeted non-song vocalizations (12/17). Similar to when these research questions were explored independently, studies exploring both characterization and occurrence had a wide range of methodologies with few commonalities between them (APPENDIX A TABLE A-10). Some studies (7/17) undertook the same analysis methodology for both research questions (e.g., Stafford et al. 2007b, Leroy et al. 2017), but the majority utilized two largely unrelated methodologies (APPENDIX A TABLE A-10). For the question of occurrence, the most common method was a combination of manual and automated detection (8/17), though specific protocols varied across studies. For example, Clark et al. (2002) manually validated 1 hr every 18 days of data, whereas Vu et al. (2012) manually reviewed all automated detections. For the question of characterization, the most common method was partial manual (11/17) with an emphasis on high signal-to-noise ratio (SNR) vocalizations, where what was considered ‘high’ SNR varied across studies. Again, specific analysis protocols varied from a selection of 1 hr per day (Oswald et al. 2011) to a random selection of 6 days per month (Vu et al. 2012) (APPENDIX A TABLE A-10). The percent of acoustic data manually reviewed was often unclear as it was guided by automated detectors, but values ranged from <1% to 100% to determine occurrence and from 1.9% to 11% for characterization analysis (APPENDIX A TABLE A-10).

2.5.1.2 STUDIES TARGETING ALL SPECIES PRESENT

Of the 94 big PAM data baleen whale papers reviewed, only nine targeted all species present in the acoustic data and of those, only five described the occurrence of three or more species (APPENDIX A TABLE A-11; Figure 2.4). Multi-species studies used data ranging in timespan from 1–6 years with the majority (6/9 studies) spanning 1–2 years. Occurrence was investigated in every all-species study, with McDonald (2006) also investigating density and Nieukirk et al. (2004) also characterizing vocalizations. Methodologies to determine occurrence varied across studies, with the percent of data manually reviewed ranging from 5% to 100% (APPENDIX A TABLE A-11). The most commonly used method to investigate occurrence of all baleen whale species was a combination of manual and automated techniques (3/9 studies; APPENDIX A TABLE A-11) where protocols included manually reviewing a portion of each file (Hannay et al. 2013), reviewing 20 files per species with varying automated detector counts (Frouin-Mouy et al. 2017), or selecting data at random from within regions that were suspected to have unreliable automated detections (De Vreese et al. 2018).

2.5.1.3 DESCRIBING AUTOMATED DETECTOR PERFORMANCE

The description of automated detector performance in baleen whale big PAM studies was variable across the literature reviewed. Of the 53 studies that incorporated automated detectors, 25 made no commentary on automated detector performance. Three studies commented on detector performance (e.g., noted that automated detector(s) may have missed some vocalizations or performed poorly), but performance was not calculated, or, if it was, the results were not presented (Širović et al. 2004, Stafford et al. 2005, Stafford et al. 2011). Five studies commented on how the automated detector(s) performed in previous studies but did not calculate performance for their data set (Table 2.1). Some aspect of automated detector performance was calculated and presented in only 20 of the 53 studies that used automated detectors (Table 2.1).

Table 2.1. Summary of metrics used to describe automated detector performance for each species group (species) where '-' indicates the metric was not described. Metrics include false negative rate (FNR), false positive rate (FPR), precision (P), recall (R), and accuracy (ACC). This summary only includes the 25 studies that provided information on automated detector performance (28/53 studies did not and are not included here).

Species	FNR (%)	FPR (%)	P (%)	R (%)	ACC (%)	Study
Blue	1.0	1.0	-	-	-	Gavrilov and McCauley (2013)
	-	-	67.0–95.0	77.0–96.0		Širović et al. (2015b)
	0.0–9.4	17.6–100.0	-	-	-	Balcazar et al. (2015)
	-	14.6–36.6	-	-	-	Tripovich et al. (2015)
	6.0–33.0	3.0–13.0	-	-	-	Buchan et al. (2015)
	~1.0[a]	~1.0[a]	-	-	-	Gavrilov et al. (2018)
	<0.002	-	-	-	-	Buchan et al. (2018)
	<5.0[a]	<5.0[a]	-	-	-	Jolliffe et al. (2019)
Bowhead	-	-	84.0	22.0	-	Hannay et al. (2013)
Bryde's	10.0	50.0	-	-	-	Kerosky et al. (2012)
Fin	21.0	20.0	-	79.0		Morano et al. (2012b)
	-	0.0	-	35.3	-	Tsujii et al. (2016)
Humpback	6.0–11.0	-	-	-	-	Vu et al. (2012)
	-	-	-	90.0	-	Kowarski et al. (2018)
	-	8.0	-	68.0	85.0	Español-Jiménez and van der Schaar (2018)

Species	FNR (%)	FPR (%)	P (%)	R (%)	ACC (%)	Study
Minke	-	5.0	-	22.0–100.0	-	Oswald et al. (2011)
	27.0 (0.0–51.0)	-	-	-	-	Risch et al. (2013)
	27.0[a]	-	-	-	-	Risch et al. (2014a)
	-	11.0	20.0	74.0	-	Risch et al. (2019)
Right	-	-	-	15.0	-	Mellinger et al. (2004)
	7.0–19.0	-	-	-	-	Mussoline et al. (2012)
	-	-	-	75.0[a]	-	Morano et al. (2012a)
	36.2–53.6	-	-	46.4–63.8	-	Hodge et al. (2015)
	-	-	-	75.0[a]	-	Salisbury et al. (2016)
	31.0	-	-	-	-	Davis et al. (2017)

[a]Performance metric based on previous research

The majority of studies that incorporated automation (with or without manual review) investigated acoustic occurrence (Figure 2.4), with the exception of three that investigated characterization only (Delarue 2008, Magnúsdóttir et al. 2015, Rekdahl et al. 2017). None of the characterization studies reported automated detector performance, which is unsurprising given that automated detector performance would not impact the reliability of their results as they simply used the automated detectors to find signals that were then manually characterized.

Different terminology was used across studies to describe the same automated detector performance metric (see performance metric definitions and formulas summarized in Figure 2.5); in some cases, the definition was assumed when equations were not provided. False negative detection errors, missed call rate, false negative percent, misdetection rate, rate of missed detections, and missed detection rate were all assumed to refer to FNR. Rate of false detections, false detection rate, negative positive rate, false alarm rate, and false positive percent were all interpreted as FPR. Correct detection rate, percent identified, percent of calls found, true positive percent, and percent probability of detection were interpreted as R.

		Detector	
		Detected	**Not detected**
Truth	**Detected**	*TP* True positive	*FN* False negative
	Not Detected	*FP* False positive	*TN* True negative

$$\text{False negative rate} = FNR = \frac{FN}{TP+FN}$$

$$False\ positive\ rate = FPR = \frac{FP}{FP+TN}$$

$$Recall = R = true\ positive\ rate = TPR = \frac{TP}{TP+FN}$$

$$\text{Precision} = P = \frac{TP}{TP+FP}$$

$$Accuracy = \ ACC = \frac{TP+TN}{TP+TN+FP+FN}$$

$$\text{F-score} = 2\frac{P\ x\ R}{P+R}$$

$$Matthews\ Correlation\ Coefficient =$$
$$MCC = \frac{TP\ x\ TN - FP\ x\ FN}{\sqrt{}(FP+TP)(TP+FN)(TN+FP)(TN+FN)}$$

Figure 2.5. Detector performance metric definitions and formulas for a binary detector/classifier. Where a detector (automated or manual) is binary if a positive or negative result is defined for each unit (e.g., acoustic file or period of time). Where number of detections is given rather than a binary output, TN is generally not defined. When considering automated detector performance, the manual analysis results (Truth) are compared to automated detector results (Detector).

The performance metrics varied across studies. FNR, FPR, and R were the most commonly reported metrics (Table 1). P was reported in three instances, and ACC was only described on one occasion (Table 2.1). For some studies, describing FPR, R, or P was unnecessary as every automated detection was manually checked and the FP were removed (APPENDIX A TABLE A-7). Some authors plotted true positive rate against false positive rate to create ROC curves (Vu et al. 2012, Hodge et al. 2015, Tsujii et al. 2016, Español-Jiménez and van der Schaar 2018). The values of performance metrics varied greatly across metrics and species (Table 2.1). With an ideal value of 0%, FNR ranged from 0%–54% and FPR from 0%–100%. Conversely, with an ideal value of 100%, P and R ranged from 20%–95% and 15%–100%, respectively (Table 2.1). Wide ranging values were in some cases reported within studies. For example, Balcazar et al. (2015) reported an FNR of 0%–9% and FPR of 18%–100%, depending on the type of blue whale vocalization targeted by the automated detector, the location of the acoustic recorders, and the year of the recordings. Hodge et al. (2015) similarly concluded that right whale automated detector performance varies by location with R values of 46%–64% and FNRs of 36%–54%. Risch et al. (2013) found that minke whale FNR for automated detection ranged from 0%–51%, depending on vocalization quality in the recorded data. No species consistently had better automated detector performance than others, though such comparisons are challenging given the range in metrics employed, automated detectors applied, vocalization types, and variability in number of studies per species (Table 2.1).

2.5.1.4 TERMINOLOGY ASSOCIATED WITH DATA ANALYSIS METHODS

An inconsistency in terminology related to analysis methods in big PAM data was apparent throughout this literature review. For example, one study may describe false positives while another describes incorrect detections, two equivalent detector performance metrics. Human manual analysis of data was referred to in a variety of ways throughout the literature including ‘manually’, ‘visually’, and ‘aurally’ ‘examined’, ‘viewed’, ‘logged’, ‘inspected’, ‘analyzed’, and ‘detected’. Automated analysis was described as ‘autodetection’, ‘automated detection algorithms’, ‘automatically detected’, and ‘search algorithm’. The terms ‘manual’, ‘visual’, and ‘aural’ most commonly referred to some manner of human analysis, while the term ‘automated’ indicated the use of an algorithm. ‘Detected’, ‘detector’, and ‘detection’ were used interchangeably between manual and automated methods.

2.6 DISCUSSION

This systematic literature review of baleen whale PAM studies revealed a shift in methodologies applied to increasing volumes of data collected. With the use of modern technologies allowing for the remote autonomous collection of large volumes of acoustic data, the data analysis methods have appropriately shifted from predominantly relying on human analysts to methods incorporating both automated and manual techniques (Figure 2), a trend similarly observed in other fields tackling big data (Lewis et al. 2013, Sivarajah et al. 2017).

Big PAM baleen whale studies were largely limited to humpback, blue, fin, and right whales, with a small proportion of research investigating more than one species type at a time. The bias in reporting toward these species likely reflects a combination of factors, including their conservation status, distributions that overlap or conflict with human activity, propensity towards being vocally active and thus captured on recorders, or public interest. For example, the acoustically prolific humpback whale song first became famous in the 1970s, and now has a great deal of public and scientific interest (Payne and McVay 1971). Conversely, other baleen species are in locations where it is more difficult to collect data such as the bowhead whale in the Arctic (Blackwell et al. 2007, Stafford et al. 2012, Charif et al. 2013) or have vocalizations that are more rare, poorly understood, or difficult to study acoustically such as the Omura's whale (*Balaenoptera omurai*) (Cerchio et al. 2015). As more work describes the sounds of these species, their presence in the literature will likely increase.

One of the great benefits of PAM data collection is that it captures signals from all species acoustically active in the area that vocalize within the parameters of the recording system. Therefore, by restricting research efforts to only describing the occurrence of a single species, a practice that likely reflects many factors including budget, time, access to different automated detectors, and priorities, researchers are not fully utilizing the investment they have made in data collection. Thus far, most multi-species studies involve fin and blue whales and low sampling rate data. This is unsurprising given that these species produce regular, predictable, species-specific acoustic signals for which reliable automated detectors can be more easily developed relative to other baleen whales such as humpback whales, which produce more varied signals that can change considerably over time (Rekdahl et al. 2017). Further, blue and fin whales produce low-frequency signals that can be captured by recorders sampling at 100 or 250 Hz, requiring less power and memory storage in recording devices. However, acoustic recorders are now sufficiently powerful to sample at higher rates for long durations, allowing for a greater range of signals to be captured and more species to be described (Moloney et al. 2018). While few studies in the present review explored all species acoustically present, high sampling rates in new generation recorders, an increasing knowledge of marine mammal vocalizations allowing more species to be identified, and an impetus towards ecosystem studies (Sherman et al. 2005) should lead towards more multi-species studies. The development of more automated detectors, or suites of automated detectors that capture and differentiate many types of acoustic signals could encourage more multi-species studies. Worth noting, the present review could not effectively differentiate between studies that investigated and reported on a single species and those that investigated all species but reported on species separately across publications. Therefore, the practice of multi-species analysis may be more common than is perceived here. As research groups include more species, putting greater strain on analysis efforts, the shift to utilizing a combination of automated and manual analysis techniques is expected to continue, as was observed in studies that investigated all acoustically active species in this review.

While a trend toward incorporating automation into big PAM baleen whale analysis methods was observed, protocols showed great variation across studies, which likely reflects differences in research goals, time, budget, acoustic signal(s) of interest, and experience of research groups. Some variation may be due to different requirements from the journal of choice for publication, with some potentially requiring more stringently described methodologies (e.g., automated detector performance evaluation) than others. The acoustic research community must work to standardize methods among different projects to increase comparability/consistency across studies (Mellinger et al. 2007b). Therefore, I provide the following recommendations to encourage future research towards this goal.

2.6.1 Recommendations

Recommendations for future work on baleen whale PAM are based on the present literature review as well as recommendations from other fields that utilize big data. Suggestions seek to find a balance between 1) being reasonable and achievable for researchers, regardless of budget and time restraints, 2) maintaining consistency with previous baleen whale PAM literature, and 3) achieving standards utilized beyond the marine PAM field to encourage interdisciplinary consistency (e.g., PAM in the terrestrial realm). In many instances, our recommendations are limited by a lack of consistency observed in the literature (in big PAM data or other big data studies). These should therefore not be considered hard and fast rules, but rather a starting point to a larger methodological discussion within the PAM data community.

2.6.1.1 RECOMMENDATION 1: METHODOLOGY FOR CHARACTERIZATION STUDIES

For researchers seeking to characterize baleen whale acoustic signals or acoustic behaviour, I recommend analysis driven by the SNR of acoustic signals. This was commonly employed in studies that investigated both occurrence and characterization in the present literature review. By restricting characterization to signals of high SNR, researchers reduce the chance that they misidentify, misclassify, or inaccurately characterize the signal (Mellinger 2004). The method of calculating SNR and what is considered “high” must be clearly defined in the study. One approach is to compare signals to the sound level of the appropriate frequency band (Castellote et al. 2012a, Gavrilov et al. 2012), which can be made more specific by using the ambient sound immediately before the signal (for the same duration of the signal) (Kowarski et al. 2019). There is arguably value to additionally characterizing low SNR signals if the quality and context is such that the researcher can reliably identify species. If the characteristics of lower SNR vocalizations are shared with the acoustics community, future researchers will be better able to classify faint signals in their own data, which can be particularly important for endangered or rare species. Where researchers include varying SNR vocalizations in characterizations, they should clearly specify and differentiate these in their results. Automated methods can be utilized to identify high SNR signals for manual review, though effective automated detectors may not be available before a signal has been adequately characterized. Where automation is not feasible to guide manual review, I recommend employing partial manual review to identify acoustic signals of interest with high SNR.

Partial manual review was the most common characterization method in the present review for non-song vocalizations and is arguably the most appropriate method when effective automation is unavailable, and the quantity of data is such that full manual review is unachievable. Specific protocols to select data for partial manual review and the amount of data reviewed were varied in the literature reviewed, likely reflecting different research questions, goals, acoustic signals of interest, time, and budget. While I recommend that protocols incorporate SNR, one must then decide how to ensure the sample is appropriate for the research question. For example, if a study is claiming to describe vocalizations of a species, selecting high SNR vocalizations from three days is arguably not representative as vocal behaviour may vary across space and time. Rather, vocalizations should be analyzed across time of day, day of year, and locations to increase the chance of a representative sample. Ancillary information can also be considered when determining analysis protocols such as seasonal ice cover, known migration times, and information from visual surveys.

Studies that incorporated characterization of songs commonly employed full manual review, but these were almost entirely limited to relatively small studies (2,000 hr or less of acoustic data) and may become increasingly unrealistic for research groups to undertake in the future as data sets continue to grow. Furthermore, where a full manual review does not limit its characterization to high SNR events, it risks mischaracterization. Therefore, when full manual review is unachievable, I argue partial manual review driven by SNR (or vocalization quality) is sufficient for song characterization research.

My recommended guidelines for characterization methodology is summarized as follows:

1. Select vocalizations for analysis based on SNR. As a minimum the analysis should focus on high SNR vocalizations; however, describing vocalizations at all signal to noise ratios is recommended.

2. If available, use automated techniques to identify high SNR vocalizations.

3. Where automated methods are inapplicable, undertake a partial manual review, at minimum, to identify signals of interest. The manual review protocol must capture a representative sample and should consider ancillary information.

4. Include a wide temporal window (over season, day, hour) and diverse spatial locations where possible to fully capture the variability on vocalization types.

2.6.1.2 RECOMMENDATION 2: METHODOLOGY FOR OCCURRENCE STUDIES

For the question of baleen whale spatial or temporal acoustic occurrence, I recommend utilizing a combination of manual and automated methods, the most common technique observed in the present literature review. This recommendation applies to studies solely investigating occurrence and those that include additional research questions. The sole use of manual review (full or partial) would only be necessary where automated detectors are ineffective (e.g., signal is too variable, there are other sounds that interfere with automated detection) or where automated detectors cannot be developed because too little is understood about the acoustic signal of interest. Full manual review would be unrealistic for many research groups, and partial manual review inevitably restricts findings to only a portion of the data. Automated detection without the verification of manual review was rare in the literature and should be avoided. Indeed, the present review revealed that no species has consistently had high automated detector performance reported such that one could argue no manual review is required. Conclusions drawn from research studies solely reliant on automated detectors that are known to have variable performance depending on factors such as location, season, and other ocean sounds should be viewed with caution (Hodge et al. 2015, Širović et al. 2015b, Erbs et al. 2017).

The question then remains, what protocol should be followed when implementing a combination of manual and automated techniques to determine baleen whale occurrence and how can researchers effectively determine automatic detector performance? Many researchers in the present literature review opted to manually review every automated detection. This technique can result in an intensive workload where effort in terms of time and cost will vary depending on the experience level of analysts. Such effort is likely beyond the reach of some research groups and could become completely unattainable when investigating more than one or two species. Indeed, the present literature review found that no study investigating more than two species checked every automated detection. I therefore argue that, unless the number of automated detections is reasonably small or the research requirements are such that not a single false automated detection is acceptable in the results, the manual review of each automated detection or automated detection event is unnecessary. Rather, researchers should follow the trend of many big data studies and manually review a subset of data to determine automated detector performance metrics (Lewis et al. 2013, Ofli et al. 2016, Knight et al. 2017; See Recommendation 4). The topic of automated detector performance metrics is discussed further in Recommendation 3.

To effectively compare occurrence results between studies, researchers must not only aim for consistent methodologies but also consistent presentation of results, especially within species. The present literature review observed two main categories of units used in results: number of vocalizations or automated detections and presence of vocalizations or automated detections, where presence is given the same weight whether one detection happened within that timeframe or 200. Number of detections can allow a finer comparison of relative occurrence between e.g., two recording stations, but is susceptible to misrepresenting findings if detector performance (manual or automated) is variable across space or time. Presence is arguably more comparable across studies. The same automated detector or human analyst is rarely applied to multiple studies, and if they were, they would be expected to perform differently if the acoustic environment between the two studies is not comparable (Erbs et al. 2017). When there is a high density of vocalizations, this difference in performance is reduced by looking at presence rather than the number of vocalizations (e.g., Hodge et al. 2015 found that missed detections were high when assessed per vocalization but low when assessed per day). What's more, presence allows TN to be defined and calculated, which is not the case when considering number of detections (Figure 2.5). I therefore argue that presence is the preferred unit for occurrence results. In the present review, presence results were most commonly reported as hours per day or per month. Maintaining this trend would increase comparability between studies, though the appropriate unit of time analyzed and presented will depend on the specific research questions being addressed, and, with data sets growing ever larger, days per week, month, season, or year may become more achievable and common units.

In contrast to most methodologies observed in the present literature review, those investigating diel occurrence showed some consistency between studies that should continue to be upheld in future research where authors seek to directly compare studies.

Diel studies should incorporate all days where vocalizations were deemed present, define light regimes based on nautical twilight (angle of the sun), and present results as hourly mean adjusted number of vocalizations (or presence of vocalizations) per hour for each light regime. There is some discrepancy in how many light regimes are used. Most studies reviewed here used three or four, where those with three had one regime for twilight, while those with four separated twilight into dawn and dusk. Given that acoustic occurrence did vary between dawn and dusk in some studies (Mussoline et al. 2012, Kowarski et al. 2018, Kowarski et al. 2019), it seems reasonable to have them separated and to use four light regimes. These recommendations based on trends in the literature may not be applicable in all regions of the world (e.g., in high latitudes where using nautical twilight would be inappropriate) and should be adapted appropriately. Incorporating novel approaches to diel analysis could be useful, though I argue there is value in additionally presenting results as per the typical methods to allow comparison and discussion.

Our recommended guidelines for occurrence methodology are summarized as follows:

1. Use a combination of automated and manual methods where the automated detector performance is determined from the manual review of a subset of data.
2. Present results as presence (e.g., as hours per day or days per month).
3. Define light regimes for diel analysis based on nautical twilight (where appropriate), and compare the mean adjusted number of vocalizations per hour for each light regime.

2.6.1.3 RECOMMENDATION 3: AUTOMATED DETECTOR METRICS

This review highlights previous findings that automated detectors in PAM vary in performance depending on location and timeframe (Hodge et al. 2015, Širović et al. 2015b, Erbs et al. 2017). This is unsurprising given the wide range of acoustic conditions encountered in the marine realm. For example, the performance of an automated right whale upcall detector would be different in a month where right whales were the only species present than in a month where humpback whales were singing because humpbacks produce similar signals to right whales (Parks et al. 2011). I therefore propose that any application of automated techniques must be paired with manual review to determine automated detector performance, a conclusion similarly reached by Knight et al. (2017) after reviewing PAM avian literature. Where studies span numerous locations and seasons, researchers should further consider calculating automated detector performance for each circumstance as was completed by Erbs et al. (2017).

My review revealed that automated detector performance metrics are under-represented in the baleen whale PAM literature with more than half of studies that used automated detectors not describing performance. Studies that did describe performance used varying metrics that were often poorly defined in terms of formula and the unit of time being considered. This variation makes it difficult to compare results across studies, species, locations, and seasons. While FNR and FPR were the most commonly reported metrics in the present review, Knight et al. (2017) argue that P, R, F-score (Figure 5), and area under the (P and R) curve (AUC) are required for PAM studies to maintain standards with other disciplines. I concur that researchers should strive to present these metrics, particularly P and R, as F-score and AUC are aggregate metrics to represent both P and R. P provides the proportion of automated detections (or detection events per unit time) that were correct and R provides the proportion of true detections (or detection events per unit time) that were captured by the automated detector (Figure 5). Another less common metric to summarize automated detector performance is Matthew’s Correlation Coefficient (Figure 5) which has the benefit of incorporating TN, a metric not represented in P, R, F-score, or AUC, and is appropriate for the imbalanced data often seen in PAM (Boughorbel et al. 2017). TN can only be determined where automated detector output is binary (e.g., presence/absence). A formula must always be presented alongside any performance metric as well as the unit of performance (e.g., it must be clear if the metric is describing the automated detector performance per vocalization or per unit time, relative to the manual analysis). Indeed, the variation in performance metric values in the present review may be partially due to studies evaluating different units.

The significance of automated detector metrics will vary between studies as there will almost always be a trade-off between P and R. For some studies, achieving high R will be important because the acoustic signals of interest are rare or the species is endangered, but this will likely result in a lower P (Mellinger et al. 2007b, Kerosky et al. 2012, Buchan et al. 2018). Studies on species that are more vocally prolific may allow a lower R in favor of optimizing P (Mellinger et al. 2007b). Authors should indicate whether they have developed automated detectors with the intent to optimize P, R, or some metric that balances both such as F-score, AUC, or MCC.

Once performance metrics are calculated, researchers must critically interpret them and present results in a meaningful way. Where automated detector performance is found to be low, the automated detector may be deemed ineffective and either the automated detector must be improved, or an appropriate manual analysis protocol must be undertaken. At what level automated detector performance is deemed too poor will depend on the research goals. Researchers may improve or optimize automated detector results post processing. For example, some automated detectors can have confidence levels imposed, or a minimum number of automated detections per timeframe requirement can be applied (Mouy et al. 2016, Delarue et al. 2018). Presenting automated detector results alongside performance metrics will help ensure results are interpreted correctly. For example, an R of 0.50 tells the reader that the results only represent half of the true occurrence of the acoustic signal. Further, where authors understand what factors impact automated detector performance, they should present such information along with their acoustic occurrence results (e.g., anthropogenic activities, weather events, ambient sound levels).

In addition to evaluating automated detectors, researchers should strive to validate the effectiveness of the manual review, given the potential for discrepancies between human analysts that produce the ‘truth data’. This can be done by having multiple humans review the same data (at least for a subset) to calculate the agreement between them (e.g., Leroy et al. 2018b). Where only employing a single analyst is possible (given the limited resources of many research groups and scarcity of qualified individuals), papers should provide sufficient evidence that the experience of the analyst is such that the truth data can be considered sufficiently reliable.

Our recommended guidelines for automated detector metrics are summarized as follows:

1. Pair automated detector implementation with manual review to determine automated detector performance metrics.
2. Evaluate automated detector performance metrics separately for different acoustic circumstances (e.g., each season and location).
3. At minimum, evaluate P and R for each automated detector.
4. Include a formula and the unit investigated for all automated detector performance metrics reported.
5. Evaluate the reliability of the human created ‘truth data’.

2.6.1.4 RECOMMENDATION 4: DATA SELECTION TO CALCULATE AUTOMATED DETECTOR METRICS

Regardless of the research question, one of the most variable protocols observed in the present literature review was how data were selected for manual analysis to validate automated detectors. The amount of acoustic data reviewed ranged greatly with little to no consistency between studies. The manner data were selected for manual review was inconsistent. Depending on the study, data for manual validation of automated detections were selected completely randomly or was based on automated detector counts, time to capture the entire recording period, location to capture all recording sites, ambient sound, or suspicion that automated detections were incorrect. Given the known variability in automated detector performance that can occur across these variables, I recommend that researchers account for all of them when selecting data for manual validation. Proceeding otherwise could result in performance metrics that are not truly representative of the results.

The question then remains, how much data should be manually validated? This will likely be determined by the constraining factors of time, budget, and resources, but need to be sufficiently high enough to ensure a representative sample was manually analyzed. A manner to check if the sample data set is sufficiently large is to calculate the P and R of the automated detectors based on the sample, which may be 5% of acoustic data, then calculate P and R as if only 2.5% of acoustic data was reviewed. If P and R do not vary between the two sample sizes, the plateau of performance has likely been reached, and the performance metric values are reliable.

Our recommendation for samples of data selected to validate automated detectors is:

1. Samples must represent the entire breadth of conditions present in the data set of interest to effectively report on automated detector performance.

2.6.1.5 RECOMMENDATION 5: TERMINOLOGY

Terminology used to describe methods to analyze big PAM baleen whale data varied across studies, resulting in a lack of clarity when attempting to compare methods and results during the present review. For example, detections can refer to the outcome of human manual analysis, automated detectors, or both, depending on the study. Further, studies incorporating sighting surveys also have visual detections (a term also applied to manual PAM analysis). Knight et al. (2017) similarly found a lack of consistency in avian

PAM literature terminology, particularly regarding automated detector performance metrics. Future research should strive to maintain consistency and clarity. To this end, I have compiled the following guidelines that are recommended for future studies:

1. Clearly define the terminology that will be used in the paper. For example, if using an algorithm that first detects a signal, then classifies it as a vocalization, the author should clarify that the term "automated detector" refers to an automated detector-classifier. A small glossary section would add great clarity to PAM articles.

2. Qualify any use of the term "detection". For example, "manual detection" describes a human-detected signal, "automated detection" describes an algorithm-detected signal, and "manually validated detection" describes a signal that was first detected automatically then validated by a human.

3. Use the term "manual" or "human" to qualify detections from human analysts. These are more broadly applicable beyond the field of acoustic than "aural" or "visual", for example.

4. Use the term "automated" to qualify results from a computer algorithm.

2.7 CONCLUSIONS

I present a literature review of baleen whale PAM methods and propose guidelines for future work to enhance consistency and rigor of methods. The PAM community should work towards implementing consistent standards while considering the sometimes-limited resources of research groups and how requirements vary across research questions. Big data will likely continue to increase as technology matures and analysis methodologies must find the balance between adapting appropriately while maintaining consistency. Results from PAM marine mammal research, especially those investigating occurrence, can reliably inform management decisions. However, standards or best practices are required and must be upheld for findings to be considered reliable and taken into consideration as appropriate.

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CHAPTER 3 WESTERN NORTH ATLANTIC HUMPBACK WHALE FALL AND SPRING ACOUSTIC REPERTOIRE: INSIGHT INTO ONSET AND CESSATION OF SINGING BEHAVIOUR

3.1 PUBLICATION STATUS

This chapter was published in the Journal of the Acoustical Society of America in March 2019 (Kowarski et al. 2019).

3.2 ABSTRACT

Humpback whale songs have been described worldwide and studies exploring non-song vocal behaviour continue to expand; however, studies on the transition periods when whales shift to and from the seasonal behavioural state of singing are lacking and may be potentially informative regarding the proximal factors controlling the onset and offset of humpback whale male singing. Acoustic recorders collected data off eastern Canada continuously from the Bay of Fundy in fall 2015 and near-continuously off northeast Nova Scotia in spring 2016. Humpback whale acoustic occurrence and behaviour were identified by systematically reviewing a subset of acoustic recordings for presence before analyzing the highest quality recordings for behaviour. The onset of singing in the fall was gradual over a period of about 3 weeks with an intermediate form, termed "song fragment", occurring prior to full songs. In comparison, singing in the spring seemed to end abruptly with few song fragments. Song fragments could be produced by juveniles learning to sing for the first time or mature males preparing for breeding activities prior to migrating to southern breeding grounds. I propose an alternative hypothesis that the

timing and manner of transitions could be driven by physiological processes similar to those documented in songbirds.

3.3 INTRODUCTION

The humpback whale (*Megaptera novaeangliae*) is a medium-sized mysticete found in all ocean basins (Jefferson et al. 2008). It is known for its long migrations from high-latitude summer feeding grounds to low-latitude winter breeding grounds (Kellogg 1929, Mackintosh 1942, Mackintosh 1966, Norris 1967) and its acoustic behaviour. Sounds of the humpback whale have been studied globally with two overarching acoustic behavioural categories described: song and non-song calls (e.g., Payne and McVay 1971, Cerchio and Dahlheim 2001, Cerchio et al. 2001, Arraut and Vielliard 2004, Au et al. 2006, Dunlop et al. 2007, Garland et al. 2011, Stimpert et al. 2011, Rekdahl et al. 2013, Rekdahl et al. 2015).

Songs are a sexually-selected male display that occur during the winter breeding season (Payne and McVay 1971) when humpback whales migrate from high latitude feeding grounds to lower latitudes (Kellogg 1929). The precise function of singing is still debated, with proposed functions including to attract mates (Winn and Winn 1978, Tyack 1981), stimulate female receptivity (Baker and Herman 1984, Smith et al. 2008), mediate male competitive interactions (e.g., Cholewiak et al. 2018), form male coalitions (Darling et al. 2006), and/or establish dominance (Darling and Bérubé 2001). Humpback whale songs have a hierarchical structure in which discrete units (i.e., notes) are arranged in series to form stereotyped phrases, which repeat to produce themes that occur in sequence (Payne and McVay 1971, Payne et al. 1983, Cholewiak et al. 2013). Whales within the same population (region) sing a similar song that changes over time while whales in different populations sing different songs, although the rules governing song structure are similar in all ocean basins (Payne et al. 1983). In the South Pacific Ocean, Garland et al. (2011) described the spread of humpback songs across an ocean basin, an example of repeated cultural transmission across populations at a large geographic scale.

Humpback whale songs have been studied much more extensively as compared to other types of humpback whale vocal behaviour (Silber 1986, Stimpert et al. 2011, Rekdahl et al. 2013). Calls not associated with songs are produced by males, females, and calves throughout the year and have been linked to both social and feeding behaviours (Silber 1986, Cerchio and Dahlheim 2001, Dunlop et al. 2007, Stimpert et al. 2007, Zoidis et al. 2008). Such calls that have been previously associated with humpback whale social behaviours include grunts produced by calves (Zoidis et al. 2008), blows and cries produced by competing males (Dunlop et al. 2008), snorts and wops produced within and between groups (Dunlop et al. 2008), and grunts and barks that occur when groups meet (Dunlop et al. 2008). Rekdahl et al. (2013) found that some of these call types are stable through multiple years while others are more variable and are often incorporated into songs. Cerchio and Dahlheim (2001) described cries in southeast Alaska that are associated with feeding behaviour.

One aspect of humpback whale acoustic behaviour yet to be fully described is the fall (autumn) and spring transitional periods when seasonal singing behaviour waxes and wanes, respectively. The complete repertoire of vocal behaviours during these transitional periods, or “shoulder seasons”, of the year remain largely undescribed. This knowledge gap reflects a lack of available data and, more so, the difficulty in describing an inherently dynamic behavioural transition when incorporating structured songs into the seemingly less structured non-song repertoire. Humpback whale songs have been well documented on high latitude feeding grounds, largely during early spring and late autumn, and on migratory routes (Baker et al. 1985, Mattila et al. 1987, McSweeney et al. 1989, Clapham and Mattila 1990, Cato 1991, Helweg et al. 1998, Norris et al. 1999, Charif et al. 2001, Clark and Clapham 2004, Clark and Gagnon 2004, Dunlop et al. 2007, Noad and Cato 2007, Vu et al. 2012, Garland et al. 2013a, Stanistreet et al. 2013, Magnúsdóttir et al. 2014, Magnúsdóttir et al. 2015, Kowarski et al. 2017). This indicates that the onset and cessation of singing occurs pre- and post- migration to low latitude breeding grounds. Kowarski et al. (2017) suggested that vocal behaviour neither belonging to the song or non-song category occurs during transition periods. Similarly, McSweeney et al. (1989), Mattila et al. (1987), and (Garland et al. 2013a) described singing behaviour prior to migration that was not complete songs. In songbirds, transitional periods have been found to be hormonally driven, with low testosterone levels resulting in more variable vocalizations and high testosterone levels resulting in more structured songs (Smith et al. 1997). Environmental factors also play a role in some oscine species with an increased photoperiod accelerating the effects of testosterone on singing behaviour (Meitzen et al. 2007).

The present paper aims to explore the nature and timing of the Western North Atlantic humpback whale repertoire as it transitions through one fall and one spring. Western North Atlantic humpback whales overwinter from January to early April on breeding grounds in the Caribbean and Cape Verde Islands (Whitehead and Moore 1982, Martin et al. 1984, Palsbøll et al. 1997, Jann et al. 2003) and summer on a number of known northern feeding grounds including those off eastern Canada (Katona and Beard 1990, Smith et al. 1999). Songs have been detected in Canadian waters into winter months, indicating that transitions likely occur in the region (Kowarski et al. 2017). I use data collected through static acoustic monitoring techniques to explore whether the transitions off eastern Canada are abrupt, fluid over time, or if they occur in stages that can be delineated into vocal categories. By shedding light on a new aspect of humpback whale acoustics, I give an additional perspective to attempts to understand the functions of the songs and sounds of the humpback whale.

3.4 **METHODS**

3.4.1 Data collection

Acoustic data collected off eastern Canada using static Autonomous Multichannel Acoustic Recorders (AMARs; JASCO Applied Sciences Ltd.) was explored over two time periods: September to December (the "Fall 2015" data set) and during April to July (the "Spring 2016" data set). The Fall 2015 recordings were collected from the mouth of the Bay of Fundy while the Spring 2016 recordings were collected from off northeastern Nova Scotia (Figure 3.1). The deployment details and recording specifications for each data set are provided in Tables 3.1 and 3.2.

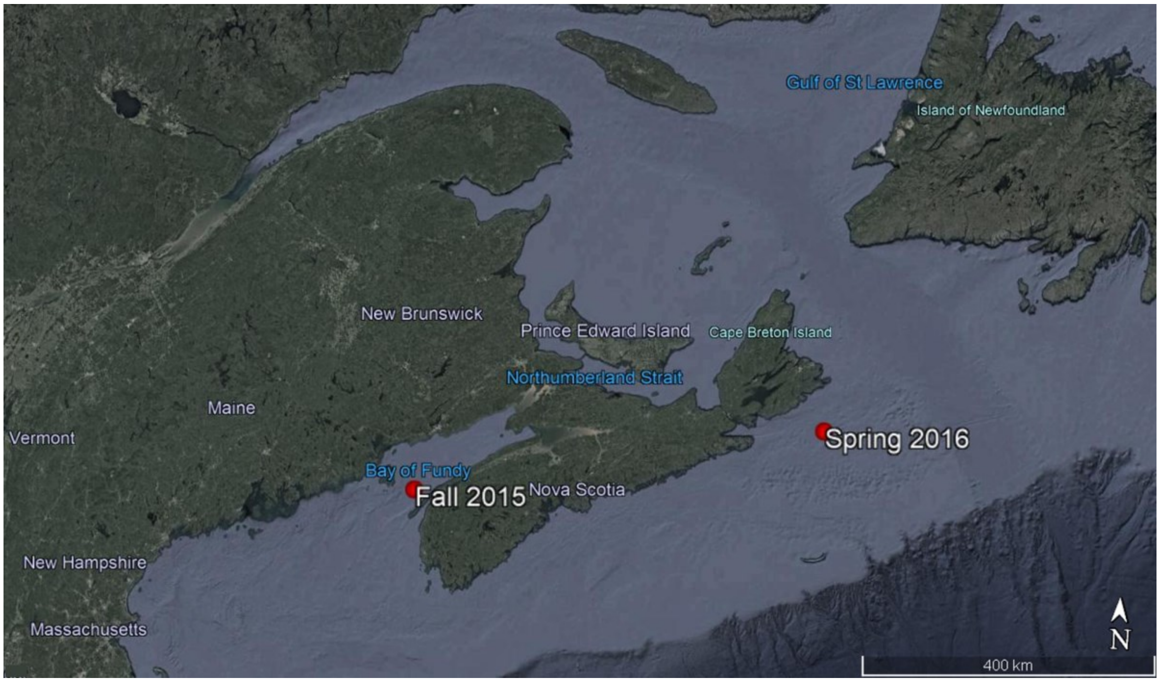

Figure 3.1. Fall 2015 and Spring 2016 stations off eastern Canada.

Table 3.1. Deployment and retrieval dates, location, water depth, and recorder position for the two recording stations.

Station	Deployed	Retrieved	Latitude (N)	Longitude (W)	Water Depth (m)	Recorder Position
Fall 2015	27 Aug 2015	1 Dec 2015	44° 33.5'	-66° 20.0'	151	On seafloor
	3 Dec 2015	28 Apr 2016	44° 33.8'	-66° 20.2'	148	
Spring 2016	3 Nov 2015	21 July 2016	45° 25.8'	-59° 46.3’	123	20 m above seafloor

Table 3.2. Recording equipment specifications and recording schedule for the two stations where hydrophone sensitivity is the sensitivity of the entire recording system.

	Fall 2015	**Spring 2016**
Hydrophone	M36-V35dB omnidirectional (GeoSpectrum Technologies Inc.)	HTI-99 omnidirectional (HTI, Inc.)
Hydrophone Sensitivity	−165 ± 3 dB re 1 V/µPa	−165 ± 3 dB re 1 V/µPa
Resolution	24 bit	24 bit

	Fall 2015	**Spring 2016**
Gain	6 dB	6 dB
Duty Cycle (min)	11.5	20
High frequency sampling rate (kHz)	375	250
High frequency duration (min)	1	1
Low frequency sampling rate (kHz)	16	8
Low frequency duration (min)	10.5	11.3
Sleep duration (min)	NA	7.7

3.4.2 Acoustic analysis

Acoustic analysis was completed in three phases. In phase 1, the occurrence (presence/absence) of humpback whale vocalizations was identified throughout the two data sets. In phase 2, the occurrence results were expanded to include the type of humpback whale vocal behaviour that occurred in high quality recordings. In phase 3, songs and any vocalizations similar to songs were analyzed in more detail.

Phase 1 occurrence analysis was completed by experienced acousticians that manually reviewed a subsample of each data set using PAMlab (JASCO; hamming window, frequency resolution: 2 Hz, frame length: 0.128 s, time step: 0.032 s). For Fall 2015, this was done by reviewing 70-second samples extracted from the center of every other 10.5 min file sampled at 16 kHz from 27 August 2015 to 15 January 2016 (62 samples 23 min apart for each day). For Spring 2016, 1-min samples extracted from the center of every 11.3 min file sampled at 8 kHz (72 samples 20 min apart for each day) from 1 April to 15 July 2016. Humpback whale acoustic occurrence was indicated by annotating the entire duration and frequency range of the fundamental frequency contour of a single humpback whale vocalization per sample. Acoustic signals were deemed humpback whale vocalizations if they aligned with characteristics previously reported in the literature (e.g. Au et al. 2006, Rekdahl et al. 2013). Effort was made to annotate the highest quality vocalization in a sample. In this manner, humpback whale acoustic presence/absence throughout the two data sets was assessed and then visualized using daily and hourly occurrence plots.

Results from the phase 1 acoustic occurrence analysis were used to guide the phase 2 analysis where vocal behaviours were analyzed and categorized. First, PAMlab calculated the signal to noise ratio (SNR) of each vocalization annotated in phase 1 by extracting the annotation sound pressure level (SPL) and the ambient SPL, where the ambient SPL was measured immediately before the annotation (using the same duration and frequency range as the annotation). The inverse annotation SPL was divided by the inverse ambient SPL and the resulting value logged to obtain the SNR. Then, for every 6 hours of data where humpback whale vocalizations occurred, I selected the acoustic file with the highest vocalization SNR. Each of the selected high-quality acoustic files (10.5 min duration in Fall 2015 and 11.3 min duration in Spring 2016) were analyzed and the presence/absence of one or more vocal categories was assigned. By limiting our analysis to a maximum of 1 file every 6 hours, I reduced the chance of re-sampling the same whale(s) over consecutive 6-hour periods. In this manner, I categorized vocalizations up to four times each day for days in which vocalizations occurred. To increase confidence of vocal category assignment, I analyzed humpback whale vocalizations in files immediately preceding and following the file of interest. In Fall 2015, where there was no gap (sleep mode) in the recorder's duty cycle, analysts could confirm humpback whale vocal behaviour using many consecutive files, while in Spring 2016, there was an inevitable data gap between recordings as the duty cycle included 8 min of sleep mode (Table 3.2). Phase 2 analysis was not carried out on data where the vocalization quality did not allow for confident classification of vocal categories.

When defining vocal categories, attention was placed on discerning vocalizations occurring in patterns or sequences from those lacking such structure. Vocal categories implemented here were largely based on those previously described in humpback whale acoustic literature (e.g. Cerchio and Dahlheim 2001, Au et al. 2006, Rekdahl et al. 2013). Six predominant vocal categories were identified and qualitatively assigned during vocal behaviour analysis: cries, cry sequences, non-patterned calls, grunt sequences, song fragments, and songs (see Table 3.3 for definitions, Figure 3.2 for exemplars). These can be further defined into the broader categories of non-song (cries, cry sequences, non-patterned calls, grunt sequences) and song vocalizations, though the placement of song fragments in this classic scheme is unclear. The temporal variation in humpback whale acoustic behaviour was visualized using bar plots of the proportional occurrence of each vocal category over 5-day periods.

Table 3.3. Definition of each vocal category.

Vocal Category	Definition
Cries	Long, tonal, often down-sweeping; occur alone or simultaneously with other cries.
Cry sequences	Repeated cries (4-37); beginning and ending often frequency modulated.
Non-patterned	Any call (e.g. moans, grunts, wops, purrs) not in a recognizable series or pattern.
Grunt sequences	≥3 grunts in sequence.
Song fragments	1 subphrase to 2+ themes not repeated.
Songs	≥3 themes repeated at least once (Frumhoff 1983, Cholewiak et al. 2013).

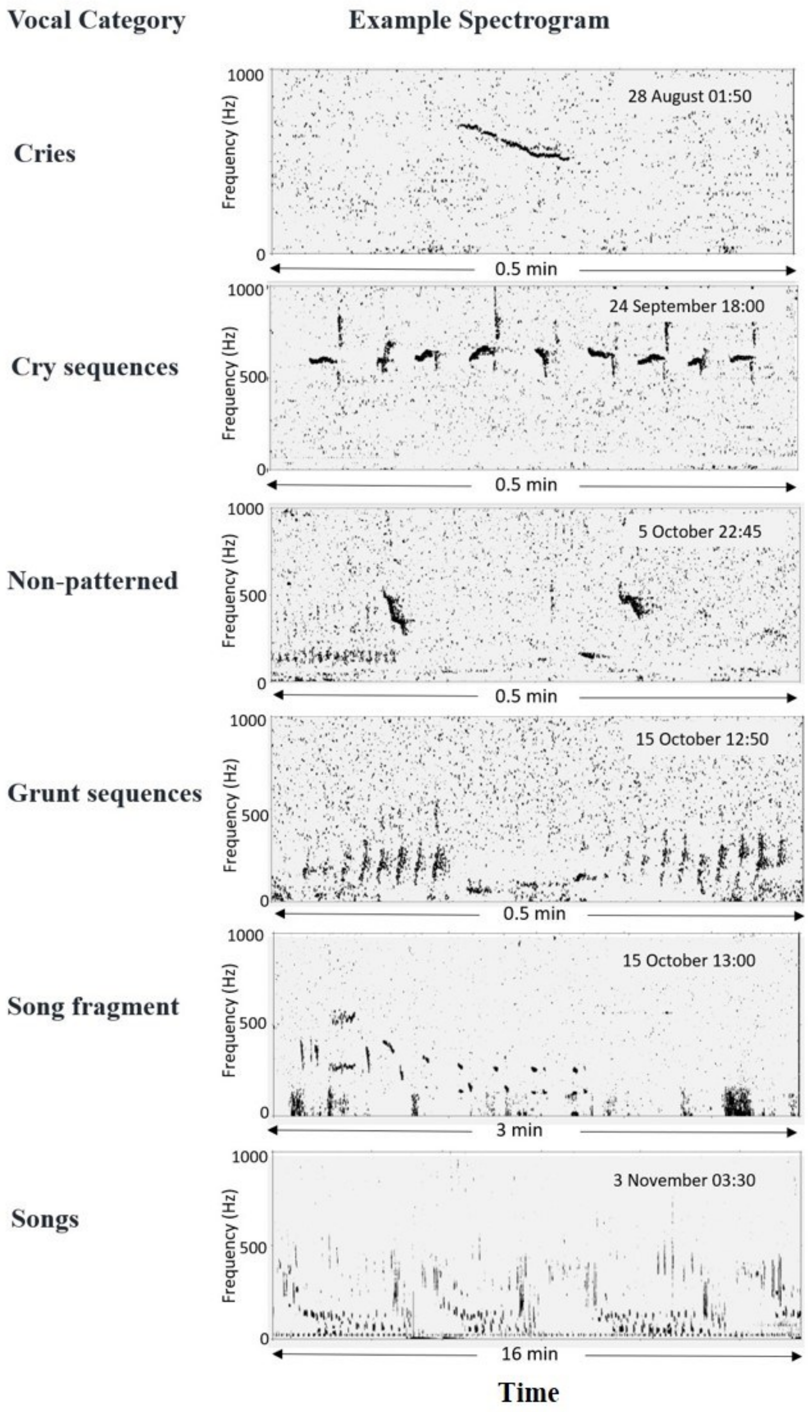

Figure 3.2. Example spectrograms (hamming window, frequency resolution: 2 Hz, frame length: 0.128 s, time step: 0.032 s) of each humpback whale vocal category.

The time-frequency domain characteristics of each non-song vocalization category were summarized. For each day, I selected the file with the highest vocalization SNR and then annotated every humpback whale non-song vocalization in the file. The duration and centroid frequency of each annotation was extracted and is summarized in Table 3.4. Duration was the difference in time between the start and end of annotations and centroid frequency was the point at which 50% of the energy was above and below a given frequency of an annotated vocalization.

Table 3.4 Number of annotations (Ann.), mean and standard deviation (SD) of vocalization duration, and mean and SD of vocalization centroid frequency for each non-song vocal category.

Vocal Category	**Ann.**	**Mean Duration ± SD (s)**	**Mean Centroid Frequency ± SD (Hz)**
Cries	629	4.6 ± 2.7	500.7 ± 85.2
Cry sequences	289	1.6 ± 0.4	578.7 ± 67.3
Non-patterned	972	1.2 ± 1.1	278.4 ± 174.7
Grunt sequences	455	0.5 ± 0.2	129.0 ± 56.9

Songs and song fragments were differentiated based on structure and complexity. Songs included 3 or more themes repeated at least once while song fragments were variable in nature with complexity and structure occurring on a continuum ranging from a single phrase or subphrase to a series of 2 or more themes not repeated in its entirety. In phase 3, I further categorized song-fragments depending on the level of song structure observed. First, I analyzed the most well defined, high SNR songs for the occurrence of different themes and phrases. I reviewed 8 songs from Fall 2015 and 4 from Spring 2016 to gain a representative library of themes and constituent phrases, for which a theme is defined as a sequence of stereotyped phrases of the same phrase type. This was challenging for the Spring 2016 data set because the whales were consistently chorusing, making it difficult to separate one song from another; however, the high quality of the songs analyzed coupled with the review of files containing chorusing provided us with high confidence that our understanding of themes and phrases was sufficient for song fragment analysis. Second, I re-reviewed the data identified as song fragments in phase 2 and, comparing it to established song themes and phrases, further categorized the vocalizations depending on the level of song structure observed into three increasing levels of complexity (Table 3.5).

Table 3.5 Levels of song fragments.

Level	Definition
Song fragment 1	1 subphrase or phrase.
Song fragment 2	1 theme.
Song fragment 3	2+ themes not repeated.

Our definition of song fragment did not require the fragment to eventually be incorporated into a song. Rather, a fragment composed of a stereotyped series of vocalizations repeated once (2 phrases) would be classified as a song fragment. The series must have some stereotyped variation (e.g., cannot be one vocalization type repeated such as a grunt or cry sequence). During analysis I noted which song fragments were observed in songs and which were not. All observed song fragments may eventually be incorporated into songs that were not recorded in the present data set (e.g., on the southern breeding grounds).

I performed a naïve matching test to ensure our protocol for differentiating between song and song fragments was repeatable. An acoustic analyst was provided our protocol, our library of themes, and all files from Fall 2015 containing either a song or song-fragment and instructed to classify each sequence into a theme category. The analyst’s results matched ours for 100% of files.

3.4.3 Diel analysis

An effort was made to explore possible diel patterns in vocal categories. The phase 2 vocal category analysis, with a maximum of 4 samples per day, resulted in an insufficient sample size for diel analysis on individual vocal categories. I instead used the results from the phase 1 occurrence analysis. I converted results from the phase 1 occurrence analysis into hourly presence/absence data and separated them into time frames per station. Every hour in a day where humpback vocalizations occurred was assigned to dawn (sun 12^{o} below the horizon to sunrise), light (sunrise to sunset), dusk (sunset to sun 12^{o} below horizon), or dark (sun is more than 12^{o} below horizon) where light period times (sunset, sunrise, nautical dusk, and nautical dawn) were calculated using Reda and Andreas (2004). For every day, I subtracted the proportion of hours containing humpback vocalizations in a 24-hour day from the proportion of hours with humpback vocalizations per light period in that day. Next, I calculated the average of these figures across the time frame of interest to determine the mean-adjusted hours with humpback vocalizations per light period. Through these calculations, I accounted for the change in light periods throughout the recording periods as well as the variation in hours with humpback vocalizations each day. I applied Welch's ANOVA to test the null hypothesis that the mean adjusted hours with humpback vocalizations were constant across diel light periods. Where Welch's was significant (P-value < 0.05), Tukey-Kramer multiple comparison tests were utilized to ascertain which light periods differed (Wiggins et al. 2005).

3.5 **RESULTS**

The phase 1 occurrence analysis revealed humpback whale acoustic presence from 27 August 2015 to 8 January 2016 in the Fall 2015 data set and from 3 April 2016 to 20 July 2016 in the Spring 2016 data set (Figure 3.3). For the phase 2 vocal behaviour analysis, 293 acoustic files from the Fall 2015 data set and 275 acoustic files from the Spring 2016 data set were selected for analysis based on having the highest SNR files within a 6-hour period. However, only vocalizations of sufficient quality could be included in the vocal behaviour analysis, and upon further examination of these files 238 were chosen to be included from the Fall 2015 data set and 175 were chosen to be included from the Spring 2016 data set. The fewer recordings analyzed from the Spring 2016 data set reflects a lower quality of vocalizations (e.g., lower SNR) compared to the Fall 2015 data set. The occurrence of vocal categories varied greatly between the two stations (Figures 3.4 and 3.5).

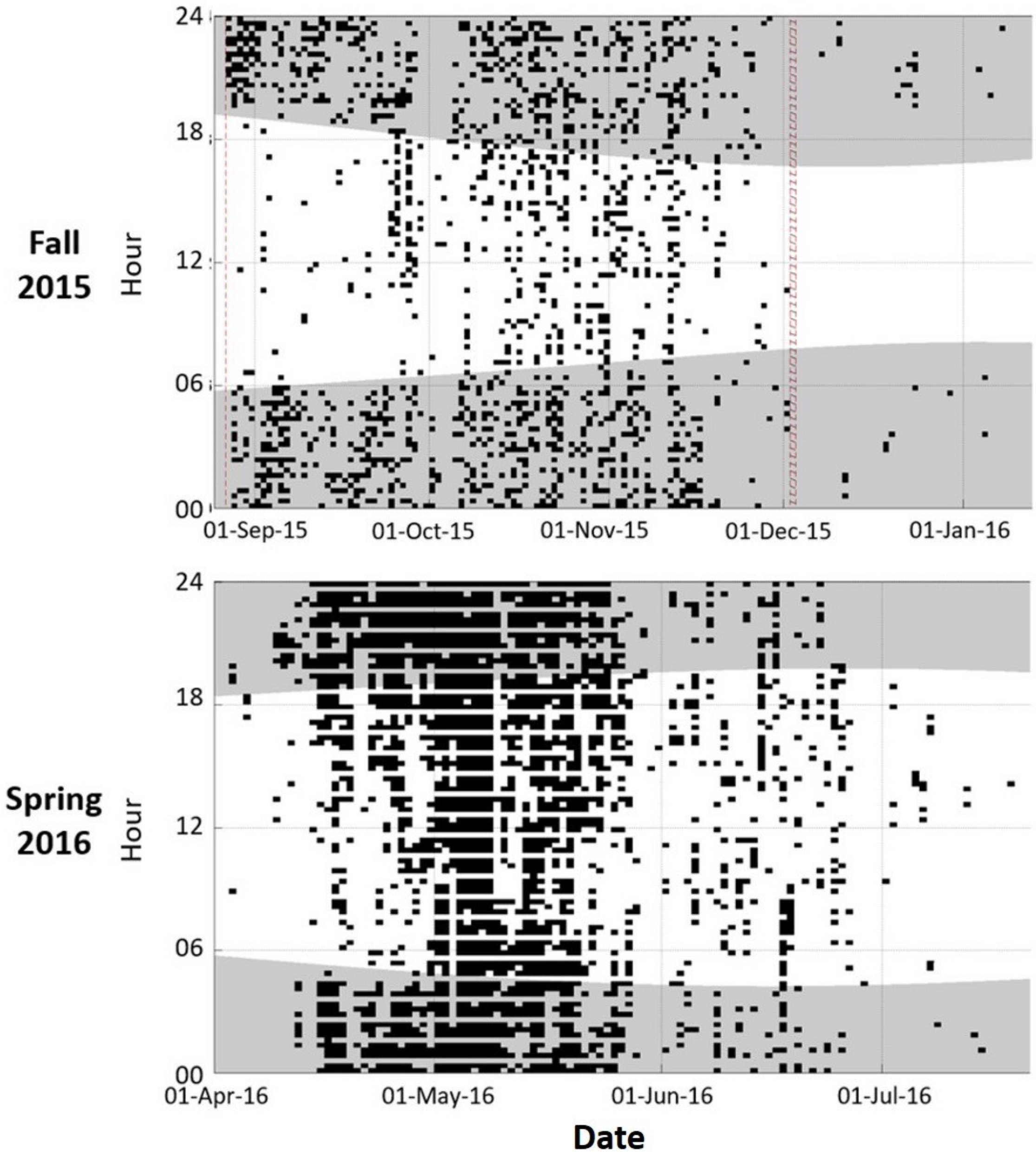

Figure 3.3. Daily and hourly occurrence of humpback whale vocalizations recorded in Fall 2015 (top) and Spring 2016 (bottom). Shaded areas indicate periods of darkness and red dashed lines indicate the deployment and retrieval dates where such dates overlap with the timeframe presented.

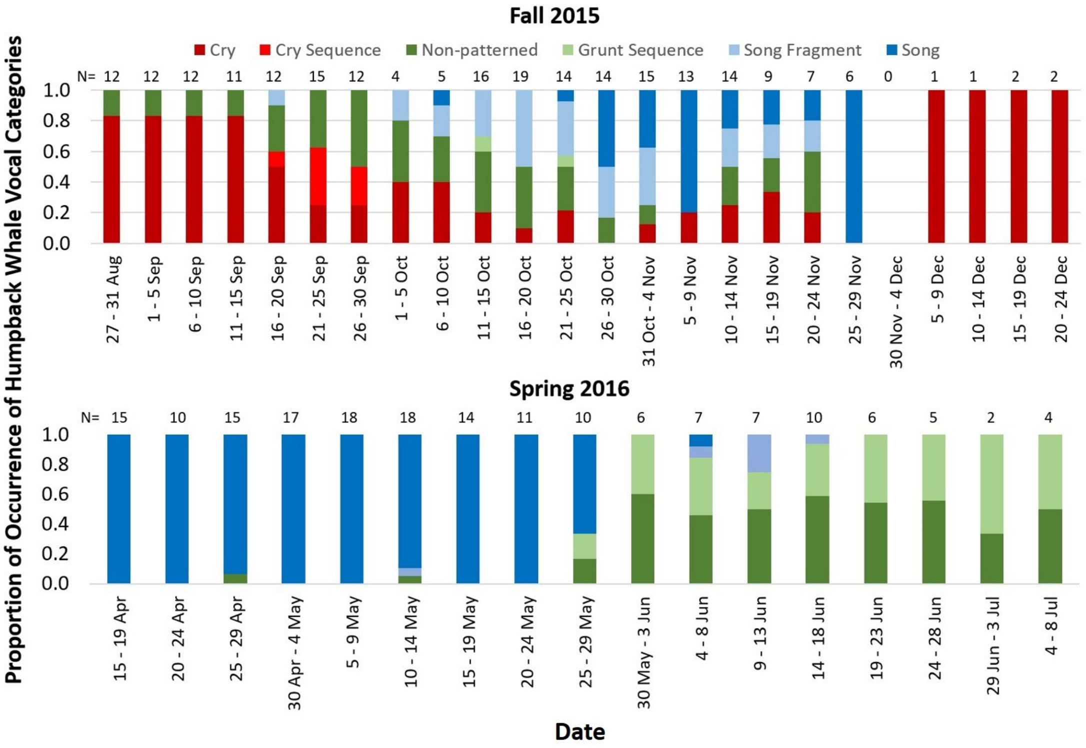

Figure 3.4. Proportional occurrence of humpback whale vocal categories over 5-day periods in Fall 2015 (top) and Spring 2016 (bottom) that were cries, cry sequences, non-patterned, grunt sequences, song fragments, or songs. The number of acoustic files analyzed in each timeframe are included (N) where acoustic files were 10.5 min in duration in Fall 2015 and 11.3 min in duration in Spring 2016.

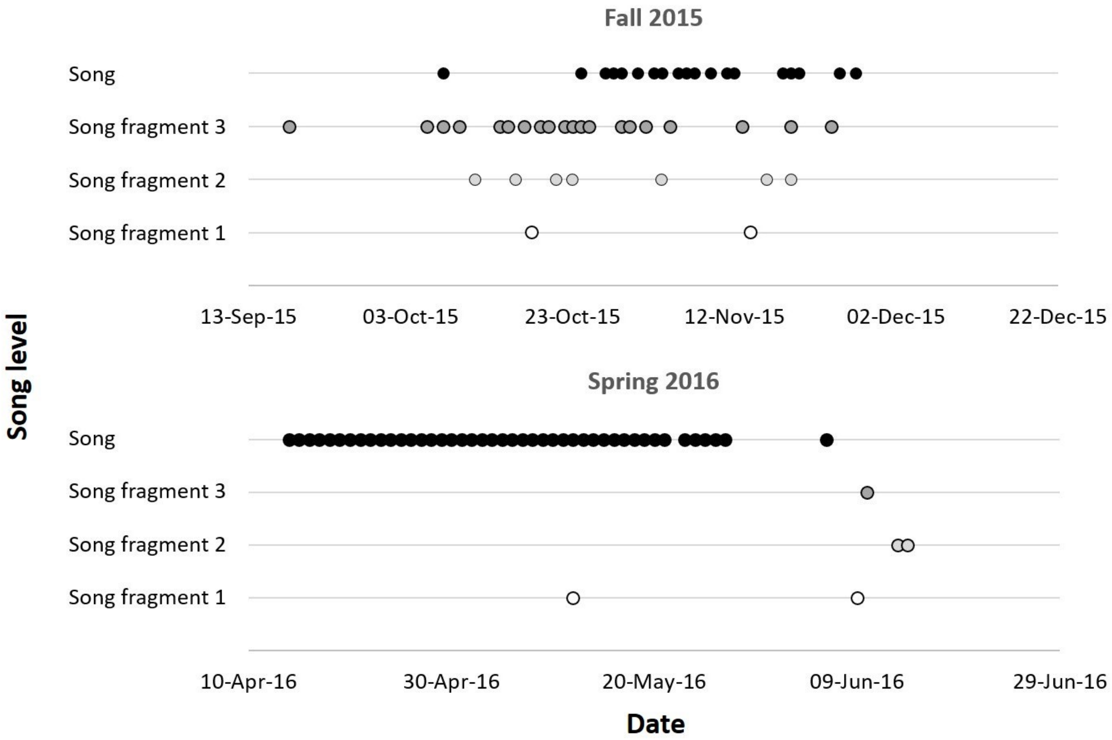

Figure 3.5. The occurrence of different levels of song fragments (1-3) and full song at the two stations.

3.5.1 Fall 2015 data set

During Fall 2015 in the Bay of Fundy, cries and non-patterned calls were present throughout the recording period with broadly overlapping distributions, while cry and grunt sequences displayed isolated temporal peaks, and song fragments and songs were found predominantly in the latter half of the fall (Figure 3.4). A clear progression throughout the season was noted: cries and non-patterned calls were the predominant vocalizations from 27 August to 25 October, with cries accounting for a greater proportion of occurrences early on. Song fragments were first recorded on 18 September and then not recorded again until 5 October, after which they became a consistently recorded vocalization through November. Complete songs were first recorded on 7

October, then were absent until 24 October, and occurred frequently between 27 October and 29 November (Figure 3.4). Six files analyzed in December contained only cries (Figure 3.4).

Complete song was preceded by song fragments: nineteen days passed between the first occurrence of song fragments and the first occurrence of songs. Song fragments with two or more unrepeated themes (level 3) were the most common song fragment type and the first observed in Fall 2015, occurring from 18 September to 19 November (Figure 3.5). Single themes (song fragment level 2) were first observed on 11 October and continued to 19 November. Phrases or subphrases on their own were observed only twice (Figure 3.5). Out of the 38 acoustic files containing song fragments, 37 had phrases/themes like those observed in songs (e.g. Figures 3.6 and 3.7), whereas 1 file had a level 1 song fragment composed of a phrase that occurred twice in the file.

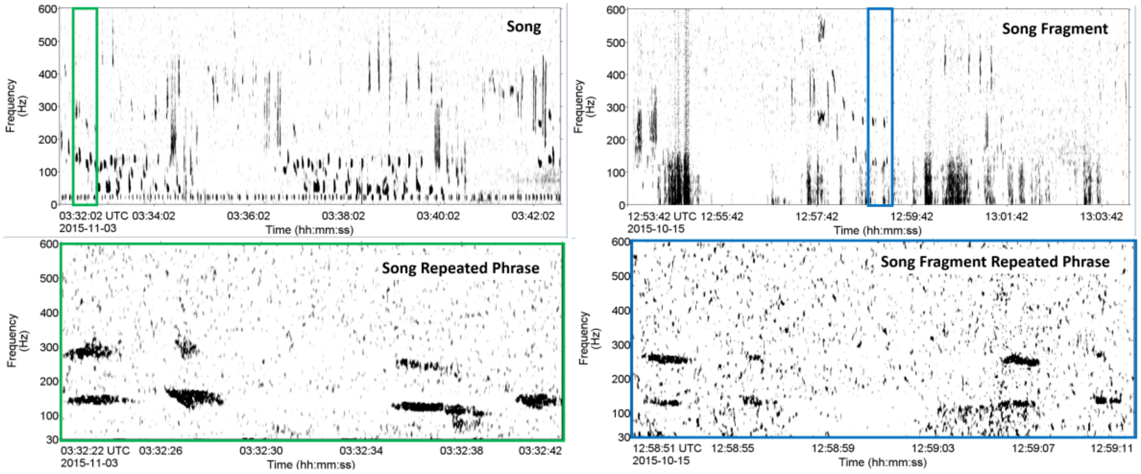

Figure 3.6. Spectrograms depicting examples of phrases observed in both a song (left; 3 November 2015) and a song fragment level 3 (right; 15 October 2015) in Fall 2015; lower panels represent details indicated within upper panels, illustrating the similarities between phrases found in songs and song fragment vocalizations (hamming window, frequency resolution: 2 Hz, frame length: 0.128 s, time step: 0.032 s).

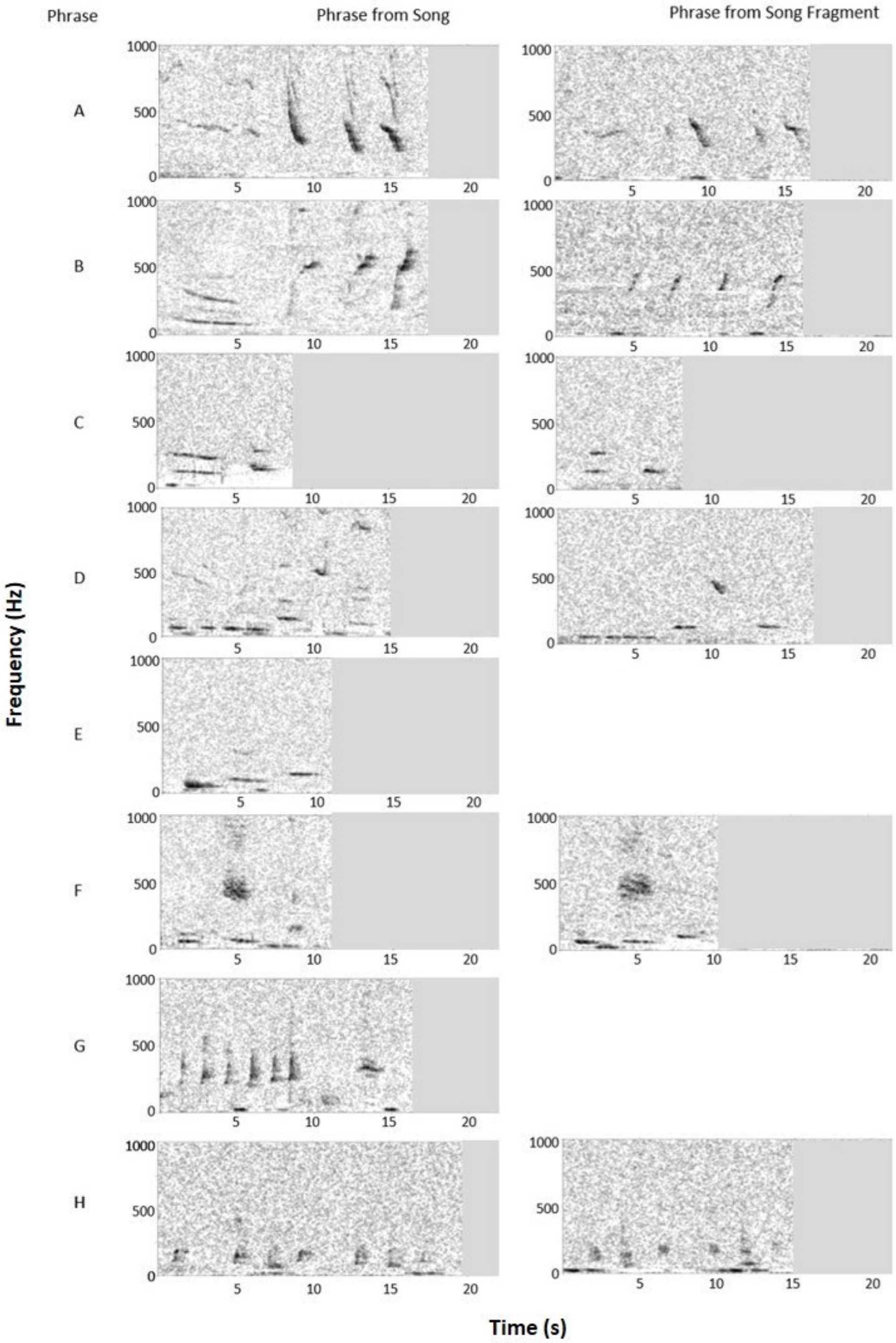

Figure 3.7 Spectrograms depicting phrases observed in songs (left) and song fragments (right) in Fall 2015 (hamming window, frequency resolution: 2 Hz, frame length: 0.128 s, time step: 0.032 s). Not all phrases from songs occurred in the song fragments analyzed. Fin whale 20 Hz vocalizations occur in many of the spectrograms.

3.5.2 Spring 2016 data set

In Spring 2016 off northeastern Nova Scotia, songs were the predominant vocal category from 16 Apr to 27 May (Figure 3.4). The remaining periods analyzed were dominated by non-patterned calls and grunt sequences. Song fragments were observed in 6 acoustic files, 5 of which occurred from 6 to 14 June after complete songs had ceased and contained phrases/themes similar to those observed in the complete songs. There were two instances of single phrases or subphrases (song fragment level 1; 12 May and 9 June), two instances of single themes (song fragment level 2; 13 and 14 June), and one instance of two or more unrepeated themes (song fragment level 3; 10 June; Figure 3.5).

The acoustic occurrence results suggest an abrupt change in acoustic behaviour in late May when humpback whale acoustic signal occurrence is drastically reduced (Figure 3.2). When coupled with the vocal behaviour results in which songs end on 27 May (apart from 6 Jun) and song fragments are limited in their occurrence, it can be inferred that the cessation of humpback whale singing off northeastern Nova Scotia in Spring 2016 was relatively abrupt in nature as compared to the song onset in the Bay of Fundy in Fall 2015 where song fragments occurred regularly prior to and during the period of song. Furthermore, in the Fall 2015 data set, non-song calls overlap greatly with the period when song and song fragments occur. This is different from Spring 2016, where song and non-song temporal distributions seldom overlap, such that non-song calls are rarely detected until song essentially ceases, though it is difficult to separate this observation from the unavoidable masking effects chorusing humpback whales have on other acoustic signals, particularly singular or non-patterned calls.

3.5.3 Diel results

Data were separated into 4 timeframes (2 in Fall 2015 and 2 in Spring 2016) chosen to correlate with periods when song and non-song vocalizations dominated (where I included song fragments in song). The results of the Tukey-Kramer multiple comparisons test revealed that when cries and cry sequences dominated, the mean adjusted hours with humpback vocalizations during light were significantly lower than dawn, dusk, and dark (Figure 3.8). In Spring 2016 when songs dominated, the mean adjusted hours with humpback vocalizations during dawn and light were significantly lower than dusk and dark (Figure 3.8). When song and song fragments dominated in Fall 2015, the mean adjusted hours with humpback vocalizations during dawn was significantly lower than dark. No significant differences between light periods were apparent in any time frames when non-patterned calls and grunt sequences dominated (Figure 3.8).

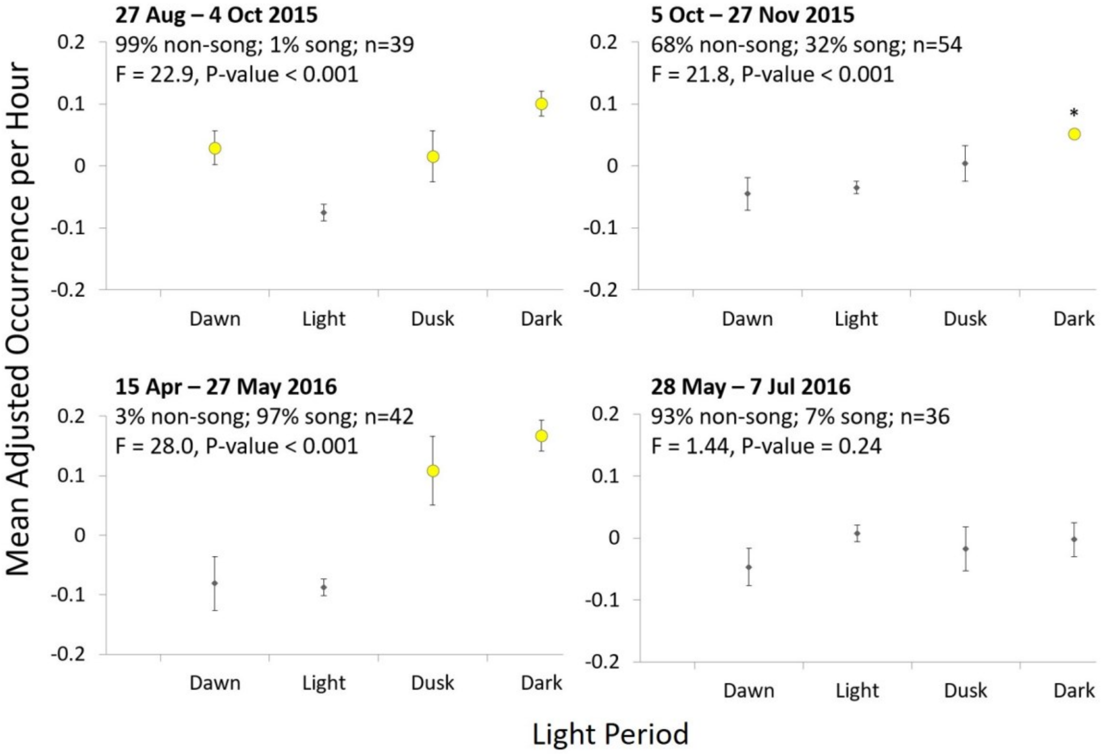

Figure 3.8. Mean adjusted humpback whale occurrence per hour for two periods in fall 2015 (top) and two periods in spring 2016 (bottom) with 95% confidence intervals in four light periods: dawn, light, dusk, and dark. Where non-song includes the vocal categories cry, cry sequences, non-patterned, and grunt sequences and song includes the vocal categories song and song fragment. Light period times were obtained from Reda and Andreas (2004). Results of Welch's test are included for each period (F and P-value) and Tukey-Kramer results are represented in colored means where different colors/sizes have significantly different values. *For 5 October to 27 November 2015, dark differed from dawn (P-value < 0.001) and light (P-value = 0.002), but not from dusk (P-value = 0.37).

3.6 DISCUSSION

Acoustic recordings from the fall of 2015 in the Bay of Fundy and the spring of 2016 off northeastern Nova Scotia captured the onset and cessation of humpback whale song production, respectively. Ideally, I would have sampled a fall and spring from the same location; however, apparent differences in residency or density of whales in these areas precluded doing so. While I had acoustic recordings both in spring 2016 in the Bay of Fundy and fall 2015 off northeastern Nova Scotia, humpback whale acoustic signals were either absent or minimal during these periods at these locations, suggesting low densities of whales, and thus did not allow for analysis of humpback whale vocalization during both periods at either location. Utilizing data from multiple sites allowed us to examine differences in the acoustic repertoire and vocal behaviour of humpback whales off eastern Canada in fall and spring, which would not have been possible from either site alone.

Vocalizations captured in the Bay of Fundy were likely produced by whales that spent weeks or months foraging in this productive feeding ground (Katona and Beard 1990). Indeed, Paquet et al. (1997) suggested around 80 animals frequent the region in summer and fall. It is unclear how humpback whales utilize the waters off northeast Nova Scotia, though the vocalizations captured in the spring of 2016 may have been produced by whales migrating to more northern feeding grounds off Newfoundland or in the Gulf of St. Lawrence (Katona and Beard 1990). Acoustic files selected for analysis in the spring were therefore more likely to be independent, sampling different individuals as they traversed the area, than in the Bay of Fundy where the same individuals are known to remain in the region for longer periods of time. These results do not indicate how any individual whale transitions its acoustic behaviour through time, but rather how the acoustic repertoire of the subset of a population transitions.

Some humpback whale vocalizations described here are indicative of certain specific behaviours or behavioural states. Non-patterned calls may be associated with social interactions and could be produced by males, females, or calves (Dunlop et al. 2008, Zoidis et al. 2008). Grunt sequences appear similar to social grunt trains described by Dunlop et al. (2008) that occur before groups merge. The lack of diel pattern during periods when both non-patterned and grunt sequence calls were predominant suggests that such social behaviour occurs throughout the 24-hour day. Indeed, the occurrence of these two vocal categories overlapped temporally both in the fall and spring data. The lack of non-patterned calls and grunt sequences in Spring 2016 when songs dominated may suggest that the majority of these animals may have been mature males, as they only moved onto social vocalizations after the cessation of song. Alternatively, other age and sex classes were present in Spring 2016, but their vocalizations were masked by singing or they were not acoustically active in April and May.

Until now, humpback whale acoustic behaviour related to foraging has only been described in a southeast Alaskan population where feeding vocalizations have been associated with coordinated foraging events on schooling herring (*Clupea pallasii*) (Jurasz and Jurasz 1979, Baker et al. 1985, D'Vincent et al. 1985, Cerchio and Dahlheim 2001). The cry sequences observed here in the Bay of Fundy match the feeding vocalizations of southeast Alaska and may similarly be linked to foraging. Grand Manan, an island located only 10 km from our recorder, has an active purse seine industry that targets aggregations of herring (*Clupea harengus*). Herring may aggregate seasonally in the region to spawn, as was historically reported (Bigelow and Schroeder 2002), or to feed. Grand Manan purse seine fishing occurred on 3, 21, 22, 23, 27, 28, and 29 September 2015 which closely aligns with our observations of cry sequences on 15, 21, 23-29 September and 14 October 2015 and further supports the Bay of Fundy as a feeding ground for humpback whales (Personal Communication, Rabindra Singh, Department of Fisheries and Oceans Canada). North Atlantic herring do not spawn in the spring, potentially explaining why cry sequences were absent from our spring acoustic data. Un-sequenced cries matching those described here have also been described in southeast Alaska (Cerchio and Dahlheim 2001) and British Columbia (personal observation), but it remains unclear if they are related to herring feeding in the same manner as cry sequences. Some instances of un-sequenced cries throughout this sample may be more appropriately grouped functionally with social acoustic behaviours (non-patterned calls and grunt sequences) which would explain the broadly overlapping distributions of cries and non-patterned calls in October and November. Whereas there was no diel variation when non-song "social" calls (non-patterned calls and grunt sequences) were predominant, a significant diel variation was found when cries and cry sequences dominated in early Fall 2015. These vocal categories may be related to foraging as many humpback prey species including herring and krill are known to undertake diel vertical movements (Blaxter and Parrish 1965, Simard et al. 1986).

The characterization of song fragments described here have not been previously defined. This vocal behaviour likely existed in other feeding ground and migratory route song data sets (Baker et al. 1985, Mattila et al. 1987, McSweeney et al. 1989, Clapham and Mattila 1990, Cato 1991, Helweg et al. 1998, Norris et al. 1999, Charif et al. 2001, Clark and Clapham 2004, Clark and Gagnon 2004, Dunlop et al. 2007, Noad and Cato 2007, Vu et al. 2012, Garland et al. 2013a, Stanistreet et al. 2013, Magnúsdóttir et al. 2014, Magnúsdóttir et al. 2015) and some authors have made observations reflecting such (e.g. Stimpert et al. 2012, Rekdahl et al. 2013, Kowarski et al. 2017). Indeed, McSweeney et al. (1989) allocated the term "partial songs" to three recordings from Alaska in the fall of 1979 and "song fragments" have been observed off Maine in the spring of 1980 (Mattila et al. 1987), but these authors did not categorize or describe the structural details of these vocalizations, or place their occurrence in the larger context of humpback vocal behaviour.

A number of explanations for high latitude humpback whale singing have been proposed (Cato et al. 2001, Clark and Clapham 2004, Stimpert et al. 2012, Garland et al. 2013a, Herman et al. 2013), three of which may lead one to expect behaviour reflective of our song fragment category: males are practicing (Clark and Clapham 2004), immature males are learning (Herman et al. 2013), and it's a hormone induced behaviour (Cato et al. 2001). Males may benefit from practicing singing in the form of song fragments before engaging in active mating behaviours, which is the ultimate goal. By only singing parts of songs, males may become proficient in their skill while continuing to allocate time and energy to foraging and socializing prior to undertaking an arduous migration. It seems these behaviours are not necessarily independent as Stimpert et al. (2012) recorded song in the presence of feeding lunges on a high latitude feeding ground. Although, if males were to produce song fragments for the sake of practice, we might expect to see the behaviour throughout the year, an observation yet to be reported in the literature.

Alternatively, song fragments may be produced by immature males learning to sing for the first time, a behaviour well described in juvenile songbirds (Eales 1985). This concept is supported by the greatly reduced occurrence of song fragments in the spring as the young males have had a full season to become proficient in singing. However, if we were observing juveniles learning a song from mature males, we would expect to see full songs prior to song fragments in the fall, so this hypothesis on its own seems unlikely, though such behaviour may have occurred beyond the range of our recorders.

Perhaps the most compelling explanation for the existence and timing of song fragment vocal behaviour is that there are physiological parameters that determine when animals produce complete songs. Such was found to be the case in several songbird species where brain nuclei have been identified that influence song production and nuclei size is associated with seasonal testosterone levels (e.g. Nottebohm et al. 1986, Kirn et al. 1989, Smith et al. 1997). Nottebohm et al. (1986) found that when young male canaries first learn to sing, there is a period of subsong as the song develops which coincides with song nuclei growth. Once a full song is produced, the nuclei are adult sized and remain constant until the end of the breeding season when song nuclei diminish to the size expected of a bird only 3 to 4 months old. The following breeding season, the bird once again goes through a period of subsong as the song nuclei enlarge, though it has already sung a complete song the previous year (Nottebohm et al. 1986). I propose that the song fragments in this study are analogous with the subsong observed in oscine birds; thus, humpback whales may similarly have a neurological song control system influenced by testosterone levels. Seasonal fluctuation would result in a period of song fragment behaviour in the fall before the neurological control system attains a state required for full song production. Cates et al. (2019) concluded that male humpback whale testosterone levels peak in the winter, are lowest in the summer, and increase and decrease through the fall and spring, respectively, so it is reasonable to expect coincident fluctuations in singing behaviour. One may expect a gradually increasing level of complexity in song fragments through the fall in support of this hypothesis, which was not observed here. Indeed, I observed a spectrum of complexity, but it did not necessarily occur temporally. Such detail may only be observable at an individual level, rather than the population level observed here. Alternatively, whales may go through a period of variable song fragment complexity as their hormones increase.

I observed a brief period of subsong/song fragment behaviour in the spring that, if our hypothesis is correct, is associated with reduction in testosterone below a certain threshold. Interestingly, the spring transition had a seemingly more abrupt cessation to singing with minimal song fragments when compared to the fall. Further spring data sets are required to confirm whether the spring transition is truly abrupt as singing males may have continued to produce songs or song fragments and transitioned gradually, but simply moved away from the area detectable by our recorder.

Both in the fall and spring, during weeks when song and song fragments occurred, humpback whale vocalizations occurred more at night than in the day. Given that the predominant source of regular ambient noise fluctuations in the Bay of Fundy is tide related (Delarue et al. 2016) and the soundscape off Nova Scotia does not follow any obvious diel patterns (Delarue et al. 2018), it is reasonable to surmise that the diel trends observed here were not simply artifacts of diel masking events, but are truly indicative of humpback whale behaviour. Similar trends were observed in singing humpback whales offshore Nova Scotia in the winter (Kowarski et al. 2018) and on breeding grounds in Hawaii (Au et al. 2000), Mexico (Cholewiak 2008), Brazil (Sousa-Lima and Clark 2008), and Angola (Cerchio et al. 2014) suggesting that this diel pattern is a characteristic of the acoustic behaviour and is not related to season, location, or masking effects. It has been suggested that the diel pattern reflects a switch in primary mating strategies where selection pressures have resulted in males utilizing physical competition in the day and acoustic sexual advertisement at night when visual displays would be less effective (Au et al. 2000).

3.7 CONCLUSIONS

In describing humpback whale acoustic behaviour in the fall and spring, I have provided insight into song initiation, that includes a period of song fragment production, and cessation, that seems more abrupt with minimal song fragments. Furthermore, I presented the first evidence of humpback whale feeding calls in a population outside of southeast Alaska and described how diel acoustic patterns vary over time. I discuss two potential proximate benefits and outcomes of high latitude song fragment behaviour: for practice and for learning of immature males. I argue that these benefits alone cannot explain our observations, and thus hypothesize that the ultimate trigger of singing onset and cessation can be explained by physiological changes (e.g., hormone levels and neurological processes) that take place prior to migration outside of the breeding grounds. Sexual selective forces have shaped much of the mating behaviour of humpback whales, and consequently the regulatory mechanisms that govern seasonal behaviour. To further explore and develop our hypothesis, this research needs to be expanded both spatially and temporally with an investigation into environmental factors that may correlate with song behaviour and trigger physiological changes as is seen in songbirds (Meitzen et al. 2007). Furthermore, acoustic tag studies of individual whales across sexes and age groups during the fall and spring season to capture individual whale acoustic transitions coupled with seasonal hormone analysis would be extremely illuminating.

3.8 ACKNOWLEDGEMENTS

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CHAPTER 4 WHERE, WHEN, AND WHY DO WESTERN NORTH ATLANTIC HUMPBACK WHALES BEGIN TO SING?

4.1 PUBLICATION STATUS

As of 5 October 2020, this chapter is under review in Bioacoustics.

4.2 ABSTRACT

At the onset of the winter breeding season, male humpback whales begin a prominent breeding behaviour, singing. Early songs are produced on summer feeding grounds prior to migration, but little is known about the proximate cues for the initiation of this behaviour, nor where or when it begins. I document the phenology of humpback whale singing along the western North Atlantic coast ranging from Newfoundland and Labrador, Canada to Massachusetts, U.S.A. through the fall-winter of 2015-16 (seven stations) and 2016-17 (three stations). Acoustic data from static recorders were categorized as containing humpback whale non-song calls, song fragments, or full songs. Singing onset was tested for correlations with latitude, temperature, photoperiod, sea surface pressure, and wind speed. First heard in September, singing occurred throughout the fall-winter, but was not regular until October. I found evidence that singing onset is correlated to latitude ($r = 0.61$, $p = 0.08$), photoperiod ($r = -0.66$, $p = 0.06$), and sea surface temperature ($r = -0.66$, $p = 0.05$). Reliable environmental cues, such as photoperiod, may produce a heritable physiological response, resulting in whales acquiring the capacity and motivation to sing, with the subsequent timing and nature of song production influenced by other factors.

4.3 INTRODUCTION

Seasonal breeding is common throughout the animal kingdom. The timing of behavioural and physiological shifts to initiate mating are species-specific, and often population-specific, typically functioning to maximize reproductive potential. Environmental cues can influence the onset of breeding behaviours (e.g., Bubenik et al. 1982, Sharp 1993, Perret and Aujard 2001, Oseen and Wassersug 2002). Social interactions, temperature, rainfall, and food can impact mating behaviour timing, with photoperiod often identified as the determinant proximate factor (Lofts and Murton 1968, Ball 1993, Inai et al. 2003, Rosa and Bryant 2003). Acoustic signals produced by males, presumably to advertise fitness and attract mates, have received attention as they can be energetically expensive or high risk (e.g., predator or competitor attraction). From insects, to frogs, birds, fish and mammals, seasonal mating vocalizations are heard globally. Here, I investigate the timing of male singing for one of the more well-studied seasonal singers in the ocean, the humpback whale (*Megaptera novaeangliae*).

Humpback whales are medium-sized mysticete whales distributed globally that make large scale seasonal migrations from the high-latitudes in the summer to feed to low-latitudes in the winter to mate and give birth, with the exception of the non-migratory Arabian Sea population (Kellogg 1929, Bettridge et al. 2015). As with many animals, numerous physiological and behavioural changes are observed in male humpback whales at the onset of the breeding season in the fall, beyond undertaking migration. Their testes size (Chittleborough 1955), testosterone levels (Cates et al. 2019), and aggressive male-male interactions (Tyack and Whitehead 1983) all increase with the onset of the breeding season.

Humpback whale vocalizations vary with season and have been most generally categorized as song or non-song. Non-song calls seem to be produced by males, females, adults, and calves throughout the year. A range of non-song vocalizations have been described and are believed to be related to social and feeding behaviours (Cerchio and Dahlheim 2001, Dunlop et al. 2008, Zoidis et al. 2008, Videsen et al. 2017). Non-song calls are simple, in that they are not organized into complex patterns (Rekdahl et al. 2017). In contrast to non-song calls, songs are produced only by males in association with the breeding season (Payne and McVay 1971, Winn and Winn 1978). Songs have complex patterns and are hierarchical in structure with discrete units forming phrases, that repeat to create themes, which together make up a song (Payne and McVay 1971, Payne et al. 1983). Songs are repeated to form song sessions that can continue for hours. While the ultimate reason for singing is successful reproduction, several proximate functions have been proposed, including to attract females (Winn and Winn 1978, Tyack 1981, Herman 2017), stimulate receptivity in females (Baker and Herman 1984, Smith et al. 2008), form male coalitions (Darling et al. 2006), establish dominance (Darling and Bérubé 2001), and/or mediate competitive interactions between males as part of a lek mating system (Clapham 1996, Cerchio et al. 2001, Cholewiak et al. 2018). Male song is predominant on warm breeding grounds, but it also occurs on the feeding grounds pre- and post- migration (Mattila et al. 1987, McSweeney et al. 1989, Magnúsdóttir et al. 2014, Kowarski et al. 2018, Kowarski et al. 2019). There is some evidence that humpback whales occur at high latitudes throughout the year, suggesting that perhaps not all individuals migrate, or perhaps that not all individuals migrate at the same time (Pomilla et al. 2014).

In the western Atlantic a population of humpback whales, thought to be distinct from their eastern Atlantic counterparts (Stevick et al. 2006), migrate between their summer feeding grounds that include the waters off eastern Canada and the U.S.A. and their winter breeding grounds of the Caribbean (Whitehead and Moore 1982, Martin et al. 1984, Katona and Beard 1990, Palsbøll et al. 1997, Smith et al. 1999, Jann et al. 2003). In the fall and winter, humpback whale songs have been recorded on known western North Atlantic feeding grounds including the Bay of Fundy, Canada, and the Stellwagen Bank National Marine Sanctuary, U.S.A., as well as in the offshore Gully submarine canyon and eastern Scotian Slope of Nova Scotia (Vu et al. 2012, Stanistreet et al. 2013, Kowarski et al. 2018, Kowarski et al. 2019). Kowarski et al. (2019) described the period of song onset in the fall in the Bay of Fundy and defined two categories of singing. The first was 'song fragments' which occurred during the early months of song onset and ranged from one phrase or subphrase to two or more themes that are not repeated. The second was 'songs' or 'full songs' which began later in the season and were defined as three or more themes that are repeated at least once, similar to the classic definitions of song (Frumhoff 1983, Cholewiak et al. 2013).

Though song onset has been described at one location in the western North Atlantic (Kowarski et al. 2019), it is unclear if the patterns observed were representative of typical song onset in other areas or how the onset of singing in the fall (autumn) occurs over larger spatial and temporal scales. Despite this, it is not known when or where seasonal song onset first occurs in the western North Atlantic nor whether it is driven by any proximate cues as has been described for many land animals (e.g., Ball 1993, Meitzen et al. 2007). Here I investigate acoustic recordings collected from static long-term recorders ranging from Labrador, Canada to Massachusetts, U.S.A. over two consecutive fall and winter seasons. I aim to provide a broad scale picture of humpback whale acoustic behaviour during this transitional period and describe where and when humpback whale singing begins. I investigate whether cues such as latitude, temperature, or photoperiod are correlated with the seasonal change in acoustic behaviour. By investigating the onset of singing, we gain further insight into humpback whale song function and shed light on connections between the acoustic behaviour of these animals and their environments.

4.4 METHODS

4.4.1 Data collection

Passive acoustic monitoring (PAM) data was collected from eight locations (stations) on the seafloor that spanned 10.9° of latitude, ranging from Newfoundland and Labrador, Canada to Massachusetts, U.S.A from the years 2015-2017 (Figure 4.1 and Table 4.1). Data were selected to be included in the present analysis where previous work (e.g. Delarue et al. 2018, Kowarski et al. 2019) found the recordings captured humpback whale vocalizations in the fall. This was the case for seven stations (1-3 and 5-8) in fall 2015 to winter 2016 (2015-16) and three stations (4, 5, and 7) in fall 2016 to winter 2017 (2016-17) (Table 4.1).

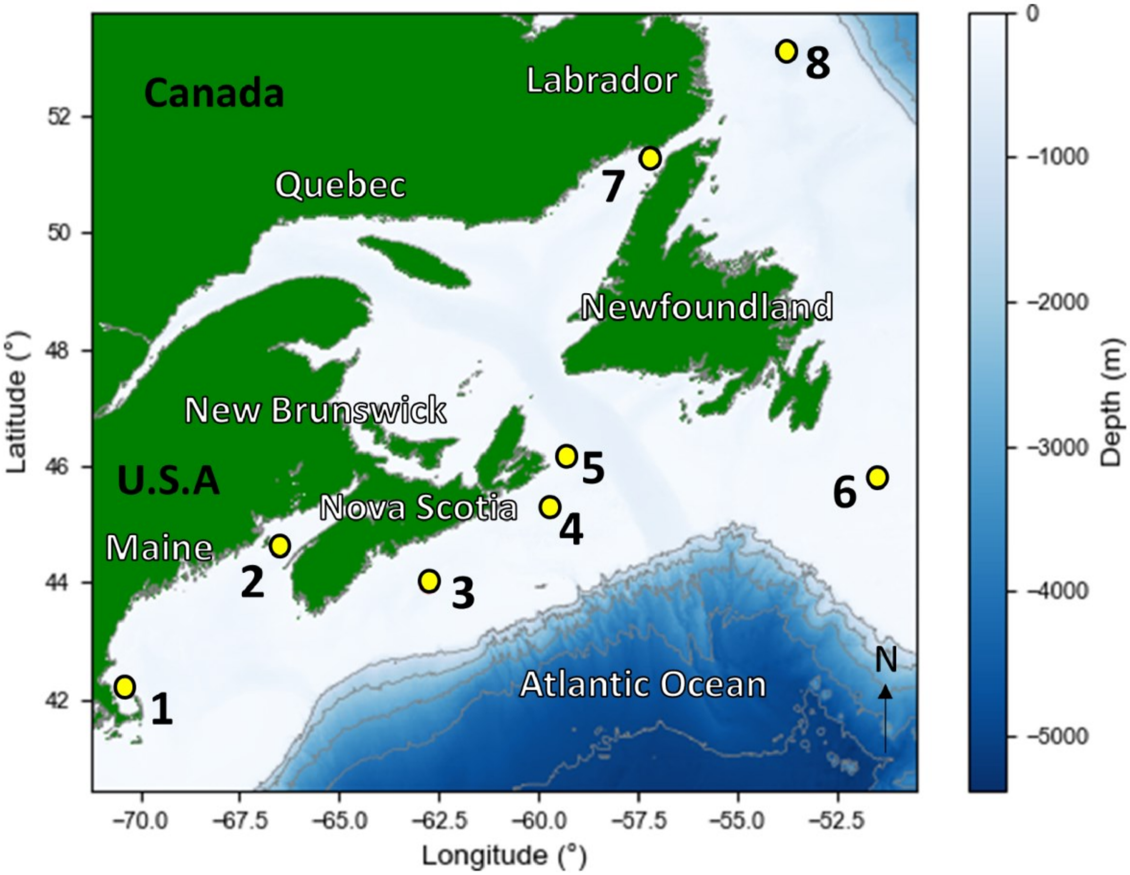

Figure 4.1. Location of eight recording stations located off eastern Canada (2-8) and the United States of America (1).

Table 4.1. Region, timeframe analyzed, deployment and retrieval dates, location, and water depth for the eight recording stations (Stn).

Stn	Region	Year(s) analyzed (1 Sep-31 Jan)	Deployed	Retrieved	Latitude (N)	Longitude (W)	Water Depth (m)
1	**Massachusetts Bay**	2015-16	14 Sep 2015	20 Feb 2016	42° 7.8’	-70° 32.0’	26
2	**Bay of Fundy**	2015-16	27 Aug 2015	1 Dec 2015	44° 33.5'	-66° 20.0'	151
			3 Dec 2015	28 Apr 2016	44° 33.8'	-66° 20.2'	148
3	**Emerald Basin**	2015-16	24 May 2015	20 Apr 2016	43° 36.5’	-62° 52.1’	200
4	**Cape Breton South**	2016-17	3 Nov 2015	21 July 2016	45° 25.8'	-59° 46.3’	123
5	**St Ann’s Bank**	2015-16	16 June 2015	1 May 2016	46° 10.1’	-59° 8.7’	74
		2016-17	23 Sep 2016	29 Oct 2017	46° 0.1’	-59° 8.5’	100
6	**Grand Banks**	2015-16	23 Aug 2015	13 Oct 2015	45° 42.0’	-51° 14.0’	78
			13 Oct 2015	19 Jul 2016	45° 42.1’	-51° 13.9’	80
7	**Strait of Belle Isle**	2015-16	3 Aug 2015	3 Nov 2015	51° 16.1’	-57° 32.3’	121
			3 Nov 2015	5 Jul 2016	51° 16.1’	-57° 32.1’	110
		2016-17	10 Jul 2016	11 Jul 2017	51° 16.6’	-57° 32.1’	110
8	**Labrador East**	2015-16	4 Aug 2015	14 Jul 2016	53° 0.9’	-53° 27.6’	582

Recordings were collected as part of four different projects coordinated by three different organizations resulting in a range of devices utilized and recording schedules applied that included both low sampling rates (2 – 16 kHz) and high sampling rates (250 – 375 kHz) (detailed recording schedules provided in Table 4.2). Data from stations 4, 6, 7, and 8 were collected as part of JASCO Applied Sciences (JASCO) Environmental Science Research Fund (ESRF) program, dedicated to describing the soundscape of the waters off eastern Canada, including the occurrence of vocalizing marine mammals (Delarue et al. 2018). Stations 3 and 5 were part of the Department of Fisheries and Oceans Canada Maritimes Region ongoing acoustic program to monitor marine mammal occurrence on the Scotian Shelf and used the same recording scheme as the ESRF data set. I previously analyzed the data at station 2 (see 2015 fall in Kowarski et al. 2019) that were supplied by JASCO. The Passive Acoustic research Group of the Northeast Fisheries Science Center (NEFSC) of the National Oceanic and Atmospheric Administration (NOAA) provided the data for station 1 which was originally deployed as part of a larger array, primarily aimed at tracking North Atlantic right whales (*Eubalaena glacialis*). Despite the range of data sources, all recordings were sufficient in duration (10 min cycles to continuous) and sampling frequency (2 to 16 Hz during low frequency cycle) to adequately capture the vocalizations of humpback whales for the purpose of the present study (Table 4.2).

Table 4.2. Recording equipment specifications and recording schedule for the eight stations.

	Station(s)		
	1	**2**	**3-8**
Recorder type	MARU[a]	AMAR[b]	AMAR[b]
Location of recorder	~2m above seafloor	On seafloor	20m above seafloor
Hydrophone	HTI-94-SSQ omnidirectional (HTI, Inc.)	M36-V35dB omnidirectional (GeoSpectrum Technologies Inc.)	HTI-99 omnidirectional (HTI, Inc.)
Hydrophone sensitivity (dB re 1 V/µPa)	-198	−165 ± 3	−165 ± 3
Bit depth	16 bit	24 bit	24 bit
Gain	6 dB	6 dB	6 dB
Duty cycle (min)	None	11.5	20
High frequency sampling rate (kHz)	NA	375	250
High frequency duration (min)	NA	1	1
Low frequency sampling rate (kHz)	2	16	8
Low frequency duration (min)	Continuous (15 min recordings)	10.5	11.3
Sleep duration (min)	NA	NA	7.7

[a]Marine Acoustic Recording Unit (Cornell); [b]Autonomous Multichannel Acoustic Recorder (JASCO)

4.4.2 Acoustic analysis

Acoustic data analysis was undertaken on recordings from 1 September 2015 to 31 January 2016 (2015-16; stations 1-3 and 5-8) and 1 September 2016 to 31 January 2017 (2016-17; stations 4, 5, and 7) (Table 4.1). Analysis occurred in two phases, following the protocol described in detail in Kowarski et al. (2019) and summarized here.

In phase 1, humpback whale acoustic occurrence was determined by the systematic review of a portion of data by an experienced analyst using PAMlab software (JASCO). Samples of data were extracted from the central temporal period of the low-frequency recording files (e.g., the middle 60 s of every 8 kHz file was extracted for stations 3-8 resulting in 72 samples 20 min apart each day; Table 4.3). The manual review of these samples resulted in the analysis of 1.2 hr per day to determine humpback whale acoustic occurrence (Table 4.3). By regularly and frequently reviewing short samples, I improved my chances of detecting humpback whale vocalizations, especially their long-duration songs, in comparison to the review of fewer, longer samples (Thomisch et al. 2015). Slight variation in sample selection across data sets was necessary due to differences in recording schedules (Tables 4.2 and 4.3).

Table 4.3. Description of samples of acoustic data systematically selected for manual review to determine humpback whale acoustic occurrence.

Station	Sample duration	Sample selection	Duration between samples	Samples per day	Duration analysed per day
1	90 sec	Center every other file	30 min	48	1.2 hr
2	70 sec	Center every other file	23 min	62	1.2 hr
3-8	60 sec	Center every file	20 min	72	1.2 hr

In phase 2, humpback whale acoustic behaviour was categorized as non-song, song fragment, or full song as per the definitions in Kowarski et al. (2019). The file from phase 1 with the highest SNR vocalization for each six-hour period (00:00-06:00, 06:00-12:00, 12:00-18:00, and 18:00-00:00) was analyzed to assign vocal categories to that period. By sampling across different six-hour periods I strived to find a balance between achieving results at a fine scale while reducing the chance of continually resampling the same individual; however, it is expected that the same vocalizing animal was occasionally sampled in consecutive timeframes. Multiple vocal categories could be assigned to the same acoustic file. For example, non-song and full song could be identified within the same timeframe where the analyst either identified signals outside of the pattern of the song or at a different SNR. When multiple songs occurred simultaneously, it became difficult to identify coinciding non-songs, thus the analysis was biased towards under-identifying non-songs. In the duty cycled data, where the recorders regularly entered sleep mode, it was at times challenging to differentiate song fragments from full songs. Where two or more complete song cycles occurred within one file, the file was categorized as full song. Where the song was so long that two or more full cycles could not be observed within a single file, the analyst would expand analysis to the preceding and following file. If either also had singing, it was assumed the behaviour continued through any periods without recordings and were categorized as full song. Where the adjacent files did not have singing, the vocalizations were categorized as song fragment. Any files with vocalizations too low in SNR to confidently discern a vocal category were categorized as unknown. The vocal categories assigned to each six-hour period of each recording day were plotted for all datasets. A naïve matching test performed on station 2 in Kowarski et al. (2019) revealed that this method of separating humpback whale vocalizations into categories is repeatable with a match rate of 100% between two analysts.

4.4.3 Defining song onset

Defining the onset of humpback whale singing behaviour in the fall required some consideration given the inherent limitations of PAM data. I could not be certain when the first song occurred in that region (e.g., the whale might not have been within range of a recorder), and it was difficult to discriminate song fragments from full songs where data were not recorded continuously. Therefore, for each of the ten data sets (seven in 2015-16 and three in 2016-17) I had four definitions of song onset:

1. The first day singing was confirmed
2. The first day singing became regular
3. The first day full song was confirmed
4. The first day full songs became regular.

For this analysis, I considered singing as any type of song behaviour (both song fragments or full song) and 'regular' is the first day of five consecutive days with humpback whale full songs or singing present (where days lacking any humpback whale vocalizations were excluded when counting consecutive days). By investigating singing (vs just presence of full songs), any inaccuracies in our interpretation of song fragments vs full song are irrelevant. Therefore, singing onset (first occurrence and regular) analysis is considered more sensitive and is the focus of the Results. Full song onset (first occurrence or regular) analysis, as a more conservative approach, can be found in APPENDIX B.

4.4.4 Environmental variable analysis

To investigate correlations between the onset of humpback whale singing behaviour in the fall and environmental variables, data were acquired using Environmental Data Management software (EDM; JASCO; python based) that sourced NOAA's griddap server. Variables included in this analysis were chosen because they were accessible, had previously been found effective in humpback whale habitat suitability models (e.g., Bombosch et al. 2014), and/or had previously been associated with the onset of singing in other species (e.g., Lofts and Murton 1968, Rojansky et al. 1992). Chlorophyll A (CHLA) concentration (mg/m^3) was fed by the National Aeronautics and Space

Administration (NASA) at a daily resolution of 1/24th degree. Wind speed (m/s; 10 m above sea level) and sea surface pressure (kPa; SSP) were supplied by the Fleet Numerical Meteorology and Oceanography Center (FNMOC) at a six-hour resolution of ½ degree. Sea surface temperature (°C; SST) was provided by NASA, providing an average daily SST at 1/100th degree. All data were compiled and averaged daily. SSP and wind speed were additionally averaged over two-week periods to account for the large variations in these variables that can occur between days. Day length for each day of recording days was sourced from Ark software (JASCO) where Ark uses an algorithm sourced from Blanco-Muriel et al. (2001) and was calculated as the number of hours between civil dawn and civil dusk, a definition used in previous studies investigating photoperiod (e.g., Bauchinger and Klaassen 2005).

The environmental variables (CHLA, wind speed, SST, SSP, latitude, day length) at each station were strongly correlated with each other and with day of year. Therefore, values were taken not from the day of singing onset, but rather the average day of singing onset across recording sites. This was done both as the average of each year separately (see Results) and as average across both years (see APPENDIX B). Each variable was examined using Pearson's pairwise correlation analysis (R-studio Version 1.2.5019) to see how the value of the variable in question on the average day of singing onset was correlated with the day of singing onset over the ten data sets. The variable value applied was the daily average (on the average day of singing onset), except for SSP and wind speed where the averages over a two-week period (centred on the average day of singing onset) were additionally investigated.

4.5 RESULTS

Humpback whales were acoustically present in all analyzed data sets (Figure 4.2). Vocalizations were present at the onset of the analysis period in September for all data sets except off eastern Labrador (station 8), where vocalizations were not recorded until October 2015. In many areas, humpback whale acoustic occurrence continued until the end of January when analysis ceased. However, vocalizations were absent from eastern Labrador (station 8) and the Bay of Fundy (station 2) by the end of December 2015. The Strait of Belle Isle (station 7) had a marked difference in occurrence between years with vocalizations absent by mid November 2015 in 2015-16 but continuing until early January 2017 in 2016-17 (Figure 4.2).

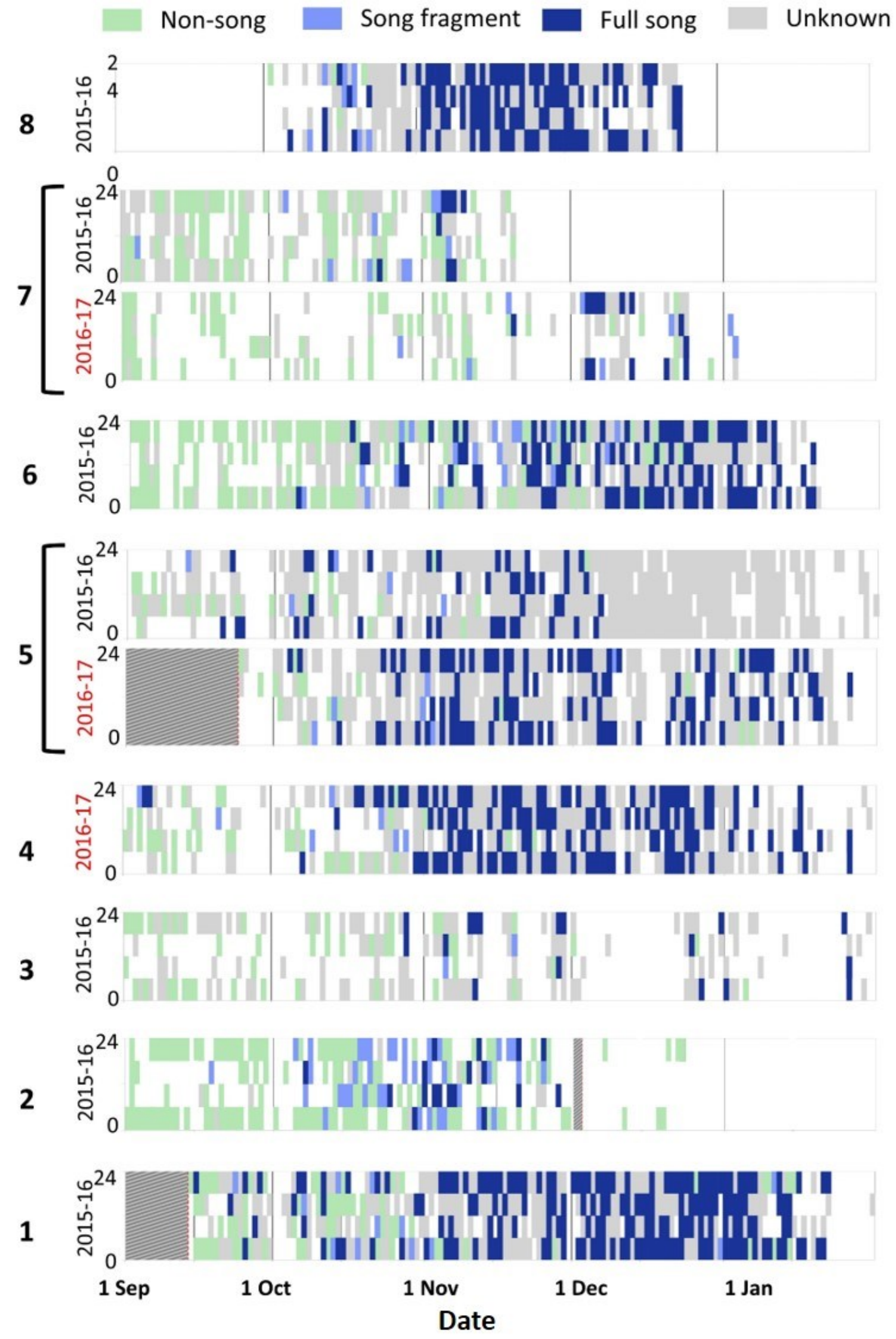

Figure 4.2. The occurrence of humpback whale vocalizations in 6 hour periods (00:00-06:00, 06:00-12:00, 12:00-18:00, and 18:00-00:00) for every day with recordings from 1 September 2015 to 31 January 2016 (2015-16) for stations 1-3 and 5-8 and 1 September 2016 to 31 January 2017 (2016-17; red) for stations 4, 5, and 7. Hashed grey periods indicate no recordings. Where mutliple behaviours were present in the same timeframe priority of behaviour presented is full song, song fragment, non-song, unknown. Unknown was assigned when vocalizations could be confidently assigned to humpback whales, but it was unclear which behaviour (non-song, song fragment, or song) was present. Stations 2 and 4 were previously analysed for Chapter 3.

The predominant humpback whale vocal category varied throughout the timeframe analyzed with non-songs, song fragments, and full songs observed in all data sets. Non-song calls were the most common vocalization category from September to November but are likely under-represented in the results once singing began. Song fragments were most common in October and November. With few exceptions, full songs were the predominant vocal category from November to January (Figure 4.2).

Singing could be heard as early as 4 September (song fragment; station 7, 2015-16) but on average, singing began on 29 September and did not become regular until 27 October (Figure 4.2 and Table 4.4). For all data sets, a lag was observed between the first day of singing and the first day of regular singing (9-51 days), with an average of 30 days before singing became regular (Table 4.4). Singing never became regular at Emerald Basin where humpback whale vocalizations became sporadic after mid-November (station 3 2015-16) (Table 4.4 and Figure 4.3).

Table 4.4. First day of singing, first day when singing became regular, the number of days between the two for each recording station and year, and the average for both years combined as well as 2015-16 and 2016-17 separately.

Station	**Year**	**First singing (full or fragment)**	**Regular singing (full or fragment)**	**Number days between first and regular singing**
8	2015-16	6 Oct 2015	22 Oct 2015	16
7	2015-16	4 Sep 2015	4 Nov 2015	61
	2016-17	27 Oct 2016	4 Dec 2016	38
6	2015-16	5 Oct 2015	5 Nov 2015	31
5	2015-16	20 Sep 2015	4 Oct 2015	14
	2016-17	4 Oct 2016	22 Oct 2016	18
4	2016-17	5 Sep 2016	26 Oct 2016	51
3	2015-16	28 Oct 2015	NA*	NA*
2	2015-16	18 Sep 2015	19 Oct 2015	31
1	2015-16	16 Sep 2015	25 Sep 2015	9
Average		**29 Sep**	**27 Oct**	**30**
2015-16		**26 Sep**	**18 Oct**	**27**
2016-17		**2 Oct**	**6 Nov**	**36**

*Singing never became regular

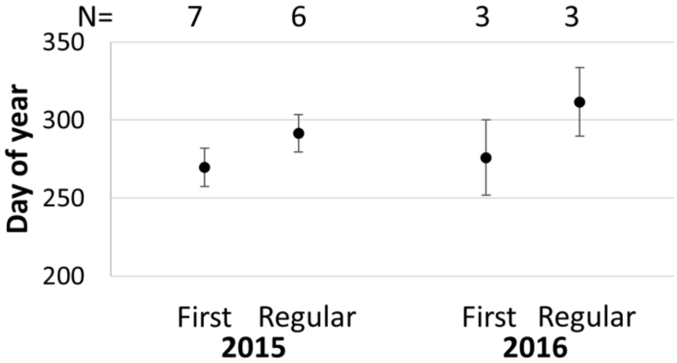

Figure 4.3. The average first day of singing and first day when singing became regular in 2015 and 2016 with 95 % confidence intervals.

Results varied when comparing singing onset between years. At St. Ann's Bank (station 5), the timing of singing onset was similar in 2015-16 and 2016-17 (Figure 4.2 and Table 4.4). In contrast, singing began notably later in the Strait of Belle Isle (station 7) in 2016-17 as compared to 2015-16 (53 days later for first day of singing and 30 days later for first day of regular singing). Cape Breton South (station 4) 2016-17 did not have recordings from 2015-16, but song onset occurred in a similar manner to nearby stations in 2015-16 (Figure 4.2 and Table 4.4).

Correlations between environmental variables and singing onset revealed slightly different results depending on the definition of song onset. While variables recorded on the average first day of regular singing (18 October in 2015-16 and 6 November in 2016-17) were not significantly correlated to first day of regular singing, some variables did have evidence of meaningful correlation with r values of SST = -0.66 (*p*=0.05), light hours = -0.66 (*p*=0.06), and latitude = 0.61 (*p*=0.08) (Figure 4.4). This suggests that humpback whales at lower latitudes, higher SST, and longer light hours may have begun singing regularly earlier in the year than those at higher latitudes, lower temperatures, and shorter light periods (Figure 4.4). The correlation between light hours and start of regular singing was largely driven by the three 2016-17 data sets (Figure 4.4). Similarly, the SST and latitude pattern are made more prominent by the late singing onset that occurred in the Strait of Belle Isle in 2016-17. In contrast to regular singing, the majority of variables recorded on the average first day of singing (26 September in 2015-16 and 2 October in 2016-17) were not approaching correlation with first day of singing (r values = -0.20 – 0.15; p values > 0.05; Figure 4.4). CHLA was marginally correlated with first day of singing (*r* = 0.54) and regular singing (*r* = -0.56), but with few data above zero driving the correlation, this trend is not strong (*p* = 0.11 and *p* = 0.12, respectively).

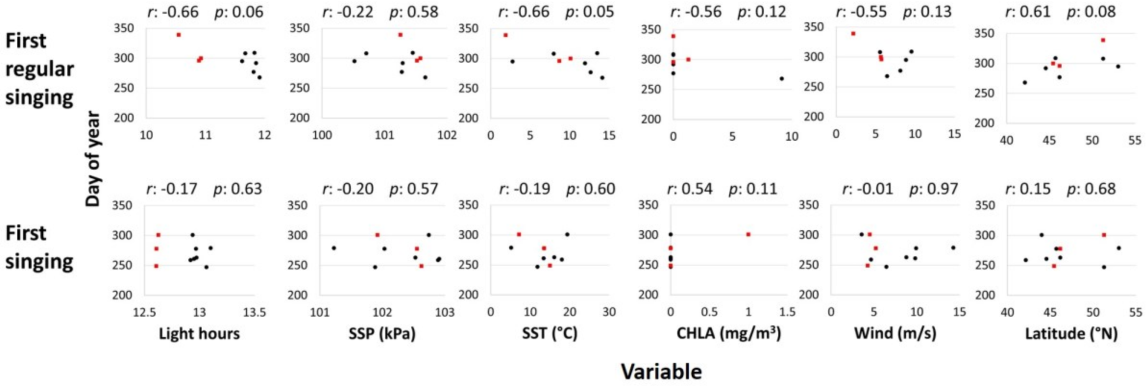

Figure 4.4. Scatterplots with the day of the year in 2015 (black circles) and 2016 (red squares) when humpback whale singing began (first occurred on bottom and became regular on top) vs variables measured on the average first day of singing or regular singing for each year. Results from Pearson's pairwise correlation are included for each plot as the correlation coefficient (r) and p value (p).

Results from our further analysis of environmental variables can be found in APPENDIX B and are summarized here. Where the variable values were taken from average singing onset across both years (29 September for first singing; 27 October for regular singing), rather than treating the years separately, and compared to first day of singing or regular singing, few strong correlations were observed (see APPENDIX B Table B-3). Light hours and latitude were once again moderately correlated to first day of regular singing with r values of -0.65 and 0.61, respectively (see APPENDIX B Table B-3). Additionally, wind speed (averaged daily) was correlated to first day of regular singing (*r* = -0.61; *p* = 0.08). In no other circumstance did wind speed or SST approach correlation to song/singing onset regardless of whether the values were averaged daily or over two weeks. When first day of full song and first day of regular full song were investigated, no correlations to variables were found (r values = -0.63 - 0.45; p values = 0.16 – 0.94; see APPENDIX B Table B-4). This was true regardless of whether variable values were averaged across both years or considered separately (see APPENDIX B).

4.6 DISCUSSION

Acoustic recordings ranging from Labrador, Canada to Massachusetts, U.S.A. captured the onset of humpback whale seasonal singing in fall 2015 at seven stations and fall 2016 at three stations. There are inherent limitations and caveats in our research design that are important to discuss and clarify. The use of omnidirectional static PAM restricted the present study to describing the acoustic behaviour of a group or population of whales, rather than how individual whales began singing. While the analysis protocol was designed to reduce the resampling of the same animal, individuals may well have been resampled over time at the same station or even across stations given the onset of migration south in the fall. With the exception of the Bay of Fundy, where 80 whales were once estimated to feed through the summer (Paquet et al. 1997), it is unclear how many whales frequent the other stations in the present study and to what extent whales remain in each area for weeks (increasing the chance of resampling) versus simply moving through during migration (reducing the chance of resampling). Resampling was not necessarily problematic to the present research questions and considering the spatial span of the stations and the restriction to analyzing high SNR vocalizations, it is likely that on any day I was sampling different individuals at different stations.

A lack of singing could indicate an absence of males, that males were present but not singing, that males were singing but during times when either recorders were in sleep mode or the data were not analyzed, or that singing males were out of detection range of the acoustic recorders, all inherent limitations to PAM. Both the duty cycled recordings and sampling regime during manual analysis were selected, in part, to increase the chance of identifying humpback whale vocalizations based on findings by Thomisch et al.

(2015). The chances of missing singing male humpback whales may have decreased throughout the season as songs became more prolific in the data, but even early in the season this species would be rarely missed given their propensity towards regular vocal activity (Thomisch et al. 2015). Given the range of soundscape characteristics of the stations (e.g., vessel noise, currents, and water depth that all impact sound propagation) (See ambient analysis in Delarue et al. 2018), it is likely that the detectability of humpback whales varied somewhat depending on station and time of year and may account for some of the variability in occurrence across stations. In previous studies using similar recorders and mooring setups offshore Nova Scotia, humpback whale vocalizations were modelled to be detectable at a range of 1 to 75 km in winter and 3 to 100 km in summer, depending on the ambient sound levels (Kowarski et al. 2018). The reduced detection range in winter is common in the North Atlantic, and is caused, in part, by an increase in adverse weather conditions, such as high wind speeds. The increase in songs into the winter despite the decrease in detection range, would suggest that the overall trends observed here were not influenced significantly by seasonal variation in detectability. Our analysis protocol and the nature of humpback whale vocalizations biased our results to highlight the occurrence of song over non-song acoustic signals where the former has higher source levels and is more prolific than the latter (Au et al. 2006, Dunlop et al. 2013a). It is unclear whether song fragments have an intermediate source level between full songs and non-songs. The bias towards identifying full song is not problematic for the present study where identifying song onset was the primary objective. Although it is important to recognize the aforementioned caveats, I was able to effectively observe humpback whale vocal behaviour through time despite these inherent limitations.

4.6.1 Occurrence and implications for migratory behaviour

Previously, humpback whales were thought to leave inshore Canadian waters by November and December (Kowarski et al. 2019) and make their way south either through a more coastal route such as Massachusetts Bay (Vu et al. 2012, Stanistreet et al. 2013) or an offshore route (Kowarski et al. 2018). They then migrate to the Caribbean where they seem to prefer the waters off the Dominican Republic over the eastern Caribbean (Stevick et al. 2018), occurring from December through June (Heenehan et al. 2019). In looking at humpback whale northern occurrence on a broader scale, I have concluded that they are common in Canada through January, even in coastal regions. These findings were unsurprising in the more southern Massachusetts Bay given previous observations by Vu et al. (2012) and Stanistreet et al. (2013). These findings indicate that individuals undertake migration at different times with some already in the West Indies in December while others remain in Canada and the U.S.A. at least through January, undergoing a later migration, short migration, or not migrating at all. Indeed, evidence suggests that in some areas, such as the Grand Banks of Newfoundland (station 6), humpback whales are present year-round (Station 7 in Delarue et al. 2018).

In south Labrador, the Strait of Belle Isle, and the Bay of Fundy, humpback whales were acoustically absent by early December, presumably having moved southward. The decrease in humpback whale occurrence during mid-November to early January at the northern stations (South Labrador and the Strait of Belle Isle) coincides with an increase during December and January previously seen in submarine canyons and the eastern continental slope area off Nova Scotia (Kowarski et al. 2018), a possible migration route for these northern individuals. It is unclear where the whales from the Bay of Fundy move after seemingly departing in December; they could travel further south through Massachusetts Bay or take an offshore route. Future PAM work in more offshore areas, especially seamounts such as those found off Bermuda combined with satellite tags would be informative.

4.6.2 Singing onset and evidence for proximate cues

Humpback whale vocalizations transitioned through the fall from being predominantly non-song to song fragments to full songs as was previously described by Kowarski et al. (2019) irrespective of where the acoustic recorders were located. This was true in both 2015-16 and 2016-17. In some cases, there was inter-annual variability in the timing of song onset, the extent of which could not be assessed given the low sample size (three stations in 2016-17). Considering the potential errors in separating song fragments from full songs in duty cycled data that include sleep mode (all stations but 1 and 2) and the challenge in identifying fragments when full songs are present, the present discussion is limited to singing results which encapsulates both fragments and full songs. More continuous, acoustic tag, or directional data sets in the future may allow these vocalization categories to be considered separately with more confidence.

There was a lag averaging one month between when singing first occurred (predominantly fragments) and when it became regular (predominantly full songs). These results strongly reinforce the previous findings of a transition period described by

Kowarski et al. (2019); this ontogeny of singing behaviour appears to be a consistent feature of at least the humpback whale population in the western North Atlantic. The onset of infrequent singing could reflect one or a combination of the following: variation among individuals with some singing earlier than others, mature males are practicing, immature males are learning, or the behaviour is hormone-induced and testosterone levels have not reached minimal threshold for more regular singing (see discussion of Kowarski et al. (2019)). If the hormonal influence is important, one could expect some environmental cue to trigger the regulatory process as has been described in other species (e.g., Bubenik et al. 1982, Asher et al. 1989, Smith et al. 1997).

The first day of singing occurred over the same time frame at all stations (September-October; average 29 September) despite the wide north-south spread of recorders (spanning 10.9° of latitude). At some stations (Massachusetts Bay and St. Ann's Bank) singing may have occurred earlier than reported, but there were no data for early September. Wind speed and SST (spanning 10.7m/s and 14.2°C, respectively) were similarly not significantly correlated with first day of singing. It is difficult to confidently ascertain whether CHLA, SSP, or light hours could impact first day of singing, given the little variation in values (1mg/m^3, 1.7kPa, and 0.5hr, respectively), rendering little statistical power. With the present data, it is impossible to know whether these initial songs are produced rarely by all males or are only produced by few individuals. These behavioural outliers may not be representative of the behavioural shift of the population. Therefore, it is arguably more meaningful to consider the timeframe when singing became regular than when it first occurred. As I delve into the trends observed here (variables correlated with regular singing) it is important to highlight that I have yet to develop methods to understand what is ‘meaningful’ to the whales. Is it first day of song fragment, first day of full song, first day of regular singing, or something else? What is ‘regular singing’ to the whales? Here, I have defined it as five days with song, an arbitrary human imposed category. Future work may well identify a better unit for song onset, but I have provided a first attempt at describing these trends.

The onset of regular singing ranged from late September to early December (averaging 27 October) and tended to occur earlier in the year at lower latitudes with longer photoperiods and higher temperatures (with some evidence of occurring earlier at higher wind speeds). Conversely, there was no indication of CHLA, and SSP correlation with regular singing, although with CHLA rarely greater than zero and SSP only ranging by 1.1 kPa across stations, statistical power was low. While the onset of regular singing was not significantly correlated to latitude, light hours, or temperature, in all cases the correlation approached significance ($p < 0.10$); given the small sample size, little statistical power of photoperiod during the fall equinox (range of only 1.4 hr between stations), and migratory nature of the whales that can move across stations, even a hint of correlation may be biologically meaningful. These trends became more obvious with the inclusion of the second year of data. Due to the small sample size and inherent variable collinearity, I could not perform a model that included all variables. The addition of further data sets in the future will help confirm or refute these perceived trends and may allow for stepwise analysis to understand the influence of each variable. It is difficult to infer causation from correlation in situ, especially when dealing with non-independent variables during the fall equinox, but I can draw from observations in other taxa.

It has been understood for decades that the number of hours with sunlight in a day affects reproduction in many, if not most, animal species outside the tropics as it provides reliable information regarding upcoming seasonal changes (Lofts and Murton 1968, Rojansky et al. 1992). In some of the more well-studied species, it has further been found that other variables can accelerate or inhibit the impacts of photoperiod. For example, for birds in temperate regions, photoperiod has been shown to influence the development of song control nuclei in the brain that affect testosterone levels (Lofts and Murton 1968, Nottebohm et al. 1986, Meitzen et al. 2007, Dawson 2013). Avian gonadal response to day length can be adjusted by any number of other factors including social interactions, weather, and food supply, but temperature seems particularly important for the gonad cycle and is related to the speed of testes development (Lofts and Murton 1968, Rojansky et al. 1992). Similarly, photoperiod has been identified as the determinant factor of seasonal breeding in sheep with temperature, social interactions, and nutrition modulating the timing of breeding (Rosa and Bryant 2003).

Humpback whale physiological and behavioural shifts may also be driven by photoperiod and modified by additional variables. All whales in the present study would experience a reliable cue (in the form of shorter photoperiods) to begin behaviours associated with the breeding season during the fall equinox (e.g., southward migration and male singing). As has been well documented in birds, the photoperiod cue may trigger the onset of an heritable physiological response in humpback whales resulting in increased testis size, increased testosterone production, and development of song control processes in the brain (Lofts and Murton 1968, Nottebohm et al. 1986, Meitzen et al. 2007, Dawson 2013). Congruent with this suggestion, historical whaling data indicates an increase in humpback whale testes size during the breeding season (Chittleborough 1955) and Cates et al. (2019) described a seasonal increase in male humpback whale testosterone levels through the fall in the North Pacific.

Once the physiological processes are triggered, the exact timing of breeding season related behaviours may then be modified by other variables, such as physical condition of the animal, an important consideration for a migratory species that largely fasts on the breeding grounds. Whales on higher latitude feeding grounds (e.g., Labrador) will undertake longer migrations northward and southward than those on lower latitude feeding grounds (e.g., Massachusetts Bay). With shorter migrations, whales in Massachusetts Bay may arrive back to the feeding grounds earlier in the spring, begin foraging earlier, and as a result, be physically prepared earlier in the fall to begin breeding behaviours when compared to their longer migrating counterparts. Additionally, whales in high latitudes may forage for longer to ensure sufficient reserves for their long migration. Indeed, Szesciorka et al. (2020) concluded that the variable timing of blue whale migrations is linked to prey availability. Information on the foraging value compared across regions would be revealing. Warmer temperatures at lower latitudes may also allow physiological changes such as testes growth to occur more quickly. The earlier onset of humpback whale singing at lower latitudes observed here has similarly been seen in birds, where those at lower latitudes with longer photoperiods begin the breeding season earlier than those at higher latitudes as gonadal maturation starts earlier and occurs faster (Dawson 2013). Additional variables not explored here could further explain the variability in humpback whale song onset observed across latitudes such as social interactions in a species where cultural behaviours are well described (Rendell and Whitehead 2001).

One population that may shed light on the question of what drives the onset of singing is the non-migratory Arabian Sea humpback whales. Little is known about this genetically distinct population, but they have been found to sing on a Northern Hemisphere seasonal cycle and female reproduction is similarly seasonal based upon examination of fetal lengths in Soviet whaling data, similar to their migratory counterparts (Mikhalev 1997, Cerchio et al. 2016). Moreover, the population is derived from a founder event originating in the Southern Hemisphere (Pomilla et al. 2014), inferring that during the adaptation to residency in the Arabian Sea, they switched breeding cycle to a Northern Hemisphere timing. Therefore, whatever drives timing in breeding must be a strong selective force. Living near the equator, these whales do not experience the variation in light hours, or variation in those variables impacted by light hours, that are experienced by humpback whales foraging in high latitudes. It may therefore be that humpback whales of a given hemisphere begin singing at around the same time due to an internal clock or even social tradition, rather than environmental cues. However, the Arabian Sea humpback whales are exposed to a biannual monsoon season that brings a range of environmental cues, including temperature changes, that could trigger singing onset. This juxtaposition of varying proximate cues is seen in bird species where temperate birds respond to photoperiod while equatorial birds respond to other cues such as rainfall (though even tropical birds maintain capacity to be influenced by light in a lab setting) (Lofts and Murton 1968).

4.7 CONCLUSIONS

This study revealed that humpback whale songs are common in coastal regions of the western North Atlantic in September to January. On average, singing began in late September and transitioned over the course of four weeks from song fragments and sporadic full songs to regular singing. Understanding this transition period can inform future PAM analysis techniques and automated detector development and application for a species with a dynamic repertoire that can be challenging to acoustically differentiate from other baleen whales. I found evidence that the onset of humpback whale regular singing occurs earlier at lower latitudes where there are longer photoperiods and higher temperatures. I propose that photoperiod may be a trigger for humpback whale breeding behaviour in the fall, but many other variables such as temperature, body condition, food availability, and social interactions likely influence the timing of song onset. Future work on other baleen whale species that sing seasonally would be an enlightening addition to this line of research. In understanding where, when, and why whales begin to sing we can piece together the significance of these behaviours, what drives them in terms of proximate and ultimate factors, and how they relate to their environment.

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CHAPTER 5 SONG ONTOGENY IN WESTERN ATLANTIC HUMPBACK WHALES: PARALLELS WITH SONGBIRDS

5.1 PUBLICATION STATUS

As of 5 October 2020, this chapter is in prep for journal submission.

5.2 ABSTRACT

The use of song as a reproductive display is common in the animal kingdom, however, for many taxa, little is known of song ontogeny. Male humpback whales produce elaborate songs on low latitude breeding grounds that originate on high latitude feeding grounds, yet songs from the two locations are rarely compared. I explore seasonal song development in the northwest Atlantic humpback whale, comparing songs from Canada to those of the Caribbean. Songs were analyzed from Canada in spring 2016 (1 station) and in fall (autumn) 2016 to winter 2017 (3 stations). In the Dominican Republic, songs were analyzed in the winter and spring of 2017 (1 station). High quality song samples were selected from long-term acoustic recordings and every phrase annotated. The song theme order, song duration, and number of phrase repetitions were compared across samples. One song theme order was common across almost all samples, with the most variability in theme order seen in November to December in Canada. Song duration gradually increased, via an increase in phrase repetitions, through the breeding season, before seemingly peaking in the Dominican Republic between January and March. I propose that humpback whale song ontogeny reflects that reported in oscine birds, with a plastic phase in the fall that could be important for learning.

5.3 **INTRODUCTION**

Vocalizations classified as songs have been described for decades in the animal kingdom in insects (e.g., Čokl et al. 1999, Simmons et al. 2001, Kindl et al. 2011, Ölveczky 2013), frogs (e.g., Leininger and Kelley 2015), bats (e.g., Behr et al. 2006), mice (e.g., Campbell et al. 2010), apes (e.g., Clarke et al. 2006), whales (e.g., Payne and McVay 1971, Cummings and Thompson 1977, Watkins et al. 1987), and birds (e.g., Byers et al. 2010, Crozier 2010, Sprau and Mundry 2010, Peters et al. 2012, Williams et al. 2013). However, for many of these taxa, little is known about the early ontogeny of songs. Indeed, only for the oscine birds has song development been described in any detail with much of the development literature restricted to when birds learn to sing for the first time (e.g., Nelson and Marler 1994).

In some species, the production of song not only develops when young birds first begin singing, but seasonally at the onset of the breeding season (e.g., Nottebohm et al. 1986). Without understanding seasonal song development, it is difficult to fully comprehend the drivers of these acoustic signals and their significance for reproductive success. Here, I explore seasonal song development in a species with one of the most elaborate mammalian songs, the humpback whale (*Megaptera novaeangliae*).

First described in the 1970's, humpback whale songs are produced by males during the winter breeding season (Payne and McVay 1971, Winn and Winn 1978) when most populations migrate from their high-latitude feeding grounds to their low-latitude breeding grounds (Kellogg 1929, Dawbin 1966). Song is a sexually-selected characteristic limited to males, and one of several tactics employed by males to gain reproductive success, although the exact function(s) within the mating system remain under debate (e.g., mate attraction vs male-male interactions; Winn and Winn 1978, Tyack 1981, Darling and Bérubé 2001, Darling et al. 2006, Smith et al. 2008, Dunlop and Noad 2016, Cholewiak et al. 2018). Songs are hierarchically structured in a classification nomenclature initially proposed by Payne and McVay (1971) that continues to be used in the literature. Discrete units (analogous to notes) make up stereotyped phrases; phrases are repeated and an uninterrupted series of like phrases is labelled a theme; and several themes are sung in sometimes invariable order to make up a song (Payne and McVay 1971, Payne et al. 1983, Cholewiak et al. 2013, Schneider and Mercado III 2019). Songs are repeated in bouts that can last for many hours referred to as song sessions (Payne and McVay 1971, Au et al. 2006, Parsons et al. 2008). Several authors have noted the similarity between the classification level of “phrase” and a typical “song” in the birdsong nomenclature, and the analogy of the repeated sequences of phrases with “eventual variety” singing behavior in some songbirds (Cerchio et al. 2001, Cholewiak et al. 2013). All whales in the same region generally conform to the same song, which changes through time via social learning and progressive cultural evolution, with songs and song sessions often becoming longer in duration through the breeding season (Tyack 1981, Payne et al. 1983, Cerchio et al. 2001, Garland et al. 2011). At the onset of a breeding season, the whales seem to pick up the same song that they left off singing in the previous season, implying a certain level of memorization (Payne et al. 1983). While singing is predominant on breeding grounds, this behaviour also occurs in high latitudes before and after migration, indicating that annual song development initiates before males reach the breeding grounds (Mattila et al. 1987, McSweeney et al. 1989, Magnúsdóttir et al. 2014, Kowarski et al. 2018, Kowarski et al. 2019).

Western North Atlantic humpback whales spend their winters on Caribbean breeding grounds, with some evidence that they occur more commonly in the Dominican Republic than the West Indies (Stevick et al. 2018). Summers are spent in northern feeding grounds that include the waters of eastern Canada (Whitehead and Moore 1982, Martin et al. 1984, Katona and Beard 1990, Palsbøll et al. 1997, Smith et al. 1999, Jann et al. 2003). Humpback whale song has been recorded in eastern Canadian waters in the fall and winter from Labrador to the Bay of Fundy, as well as in the spring off Nova Scotia (Kowarski et al. 2018, Kowarski et al. 2019, Kowarski et al. In Review). Two categories of singing behaviour have been described in this region during song onset in the fall: song fragments, produced early to mid fall, and full songs, produced mid fall through to the winter (Kowarski et al. 2019, Kowarski et al. In Review). Song fragments were defined as any vocalizations organized into one phrase or subphrase to many themes (that are not repeated). Full songs were defined as three or more themes repeated at least once (Frumhoff 1983, Cholewiak et al. 2013, Kowarski et al. 2019). The fall transition from non-song calls to song fragments to full songs was gradual, occurring over many weeks with about a month separating when songs first appeared and when singing became regular (Kowarski et al. 2019, Kowarski et al. In Review).

The fall transition from song fragments to full songs is likely only a small part of the picture of how songs develop seasonally. There is currently limited comparison of how the full songs that occur on feeding grounds compare to those produced on the breeding grounds. In the south Pacific, Garland et al. (2013a) recorded themes on an Antarctic feeding ground that matched those from breeding grounds in eastern Australia and New Caledonia, but these were only recorded over a few days and therefore provide only a glance into song ontogeny. The present paper uses passive acoustic monitoring (PAM) data to observe how the theme order, song duration, and number of phrase repetitions of western North Atlantic humpback whale songs changes through time both off eastern Canada and in the Caribbean. In doing so, I provide a piece to the humpback whale song puzzle, specifically how it is shared and changes through time.

5.4 METHODS

5.4.1 Data collection

PAM data were collected from four stations in the Atlantic Ocean, three in Canada (Strait of Belle Isle, St Ann's Bank, and Cape Breton South) and one in the Caribbean (Dominican Republic;

Figure 5.1; Table 5.1). Canadian recordings were collected using Autonomous Multichannel Acoustic Recorders (AMARs; 24 bit; 6 db gain) with HTI-99 omnidirectional hydrophones (sensitivity of −165 ± 3 dB re 1 V/µPa). Strait of Belle Isle and Cape Breton South data were part of JASCO Applied Science's Environmental Science Research Fund (ESRF) acoustic monitoring program (Delarue et al. 2018, Kowarski et al. 2019). Data from St. Ann's Bank were part of the Department of Fisheries and Oceans (DFO) Canada Maritimes Region ongoing PAM program. The Dominican Republic data were collected using a Marine Autonomous Recording Unit

(MARU; 16 bit; 6 db gain) with a HTI-94-SSQ omnidirectional hydrophone (sensitivity of -198 dB re 1 V/µPa) as part of the collaborative Caribbean Humpback Acoustic Monitoring Program (CHAMP) project, lead by the National Oceanographic Atmospheric Administration (NOAA) Northeast Fisheries Science Center (NEFSC) passive acoustics group (Heenehan et al. 2019).

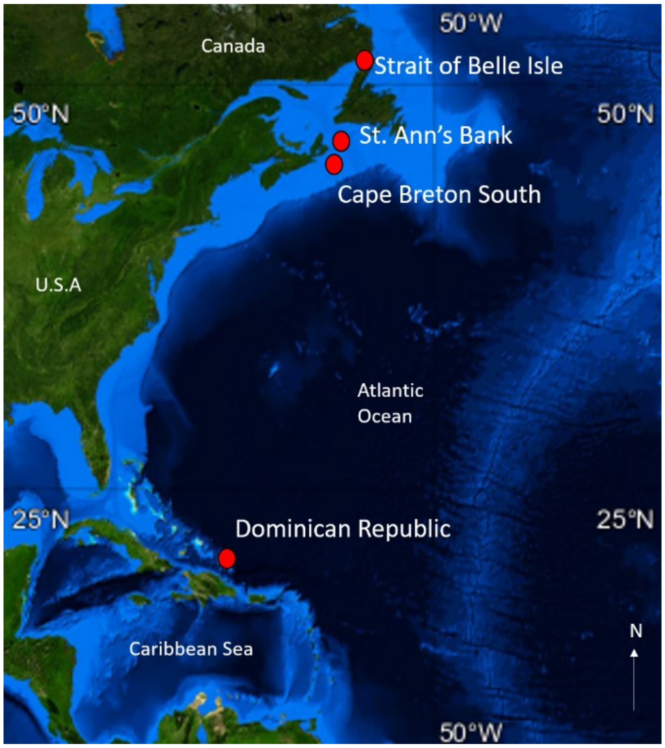

Figure 5.1 Location of four recording stations in the Atlantic Ocean.

Table 5.1 Deployment and retrieval dates, location, recorder depth, recording schedule, and acoustic recorder used to collect data from four stations.

Station	Deployed - Retrieved	Latitude Longitude	Water Depth (m)	Recorder distance from seafloor	Recording Schedule (sampling rate, duration)	Recorder
Strait of Belle Isle	10 Jul 2016 - 11 Jul 2017	51° 16.6'N -57° 32.1'W	110	20 m	250 kHz, 1 min 8 kHz, 11.3 min Sleep, 7.7 min	AMAR
St Ann's Bank	23 Sep 2016 - 29 Oct 2017	46° 0.1'N -59° 8.5'W	100	20 m	250 kHz, 1 min 8 kHz, 11.3 min Sleep, 7.7 min	AMAR
Cape Breton South	3 Nov 2015 – 9 Jul 2017[a]	45° 25.8'N -59° 46.3'W	123	20 m	250 kHz, 1 min 8 kHz, 11.3 min Sleep, 7.7 min	AMAR
Dominican Republic	7 Dec 2016 – 3 Jun 2017	20° 36.5'N 69° 49.2'W	179	1-2 m	2 kHz, continuous[b]	MARU

[a]Redeployed 21 Jul 2016; [b]15 min acoustic files

5.4.2 Song analysis

The three Canadian data sets were previously analyzed for humpback whale song acoustic occurrence (Kowarski et al. 2019, Kowarski et al. In Review). Cape Breton South recorded full songs in spring 2016 (Kowarski et al. 2019) and all three stations captured full songs in the proceeding fall to winter of 2016-2017 (Kowarski et al. In Review). While acoustic signals were of sufficient quality to identify whether a whale was singing or not in previous studies, not all occurrence results reported in these previous studies were based on calls occurring with a high enough signal-to-noise ratio (SNR) for song analysis. With the aim of identifying acoustic data of sufficiently high quality for song analysis, these previous occurrence results were used as a guide to identify data appropriate for the present research question. Acoustic data were considered 'sufficiently high quality' when 1) the humpback whale acoustic signals had high signal-to-noise ratio (SNR; at least 10 dB), 2) a song could be confidently differentiated from other songs being sung simultaneously (only one singer was present or signals from one singer were consistently louder than others), and 3) at least two song cycles from (presumably) one individual of sufficient quality were present. Every acoustic file previously found to contain at least one song note with an SNR of 10 dB or greater in the Canadian data (see SNR calculation method in Kowarski et al. 2019) was reviewed for song sessions that met this criteria. Each selected file and the four files immediately before and after it were manually reviewed to identify high quality samples for analysis, where a sample was considered a continuous series of songs (i.e., the song session) assumed to be produced by the same individual over a one- to two- hour period. When the recorders entered sleep mode (which occurred for a period of < 8 min, Table 5.1), resulting in a gap in the data, songs before and after sleep mode were assumed to be from the same individual, or sample. This assumption may be a source of some error, but it is unavoidable due to the limitations of duty-cycled data and the need to increase sample size. Samples were selected on different days to limit the chances of resampling the same whale. Therefore, any given sample can be identified by date.

While the Dominican Republic data set includes recordings from December 2016 to June 2017 (Table 5.1), I restricted analysis to the months of January and March for the present study. Humpback whale song was found to occur continuously throughout both of these months in previous analysis completed by Heenehan et al. (2019), a finding that is unsurprising given the males are known to chorus on their breeding grounds. For each month, four samples were selected for analysis spaced as far apart as possible to reduce the chance of resampling the same whale. All acoustic files from the 1st, 10th, 20th, and

30th of each month were reviewed and the highest quality sample within each day (based on the same parameters applied to the Canadian data) was selected and analysed using the same protocol as the Canadian data, but without the extra considerations for sleep mode as the Caribbean data was continuous (Table 5.1). This method of sample selection resulted in a sample size comparable to what was achieved in the Canadian data analysis. The Dominican Republic data set had a lower sampling rate (2 kHz) than the Canadian data (8 kHz), limiting my ability to observe some of the higher frequency sounds which were assumed to match those observed in Canada based on the sequence of notes. Any error resulting from this was likely minimal as most humpback whale vocalizations are captured below 1 kHz. Sixteen samples of humpback whale songs recorded in the Heenehan et al. (2019) Caribbean data set were independently analysed by a separate research team (NOAA NEFSC), resulting in the identification of all of the same phrases identified here (in both the Caribbean and Canada), thus validating the phrase classification that we present (Personal Communication, Danielle Cholewiak, NEFSC). The only variation was the start unit in some phrases which is unsurprising given the exact start of a phrase is subjective. After comparing phrases between research groups, consistency in phrase delineation was increased to ensure inter-project consistency.

Samples were manually analyzed in PAMlab (JASCO; 2 Hz frequency resolution, 0.128 s time window, 0.032 s time step, Hamming window) with each song phrase annotated (numerically), such that each song was transcribed at the phrase level. Humpback whale singing is cyclical, cycling through themes, such that where the song starts, or which is theme 1, is subjective. I selected one of the quietest periods of the song, where notes were often faint, unclear, or inconsistent as the arbitrary start of the song (containing theme 1), because I suspect this to be the time within the song cycle when the whales surfaced to breath (due to the attenuation associated with refraction in the surface layer) (Tyack 1981). Transition phrases (phrases that occur between two different phrase types; often comprised of units from both the previous and proceeding phrase) were also annotated but were not included in subsequent analysis or results. When sleep mode caused a gap in the sample, singing in the subsequent file was considered a new song (the theme at the beginning of a file was not assumed to be the phrase that followed the one at the end of the previous file when sleep mode occurred between them). Similarly, where singing ceased (or became too faint) for at least 60 sec, the singing following the break was considered a new song. In a continuous singing bout, a new song occurred when a theme began for the second time, such that no song contained two of the same theme (Garland et al. 2012).

Samples were compared temporally across the four stations in terms of theme order, song duration (start of first theme to end of last theme where the same theme never occurs twice in a song), and number of phrase repetitions within themes. Theme order was described using a numerical representation for each theme type (where theme 1 contains repetitions of phrase 1). Every unique theme order present in a sample was recorded to describe the variation in theme order within and between samples. For the Canadian data, at times the sleep mode prevented the observation of all the themes in a song. In this instance, where the theme order matched that of a full song observed elsewhere in the sample, a consistent theme order was assumed. The average song duration per sample was plotted over time for samples that captured songs from start to finish continuously. Song duration was only quantified for the most commonly observed song theme order

(1,2,3,4,5,6,7,8) to maintain consistency as recommended by Cholewiak et al. (2013). To investigate phrase repetitions, the average number of phrase repetitions per theme were calculated for each sample and were plotted over time. Themes were not included in the phrase repetition analysis when they occurred at the beginning or end of a sample, bordered on sleep mode, or bordered on a break in singing.

5.5 **RESULTS**

After restricting the Canadian data to the highest quality songs, 12 samples were analyzed: three from April-May 2016 (Cape Breton South) and nine from November 2016 to January 2017 (two from Cape Breton South, four from St. Ann's Bank, and three from Strait of Belle Isle). In the Dominican Republic, eight samples from 2017 were analyzed, four in January and four in March. This resulted in a total of 20 samples included in the present analysis. Themes 1-8 were identified at all stations (Figure 5.2) with each phrase annotated resulting in 3864 phrase annotations (themes identified through each sample included in APPENDIX C). Variants of phrases (e.g., different number of note repetitions) existed within and between samples, but followed the same general note patterns (Figure 5.2), allowing for confident delineation of phrases (Darling et al. 2019a). Theme 1 was qualitatively the most variable, especially in the Canadian data where it could be particularly faint and was initially suspected as a transition, though it was a clear theme in the Caribbean data (Figure 5.2). This perceived change in theme 1 through time may be indicative of the theme evolving through the season.

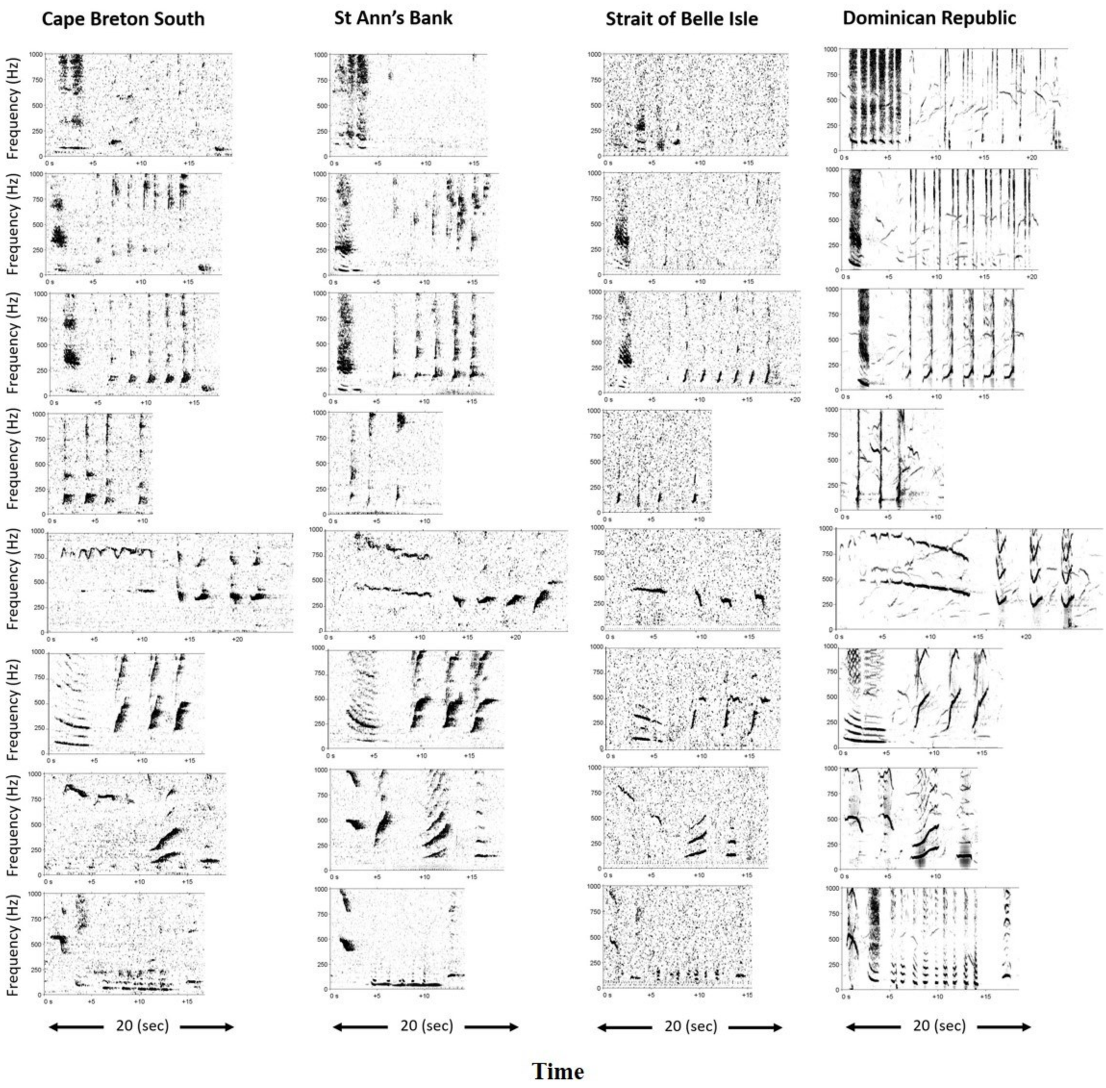

Figure 5.2 Spectrograms of exemplar humpback whale song phrases (1-8) that occurred at the four recording stations where each spectrogram has a frequency range of 0-1000 Hz and was viewed with the following PAMlab parameters: 2 Hz frequency resolution, 0.128 s time window, 0.032 s time step, Hamming window. The Cape Breton South example is from spring 2016, the St Ann's Bank and Strait of Belle Isle examples are from the fall/winter of 2016/17, and the Dominican Republic example is from the winter of 2017.

The most common theme order, which occurred in almost every sample, was 1, 2, 3, 4, 5, 6, 7, 8 (Table 5.2; henceforth referred to as song 1, 2, 3, 4, 5, 6, 7, 8). Samples in spring 2016 (April to May 2016) and late fall 2016 to early spring 2017 (6 December 2016 to 30 March 2017) almost exclusively contained song 1, 2, 3, 4, 5, 6, 7, 8. In contrast, samples earlier in the singing season in fall 2016 (21 November to 5 December), contained many different theme orders (with some themes skipped) that varied depending on which themes were left out of any given song (Table 5.2; see details in APPENDIX C).

Table 5.2 Every unique humpback whale song theme order observed for each sample (each unique day represents a sample) at the four stations. The number of songs analyzed in each sample (N) was estimated for the Canadian stations because at times only parts of songs were observed due to the sleep mode of the recording schedule. Songs are represented as starting at the lowest theme number for ease of comparability, but bouts are cyclical, and the first theme observed could be anywhere in the cycle. The most observed song (1, 2, 3, 4, 5, 6, 7, 8) is highlighted in red.

Year	Month	Day	N	Cape Breton South	St Ann's Bank	Strait of Belle Isle	Dominican Republic
2016	April	17	2	**1, 2, 3, 4, 5, 6, 7, 8**			
		19	3	**1, 2, 3, 4, 5, 6, 7, 8**			
	May	20	3.5	**1, 2, 3, 4, 5, 6, 7, 8**			
	November	21	4		1, 4, 5, 7, 8 1, 3, 4, 5, 7, 8 2, 4, 5, 6, 7, 8 1, 2, 3, 4, 5, 6, 7		
		25	3.5	**1, 2, 3, 4, 5, 6, 7, 8** 2, 4, 5, 6			
		27	4		**1, 2, 3, 4, 5, 6, 7, 8** 3, 4, 5, 6, 7, 8 2, 3, 4, 5, 6, 7, 8		
	December	5	6			**1, 2, 3, 4, 5, 6, 7, 8** 1, 2, 3, 4, 5, 6, 8 1, 2, 3, 8 1, 2, 8 2, 3, 4, 5, 6, 7, 8	
		6	3			**1, 2, 3, 4, 5, 6, 7, 8** 2, 3	
		23	3.5			**1, 2, 3, 4, 5, 6, 7, 8**	
		29	6		**1, 2, 3, 4, 5, 6, 7, 8**		
2017	January	1	6				**1, 2, 3, 4, 5, 6, 7, 8** 1, 2, 4, 5, 6, 7, 8
		9	2.5		**1, 2, 3, 4, 5, 6, 7, 8**		
		10	6				**1, 2, 3, 4, 5, 6, 7, 8**
		16	3	1, 2, 3, 4, 5, 7, 8			
		20	5				**1, 2, 3, 4, 5, 6, 7, 8**
		30	6				**1, 2, 3, 4, 5, 6, 7, 8**
	March	1	5.5				**1, 2, 3, 4, 5, 6, 7, 8**
		10	5				**1, 2, 3, 4, 5, 6, 7, 8**
		20	6				**1, 2, 3, 4, 5, 6, 7, 8**
		30	5.5				**1, 2, 3, 4, 5, 6, 7, 8** 1, 2, 3, 5, 6, 7, 8 1, 2, 3, 7, 8

Song duration (for songs with theme order 1, 2, 3, 4, 5, 6, 7, 8) and repetition of phrases varied through time (Figures 5.3 and 5.4). Song 1, 2, 3, 4, 5, 6, 7, 8, was shortest in November and December 2016 in Canada, early in the singing season, lasting only 5 to 6 min. It was longest in March 2017 in the Caribbean, lasting up to 25 min, and the few samples in spring 2016 in Canada were an intermediate duration (6 to 10 min) (Figures 5.3 and 5.4). The increase in song duration through the fall and winter was gradual, potentially peaking at some point in February or March, though more samples are required to confirm this. The changing song duration through time was caused by an increase in phrase repetitions observed in almost all themes (where phrase repetition results were not restricted to song 1, 2, 3, 4, 5, 6, 7, 8; Figures 5.3 and 5.4). Indeed, early in the singing season, many themes only contained one to two phrases, while late in the season a single theme could contain 10 to 40 phrases (Figure 5.4). For many themes, the number of phrase repetitions peaked in the winter and began decreasing again in late March 2017 (Figure 5.4).

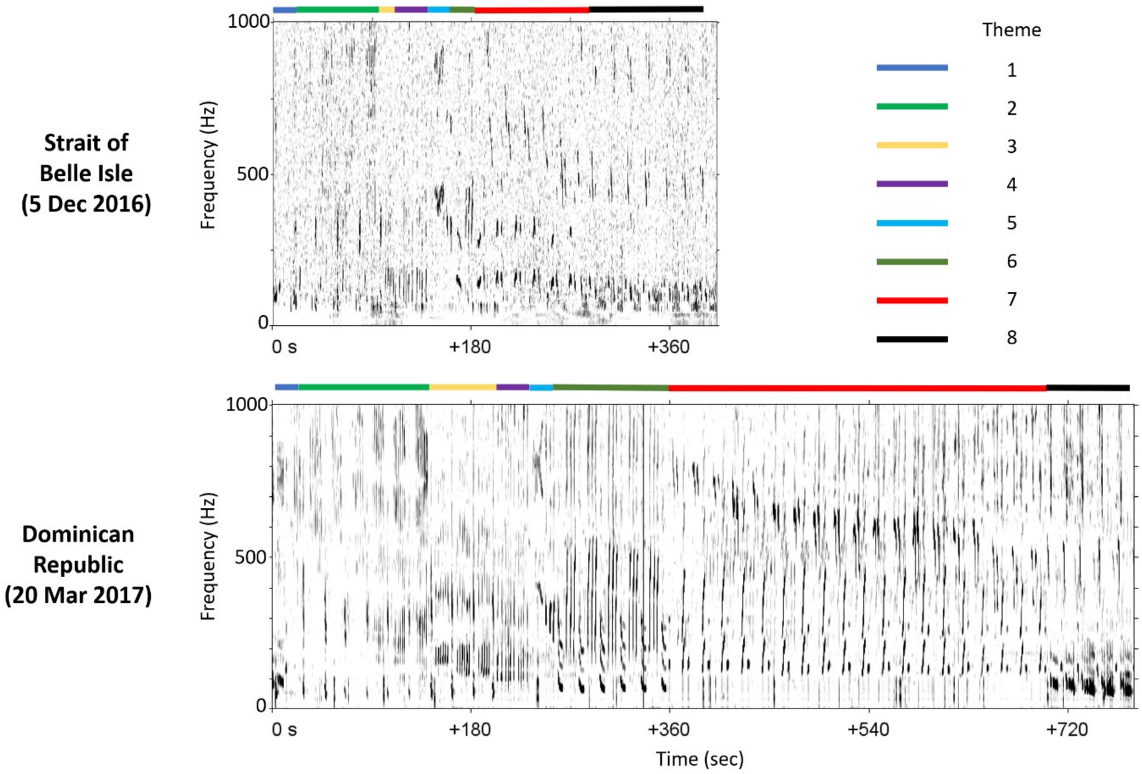

Figure 5.3 Spectrogram of an exemplar humpback whale song recorded in December 2016 in Canada (top) and a song recorded in March 2017 in the Caribbean (bottom) with the themes (1-8) colour coded for each song (2 Hz frequency resolution, 0.128 s time window, 0.032 s time step, Hamming window).

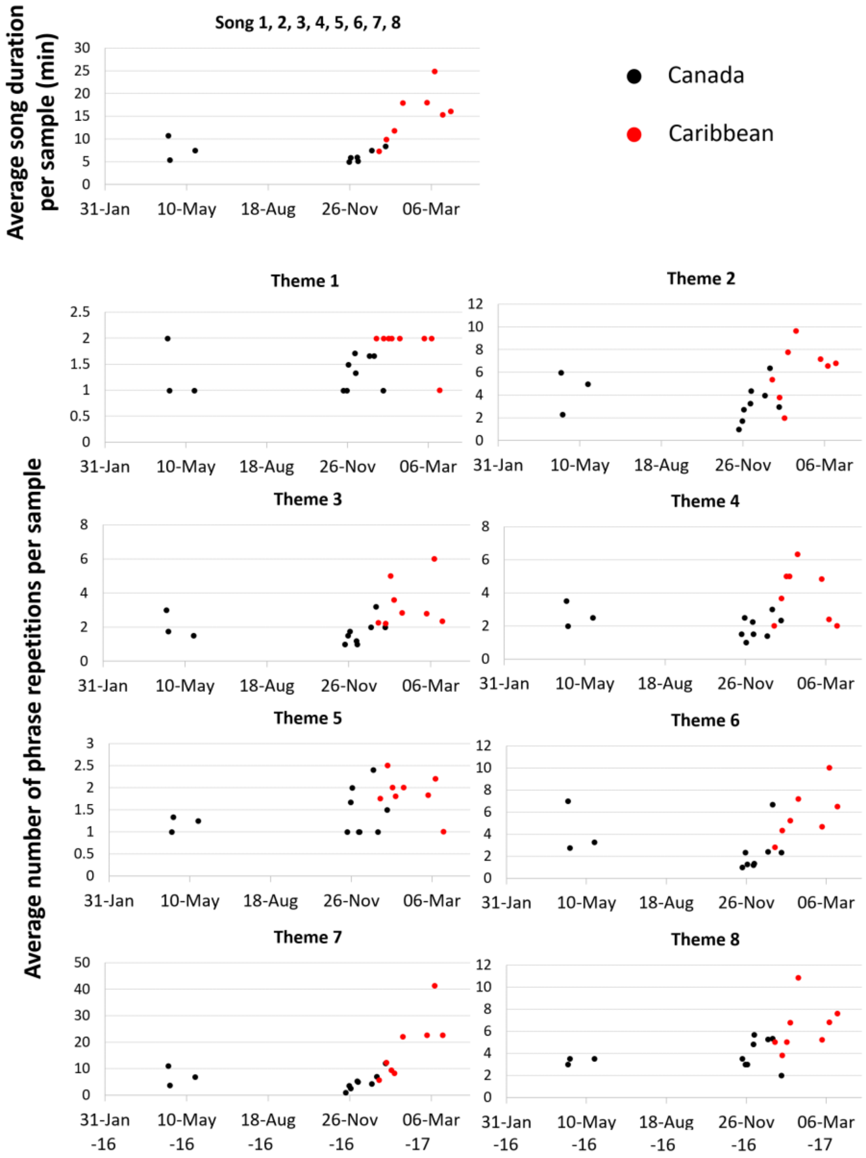

Figure 5.4 The average humpback whale song duration per sample of the most commonly observed song (top) and the average number of phrase repetitions per sample for each theme (bottom) recorded at three stations off eastern Canada (black) and one station in the Caribbean (red).

5.6 DISCUSSION

Acoustic recordings captured western North Atlantic humpback whale songs at the end of the 2015-2016 winter breeding season (in Canada during the spring), at the start of the subsequent 2016-2017 breeding season (in Canada through the fall and early winter), and into the peak of the 2016-2017 winter breeding season (in the Caribbean in winter to early spring). Unfortunately, I did not have access to data recorded in February from the Dominican Republic, and songs were not captured in high latitude recordings in the spring of 2017, preventing me from observing an entire breeding season. The sample size included in this analysis was small (20), especially for the Canadian stations (3-5 per station) where it proved challenging to find singing bouts of sufficient quality for reliable song analysis. Ideally, I would have analyzed numerous samples spread evenly over the recording period (such as was done in the Caribbean by examining songs from every 10 days), but, while songs occurred throughout these Canadian data sets (Kowarski et al. 2019, Kowarski et al. In Review), few were sufficiently high SNR with enough song repetitions to be suitable for analysis. The Caribbean data revealed a different set of challenges, with so many whales chorusing at the same time, the difficulty lay in finding a timeframe where an individual was consistently and obviously closer to the recorder than other singers to allow a single song to be tracked. The low availability of quality song samples in Canada could reflect 1) there being fewer individuals in the recorder area 2) the males in the recorder area are generally less motivated to sing, therefore fewer singing males relative to peak breeding season, reducing the chances of one singing near a recorder, 3) those males that do sing are also less motivated to produce full song (e.g., the song fragments described in Kowarski et al. 2019), or 4) singing males are less motivated to produce loud songs such that there is a continuum in source levels (SLs) where non-songs have the lowest SLs, mid-season songs have the highest SLs, and early- and late-season songs have intermediate SLs (Au et al. 2006, Dunlop et al. 2013a). The number of songs per sample were lower in Canada compared to the Dominican Republic which can be explained, in part, by the whales singing shorter song sessions (Tyack 1981, Vu et al. 2012). Regardless, even with the small sample size over a single breeding season, I was able to observe obvious temporal trends in several aspects of humpback whale song. Most clearly, they became longer and less variable through the breeding season.

My observations of song development are discussed usefully within the framework of the most well described song development process in the animal kingdom, bird song. Analogies have been drawn between bird song and humpback whale song in previous studies, with the functional unit of the bird song equivalent to a humpback whale song phrase (Cerchio et al. 2001, Cholewiak et al. 2013, Allen et al. 2018, Cholewiak et al. 2018, Garland and McGregor 2020). Bird song development after hatching has been described in three consecutive phases: subsong (quiet babbling), plastic (variable, non-stereotyped) song, and crystalized (stereotyped or stable) song (Thorpe and Pilcher 1958, Clark et al. 1987). These song phases are driven by an increase in testosterone levels in the young male birds that effect song control brain nuclei (Lofts and Murton 1968, Nottebohm et al. 1986, Meitzen et al. 2007). Some bird species maintain their crystallized song through their life (closed-ended or age-limited learners) while other bird species are more reminiscent of humpback whales as they continue to learn new songs through adulthood (open-ended learners) and seasonally produce non-stereotyped song early in the breeding season (Marler et al. 1988, Van Hout et al. 2009). Similar song development phases and associated plastic physiological processes that occur in the first year of a bird’s life, take place seasonally for adult birds that sing during the breeding period on an annual cycle (Nottebohm et al. 1986, Marler et al. 1988, Van Hout et al. 2009, Alliende et al. 2017). In adult canaries, Nottebohm et al. (1986) found that song control nuclei in the brain grow during subsong and plastic song phases before reaching peak size when crystalized song is produced. This nuclei size is maintained through the canary breeding season before reducing to the size of that seen in 3- to 4-month-old birds at the end of the breeding season. Song nuclei remain reduced in size until the subsequent breeding season when they once again begin to grow.

The initial subsong period of bird song development is reminiscent of the song fragments described early in the singing season in humpback whales (Kowarski et al. 2019, Kowarski et al. In Review). Indeed, while the earliest song analyzed here was in November, singing behaviour began as early as September (Kowarski et al. 2019, Kowarski et al. In Review), but was not defined as 'full song'. These song fragments were analyzed in more detail in the Bay of Fundy in fall 2015 (Kowarski et al. 2019) and were almost always composed of phrases that later occurred in full songs. Most of these 2015 song fragments were composed of one or two themes that were not repeated. Future work to look closely at early season song fragments on a broader scale and gain an understanding of which themes are heard first would be revealing. Early season singing behaviour outside of known breeding grounds has been recorded globally, resulting in some speculation that reproductive behaviours including mating may not be restricted to low latitudes (Mattila et al. 1987, McSweeney et al. 1989, Garland et al. 2013a, Magnúsdóttir et al. 2014, Kowarski et al. 2018, Kowarski et al. 2019). In songbirds, Riters et al. (2019) proposed that song production outside of the typical context (for mate attraction and territory defense) is 'practice' and while it is critical for successful mating as it allows for learning and maintenance, it is a form of play. Such may similarly be the case for early humpback whale singing behaviour on feeding grounds.

The second phase of bird song development termed plastic song is a period of novel combinations of song patterns or ‘combinatorial improvisation’ (Marler and Peters 1982, Nelson 1997). This plastic song was similarly observed here in November to December when the order of themes inconsistent within and between samples as different themes were skipped. Nottebohm et al. (1986) found that male adult canaries acquired most new syllables during the plastic phase of song instability. Plastic song may similarly be important for social learning and song evolution in humpback whales. Here I observed songs eventually returning to the same pattern (theme sequence) observed the previous spring, other seasons or data sets could well reveal a novel song that results from the plastic song phase.

The final phase in bird song development is when song becomes crystallized. This increase in stereotyped singing was similarly observed here where in January and March most samples contained only one order of themes which was consistent across samples. In the spring, at the end of the 2015-2016 winter breeding season, songs were also crystalized. In this particular data set the crystalized song remained unchanged in terms of theme order, but humpback whale songs have been described changing within and between breeding seasons (Payne et al. 1983, Noad et al. 2000, Cerchio et al. 2001, Garland et al. 2011) such that, their crystalized song evolves in a manner comparable to the village indigo bird (*Vidua chalybeata*) and yellow-rumped cacique (*Cacicus cela*) (Thompson et al. 1981, Cerchio et al. 2001). Having observed only one year and likely one population, it is not unsurprising that song evolution at the theme order level was not apparent here. A closer look at the unit level would almost certainly reveal more subtle changes through time (for example theme 1 seemed to have evolved by the end of March 2017) as has been described over short time periods (within a single season) in a number of studies including Payne et al. (1983), Cerchio et al. (2001), and Arraut and Vielliard (2004).

Here, I documented song duration increasing during the breeding season (changing from ~5 to ~25 min long) with some evidence of a peak between January and March that was achieved via the increased repetition of phrases for all themes. Ryan et al. (2019b) similarly reported an increase in song duration through the breeding season for the high-latitude northeast Pacific humpback whales where songs increased in duration from an average of ~5 min in October to a peak of ~10 min in January, before reducing to ~8 min in February, but song durations were not reported for March onward, so it is unclear how song duration trended for the remainder of the season. Other studies explored changes in song duration through time solely on breeding grounds and the trends were less consistent than observations at high latitudes (e.g., present study and Ryan et al. 2019b). Cerchio et al. (2001) reported an increase in song duration through the breeding season of humpback whales in Hawaii and Mexico, though only two periods were analyzed (January to February and April) and the change was less dramatic with songs in January to February ~2 min shorter than those in April. Cerchio et al. (2001) concluded that the increase in song duration in Hawaii and Mexico was attributed to both an increase in phrase repetitions and the animals singing longer phrases (a characteristic not explored here). In Hawaiian humpback whales, Payne et al. (1983) found in one year song duration increased through the early season (December to February), while in the following year it decreased (November to February), with the trends reflected in the number of phrases per theme. However, Payne et al. (1983) did not limit their duration analysis to songs of the same theme order, and noted introduction of new themes during within-season song evolution which would have effected their song duration results. It may be that early season songs on high latitudes follow more annually consistent trends (e.g., increasing in duration) than those on low latitudes where songs are well developed and are undergoing evolution.

The longest songs in the present study by far, were observed in the Dominican Republic. Miller et al. (2000) found that humpback whales increased song length (by producing longer themes as described here) in response to sonar, potentially as a strategy to compensate for the auditory interference of the sonar. The many simultaneous singers on the Dominican Republic breeding ground may cause interference in the audibility of each individual song and, much like with sonar, to compensate, the whales sing longer songs. Fournet et al. (2018c) found that humpback whales increased the source level of their vocalizations in response to louder ambient environments (natural or otherwise). It is therefore reasonable to assume that in the Dominican Republic, where chorusing whales increase ambient sound levels, humpback whales produce not only longer, but louder songs. The challenge of differentiating between chorusing singers was one faced by the analysts of the present paper, it is thus not unlikely that it is similarly faced by conspecifics. It is important to emphasize the trends observed here regarding song duration are based on a small sample size, one season and this is only one of a myriad of song characteristics that can change through time. Therefore, while the above explanation regarding auditory interference is valuable and can inform future research questions, it is likely only part of many contributing factors that influence singing behaviour.

An additional explanation for the trends in singing observed here are the physiological processes of the male humpback whales. Male humpback whale testis size has been reported to increase during the breeding season and testosterone levels peak in January and February in North Pacific humpback whales, which corresponds to the timing of the long song durations and more stereotyped songs in terms of theme order observed here (Chittleborough 1955, Cates et al. 2019). The physiological changes that are known to control many aspects of seasonal singing in birds, may similarly apply to male humpback whales (Lofts and Murton 1968, Nottebohm et al. 1986, Meitzen et al. 2007, Dawson 2013, Kowarski et al. 2019). Indeed, as testosterone levels begin to increase in the fall, whales produce song, but they may not yet be able (or motivated) to consistently sing the same pattern until testosterone levels reach some threshold. Future work at the individual singer level for song development in relation to testosterone levels and other physiological processes would be revealing.

5.7 **CONCLUSIONS**

This study has provided a glimpse into seasonal song development of humpback whales. As previously described by Payne et al. (1983), male humpback whales sang the same song in the fall as they did the previous spring in Canada. However, they did not simply ‘remember’ and continue singing in the same manner as they left off. Rather, they went through a period of plastic song, where the order of the themes was varied as different themes were omitted, that is potentially related to intermediate testosterone levels and could be an important time for song evolution and social learning. After a few months of plastic song, humpback whales returned to consistently singing the same song that was produced the previous spring. Even then, song behaviour did not go unchanged, but rather increased in phrase repetitions gradually through time. However, these trends are based on a small sample size and should be confirmed with additional data across time for multiple breeding seasons. This work highlights the importance of including high latitude songs in the observation of humpback whale song change through time, without which, such telling trends may not be apparent.

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CHAPTER 6 DISCUSSION

The song of the humpback whale has long captivated the public as well as scientists. Researchers have dedicated their life's work to understanding this elaborate and complex acoustic display. Yet, many questions remain; among them, why do they sing and what evolutionary pressures have selected for complexity, plasticity, and conformity? Humpback whales are arguably the best studied baleen whale species, owing largely to their regular occurrence in shallow coastal habitats and lack of aversion to vessels. Research projects spanning decades using shore-based, vessel-based, aerial-based, and/or underwater observations have been ongoing in regions like Hawaii, Alaska, and Australia. Humpback whales have been observed visually and acoustically, they have been photo-identified, tagged, tracked, and followed (e.g., Frankel and Herman 1993, Videsen et al. 2017, Allen et al. 2018, Fournet et al. 2018a, Stevick et al. 2018, Darling et al. 2019b). They have been exposed to sounds, both from conspecific playbacks and anthropogenic noise sources (e.g., Frankel and Herman 1993, Dunlop et al. 2013b). Yet there has not been a single report of observed copulation, nor of singing, that would yield unequivocable conclusions regarding cause and effect (Herman 2017). It seems that despite the best efforts of the scientific community, humpback whales have managed to maintain an air of mystery.

Humpback whale behaviour has caused challenges and frustrations within the broader field of marine passive acoustic monitoring (PAM). Indeed, mention humpback whales to a team of big data PAM researchers and you will be met with a series of sighs, face palms, and groans of defeat! How do you effectively analyze a complex and dynamic acoustic repertoire that is incompletely understood/described? Add the fact that humpback whale acoustic signals change through time and overlap with the characteristics of right, fin, bowhead, sei, and killer whales, as well as some seals and you find experts worldwide both amazed and infuriated by the beautiful sounds of the humpback whales.

My thesis considers the challenge of big PAM data analysis methods for baleen whales before diving into an undescribed aspect of the humpback whale acoustic repertoire, how singing seasonally ends in the spring and develops in the fall. This work can be used to inform our understanding of humpback whale singing behaviour, but also provides valuable information for big PAM data analysis techniques. The questions and challenges that I have mentioned regarding humpback whales are daunting, and I do not claim to have overcome queries pondered for years in a single thesis. Rather, I provide a new outlook on old questions - a shift from why do they sing on breeding grounds to why do they start singing at all?

6.1 SUMMARY OF FINDINGS

A review of baleen whale literature that utilized big PAM data revealed a range of protocols across different research questions. Methodologies ranged from the review of all acoustic data by a human analyst to the application of solely automated methods. Areas needing improvement were identified including a lack of consistency in automated detector evaluation and protocol terminology. I provided recommendations to promote reliable methods that are achievable for many research groups and comparable across projects and sectors. This review can inform discussions in the PAM community to determine minimum standards and best practices. Where vocalizations were not adequately described or effective automated detectors did not exist, analysis methods leaned much more toward the application of manual review. Such was the case for the remainder of my thesis, where I undertook manual analysis to understand a poorly understood dynamic repertoire.

Acoustic recordings collected in the western Atlantic from as far north as Labrador, Canada to as far south as the Dominican Republic were used to analyze humpback whale vocalizations from 2015-2017. Recordings were collected by numerous research programs with only the Dominican Republic data set aimed at humpback whale research. In this respect, this thesis is an excellent example of the value of PAM data well beyond its original intention and the unique information that can be gained from a research community that encourages the open sharing of data and knowledge.

Humpback whales were acoustically present through the fall and early winter from Newfoundland and Labrador to Massachusetts Bay. Song onset, the transition into the winter singing season, began in these northern waters. Song development was found to be gradual, occurring over many weeks on a continuum of increasing organization, to which I defined and applied vocal categories (e.g., non-song, song fragment, full song) for ease of description. Song initiation generally began with song fragments, pieces of incomplete songs that occurred through the fall. Singing started off sporadic, beginning around late September, and did not become regular until late October, by which time full songs were heard. There seemed to be correlations between the onset of regular singing with latitude, photoperiod, and temperature; with singing occurring earlier at lower latitudes where there are longer days and warmer waters. Full songs were initially inconsistent in terms of theme order, with one or more themes skipped in any given song. These plastic songs occurred through to December before taking on a more consistent order that matched that of the previous spring. The songs on the Dominican Republic breeding ground in January and March were more crystalized in terms of theme order. The duration of songs, driven by phrase repetitions, increased gradually from November to March. The cessation of singing in the spring was only captured on one recorder in Canada in 2016. Song cessation was abrupt compared to song initiation, with songs all but absent after late May and minimal song fragments apparent. Spring songs, late in the breeding season, were crystalized in terms of theme order and had an intermediate duration between that of early-season and mid-season song. One of the data sets was analyzed for diel patterns and I concluded that songs occurred more at night than during the daytime, like what has been found previously (e.g., Au et al. 2000, Kowarski et al. 2018).

6.2 IMPLICATIONS FOR PAM DATA ANALYSIS METHODS

Seasonal humpback whale song development should be considered in future PAM analysis whether researchers are looking at species acoustic occurrence or characterization of song. The effectiveness of automated detectors, be it for humpback whale signals or those of other species with overlapping calls, will be impacted by the timing, nature, and location of humpback whale song development. Future researchers can incorporate this new understanding of song onset and cessation into their work in a number of ways including a) developing automated detectors that are either season-specific or incorporate confidence thresholds that account for season, b) applying additional manual review to data collected in more challenging seasons like the fall (autumn), c) developing automated detectors that are sensitive to context including place, time, chance of detecting humpback whale song vs non-song vocalizations. For human analysts, understanding when to first expect singing behaviour and what it will look like is helpful. It would be beneficial to review songs later in the season and gain some understanding of the themes present, before determining when humpback whales are present early in the season. This will allow an analyst to discern between a song fragment and the vocalizations of other species with greater confidence.

For researchers aiming to characterize humpback whale songs for a particular place and time in PAM data, considerations should include seasonal song development. Using songs early in the season as an exemplar for a given season could produce misleading results. Furthermore, applying the practice of determining the average song of a sample (e.g., Garland et al. 2012) would be inappropriate for the plastic early-season songs. Any investigation into song length or phrase repetition should consider where in the season to sample. The ever-changing continuum of humpback whale songs in terms of how many themes are produced, what themes are produced, and song length should further be considered in any work looking at using song properties (e.g., song duration, number of units) for density estimation.

6.3 IMPLICATIONS FOR WHY THE HUMPBACK WHALE SINGS

6.3.1 Bird brain?

Humpback whale songs have been placed in the context of bird songs for years (Tyack 1981, Cerchio et al. 2001, Cholewiak et al. 2013, Allen et al. 2018, Cholewiak et al. 2018, Garland and McGregor 2020), largely because some bird species have song characteristics somewhat similar to humpback whales. Furthermore, bird songs have been studied in great depth, both in lab and field settings, in a manner that is unachievable for the large, free-ranging humpback whales. Indeed, the vast amount of research on oscine birds has deemed them the model species when it comes to song, but how analogous are the song processes employed by these evolutionarily disparate groups? Could convergent evolution have produced the same mechanisms in both birds and marine mammals? Fee and Goldberg (2011) believe so, drawing parallels between mammalian and songbird basal ganglia circuitry for vocal and motor learning. If comparable processes were at play across these different groups, I would expect to see the same behavioural and physiological trends through the song season.

Many aspects of the humpback whale vocal repertoire described in the present thesis aligns with that of the canary (*Serinus canaria*), an open-ended learner that undergoes seasonal song development. At the onset of the breeding season, both species produce song fragments, or subsongs, for a period before transitioning into static songs and finally producing crystalized songs during the peak breeding season (Nottebohm et al. 1986). Vellema et al. (2019) found that once songs are developed, canaries can retain that vocal motor memory for an extended period, such that songs can be recovered. Humpback whales beginning to sing in the fall of 2016 returned to the same song they had sung the previous spring, indicating a level of memorization. For many bird species, the onset of seasonal singing has been linked to physiological changes that are influenced by environmental cues, primarily photoperiod (Lofts and Murton 1968, Nottebohm et al. 1986, Meitzen et al. 2007, Dawson 2013). I have similarly found evidence that the onset of humpback whale regular singing in the western North Atlantic is correlated with daylight hours. While my findings certainly support a similarity between at least some songbirds and humpback whales, it lacks a link between the physiological processes of the species.

By a convenient coincidence, over the course of the present thesis, a fascinating line of work has emerged from the North Pacific and eastern Australia where Cates et al. (2019) and Mingramm et al. (2020) have investigated the hormone levels of humpback whales, respectively. Male testosterone levels were found to increase through the breeding season, peaking in January and February (Cates et al. 2019), a pattern that reflects that of song development observed here with song length and crystallization being highest between January and March. This trend in testosterone levels and its relationship with song is well described in many oscine bird studies where hormone levels impacting the development of song control brain nuclei which develop through the breeding season before once again reducing in size (Lofts and Murton 1968, Nottebohm et al. 1986, Meitzen et al. 2007, Dawson 2013). Such a link between testosterone, inherently connected to reproductive readiness, and song has implications for the sexual selection of singing behaviour. Indeed, females could use song as a cue for mature males. Mingramm et al. (2020) found principal male escorts of females to have higher testosterone levels than that of secondary escorts.

Given the ethical and logistical challenges in manipulating humpback whale brains, we may never be able to state unequivocally that humpback whale song and bird song are controlled by similar or analogous physiological processes. However, there is mounting evidence that this is at least partially true. Therefore, in considering why the humpback whale sings, researchers must consider that part of the answer is that they are physiologically capable and motivated to do so. It seems songs are rare in the summer and absent from females, because they are less motivated of producing song.

This similarity between bird and humpback whale song systems has implications for the selective forces acting on humpback whale song, as findings in avian literature could be extremely informative and should be taken into consideration in future research. For example, Robinson et al. (2019) reviewed the song systems of closed- and open-ended learning songbirds and proposed that female selection for large repertoire size and elaborate songs resulted in the evolution of open-ended learners and plastic song in adults. Plastic song in oscine birds was further correlated with polygynous mating systems which have been described in humpback whales (Cerchio et al. 2005, Robinson et al. 2019).

6.3.2 Does motivation for singing depend on context?

The change in song production through the breeding season is likely connected not only to physiological changes (e.g., producing fragments when testosterone levels are low and stereotyped full song when levels are high), but also to the whales singing for different reasons in different contexts.

High latitude humpback whale singing has been recorded globally, but it is unclear if this indicates that these areas are also important for mating (Mattila et al. 1987, McSweeney et al. 1989, Magnúsdóttir et al. 2014, Kowarski et al. 2018). Here, I found that while singing began early in the season, it looked quite different than what was observed later in the season (in high or low latitudes). Ryan et al. (2019b) and Magnúsdóttir and Lim (2019) similarly saw a progression through the breeding season in high latitudes. Riters et al. (2019) concluded that in songbirds, songs produced outside of the context of territory defense and mate attraction are an important form of play that is stimulated by intrinsic reward mechanisms and is key for song learning and maintenance. The idea that migratory routes and feeding grounds are important places for song learning has similarly been proposed by Payne et al. (1983), Garland et al. (2013a), Owen et al. (2019), Mcloughlin et al. (2018), and Magnúsdóttir and Lim (2019). Early season plastic songs in canaries are when most new song syllables are acquired (Nottebohm et al. 1986). This period of song instability may also be important for humpback whales, allowing for social learning and song evolution.

In the peak of the breeding season off the Dominican Republic, the longest and most stereotyped humpback whale songs were produced. During this time, humpback whales may have produced longer (and potentially louder) songs to compensate for being masked by conspecifics. They have been found to undertake such strategies in other contexts (e.g., in the presence of anthropogenic sound) in response to conflicting acoustic signals (Miller et al. 2000, Fournet et al. 2018c).

6.4 FUTURE WORK

The work presented here contributes to the fields of humpback whale behavioural ecology and marine PAM. Additional research, including expanding the present work, would be very informative for interpreting PAM data and understanding humpback whale vocal changes over space and time. Here, I have looked at the population or regional level of vocal change through the singing season. Tracking individuals, especially juvenile males, through time using acoustic tags could be extremely revealing. It would be particularly interesting to understand how a humpback whale song develops for the first time as a calf matures. Linking such studies directly with hormone analysis (rather than inferring it across populations) could confirm the assumptions made here. There is an abundance of information on song development to be gained from other singing baleen whale species. For example, blue whales seem to have more variation in their calls during early singing (Ward et al. 2017).

6.5 CONCLUSIONS

Even though humpback whales have delighted people on the eastern seaboard of the U.S.A. and Canada for generations, little research has been completed on the singing behaviour of this population relative to other regions where humpback whales congregate (e.g., Hawaii, Alaska, and Australia) (Payne and Payne 1985, Magnúsdóttir and Lim 2019). Even for the present research, the primary objectives of the acoustic data used was not to identify humpback whale vocalizations. Instead, research has focused on more at-risk species. While focusing on animals known to be at risk is certainly critical, ignoring those with a larger ecological impact in terms of biomass, acoustic contributions to ambient environment, and trophic level organization (Haro et al. 2020) prevents a full understanding of a complex ecosystem. For example, we did not previously know that humpback whales were so common throughout Canadian waters in the fall and winter, nor that this represents a potentially important time for them in terms of song development, practice, and learning.

By including acoustic recordings from both high and low latitudes, a more complete picture of humpback whale song change through time has been presented than would be gained from exploring a single location. Song development occurred on a continuum, gradually transitioning from song fragments in early fall to plastic songs, before acquiring a more stereotyped order. It was these crystalized songs that were observed on the southern breeding ground, increasing in duration through the season. Knowledge gained from the literature on bird song has been valuable in interpreting the present findings. In describing seasonal humpback whale song ontogeny, the present work has informed future PAM research and provided a few new pieces to the humpback whale puzzle which is slowly becoming clearer.

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APPENDIX A Chapter 2

A.1 Methods

In Web of Science the “All Databases” option was used with the below query on 10 June 2019. TOPIC: (("Passive Acoustic Monitoring" OR "Passive Acoustic*" OR Acoustic* OR PAM)) AND TOPIC: ((baleen OR mysticete* OR whale*)) AND TOPIC: ((method* OR analys* OR automated OR computation* OR algorithm* OR manual OR human-in-the-loop OR precision OR recall OR Fscore OR detector* OR optimization OR validation OR evaluation OR review)) NOT TOPIC: ((shark* OR localiz* OR localis*)).

Keywords were applied to the “Topic” category that searches titles, abstracts, keywords, and more. Effort was made to exclude localization studies at this stage as analysis techniques for localization are more specialized than the breadth of the present review. The initial query was meant to be inclusive, with little exclusions in terms of species, date, or topic. The query resulted in 1,557 references (titles and abstracts) that were extracted via EndNote and loaded into Covidence. Four studies were highlighted as duplicates by Covidence and were removed.

Within the Covidence platform, relevant studies were narrowed down in two steps. First, the title and abstract of the remaining 1,553 studies were screened for topics covering baleen whale PAM. Second, the resulting 469 potentially relevant studies underwent a full text review and were subjected to eligibility criteria (TABLE A-1). Data (first author, publication year, and title) from the remaining 166 studies (TABLE A-2) deemed relevant were extracted to Excel from the Covidence platform.

Through a detailed full text review, information on relevant variables to address the present review questions was collected from each article and recorded in Excel (Tables A-3 and A-4). Each literature question was investigated in the manner summarized in TABLE A-4 with recommendations for future work in PAM of baleen whales included in the discussion.

TABLE A-1. Exclusion and inclusion criteria applied to the 469 potentially relevant studies during the full text review.

Inclusion Criteria	**Exclusion Criteria**
• Report on one or more mysticete species. • Utilize PAM techniques. • Be peer-reviewed.	• Study purely describing automated detector development or methodology. • Review or overview article. • Study that utilized results from previous study. • Article commenting on previous research. • Study describing real-time data analysis. • Modeling or simulation study. • Study purely describing soundscape or ambient sound. • Study published 2000 – 2019. • Localization study.

TABLE A-2. 166 Studies included in the literature review.

References

Arraut and Vielliard (2004)
Au et al. (2000)
Balcazar et al. (2015)
Boisseau et al. (2008)
Bort et al. (2015)
Bouchard et al. (2019)
Buchan et al. (2010)
Buchan et al. (2014)
Buchan et al. (2015)
Buchan et al. (2018)
Burnham and Duffus (2019)
Calderan et al. (2014)
Castellote et al. (2012b)
Castellote et al. (2012a)
Cato et al. (2001)
Cerchio and Dahlheim (2001)
Cerchio et al. (2001)
Cerchio et al. (2014)
Charif et al. (2013)
Cholewiak et al. (2018)
Clark et al. (2002)
Clark et al. (2010)
Garland et al. (2013b)
Garland et al. (2015)
Garland et al. (2017)
Gavrilov et al. (2012)
Gavrilov and McCauley (2013)
Gavrilov et al. (2018)
Goldbogen et al. (2014)
Gridley et al. (2018)
Halliday et al. (2019)
Handel et al. (2012)
Hannay et al. (2013)
Harris et al. (2013)
Heimlich et al. (2005)
Helweg et al. (2005)
Hodge et al. (2015)
Jacobs et al. (2019)
Johnson et al. (2015)
Jolliffe et al. (2019)
Kerosky et al. (2012)
Klinck et al. (2012b)
Kot et al. (2012)
Kowarski et al. (2018)
Mellinger et al. (2007a)
Mercado (2016)
Mercado (2018)
Miksis-Olds et al. (2008b)
Miksis-Olds et al. (2018)
Morano et al. (2012a)
Morano et al. (2012b)
Munger et al. (2008)
Munger et al. (2012)
Murray et al. (2014)
Mussoline et al. (2012)
Nieukirk et al. (2004)
Nieukirk et al. (2012)
Oleson et al. (2003)
Oleson et al. (2007)
Oleson et al. (2014)
Oswald et al. (2011)
Oviedo et al. (2008)
Pace et al. (2010)
Paniagua-Mendoza et al. (2017)
Parks and Tyack (2005)
Parks et al. (2007)
Samaran et al. (2013)
Sciacca et al. (2015)
Simão and Moreira (2005)
Simon et al. (2010)
Širović et al. (2004)
Širović et al. (2006)
Širović et al. (2009)
Širović et al. (2015a)
Širović et al. (2015b)
Širović et al. (2017)
Soldevilla et al. (2014)
Stafford et al. (2001)
Stafford et al. (2004)
Stafford et al. (2005)
Stafford and Moore (2005)
Stafford et al. (2007b)
Stafford et al. (2007a)
Stafford et al. (2009)
Stafford et al. (2011)
Stafford et al. (2012)
Stimpert et al. (2007)
Stimpert et al. (2011)

References

Darling and Sousa-Lima (2005)
Darling et al. (2006)
Darling et al. (2012)
Davis et al. (2017)
Delarue et al. (2009)
Delarue et al. (2013)
De Vreese et al. (2018)
Dombroski et al. (2016)
Dombroski et al. (2017)
Dunlop et al. (2007)
Dunlop et al. (2010)
Dunlop et al. (2014)
Dunn and Hernandez (2009)
Edds-Walton (2000)
Español-Jiménez and van der Schaar (2018)
Eyre and Frizell (2012)
Fournet et al. (2015)
Fournet et al. (2018a)
Fournet et al. (2018b)
Frouin-Mouy et al. (2017)
Kowarski et al. (2019)
Lammers et al. (2011)
Leroy et al. (2016)
Leroy et al. (2017)
Leroy et al. (2018a)
López-Urbán et al. (2018)
Macknight et al. (2001)
Madhusudhana et al. (2019)
Maeda et al. (2000)
Magnúsdóttir et al. (2015)
Mahanty et al. (2015)
Marcoux et al. (2017)
Marques et al. (2011)
Matsuo et al. (2013)
Matthews et al. (2014)
McCordic et al. (2016)
McDonald (2006)
Melcon et al. (2012)
Mellinger et al. (2000)
Mellinger et al. (2004)
Parks et al. (2011)
Ponce et al. (2012)
Rankin et al. (2005)
Rannankari et al. (2018)
Rayment et al. (2018)
Rebull et al. (2006)
Recalde-Salas et al. (2014)
Rekdahl et al. (2015)
Rekdahl et al. (2017)
Rice et al. (2014)
Risch et al. (2012)
Risch et al. (2013)
Risch et al. (2014b)
Risch et al. (2014a)
Risch et al. (2019)
Romagosa et al. (2015)
Root-Gutteridge et al. (2018)
Ryan et al. (2019a)
Salisbury et al. (2016)
Samaran et al. (2010)
Tellechea and Norbis (2012)
Tervo et al. (2011)
Thomisch et al. (2016)
Tripovich et al. (2015)
Trygonis et al. (2013)
Tsujii et al. (2016)
Tyson et al. (2007)
Vanderlaan et al. (2003)
Videsen et al. (2017)
Vu et al. (2012)
Ward et al. (2017)
Webster et al. (2016)
Webster et al. (2019)
Whitt et al. (2013)
Wiggins et al. (2005)
Wright et al. (2018)
Wright et al. (2019)
Zoidis et al. (2008)

TABLE A-3. Data collection scheme for all studies and restricted to those with more than 1000 hr of acoustic data (1000 +).

Articles	Variable	Data collected
All	Data analysis method	Coded as a) full manual (no automated detector, manually reviewed all acoustic data collected), b) partial manual (no automated detector, manually reviewed a subset of the acoustic data collected), c) automated (employed an automatic detector, did not manually review any data), d) manual and automated (employed some combination of automated and manual analysis), or e) unclear (method employed could not determine confidently from article).
	Data volume	Calculated or estimated in hr and coded as a) unclear (could not determine confidently from article the data volume), b) 0–10 hr, c) 11–100 hr, d) 101–1000 hr, e) 1,001–10,000 hr, f) 10,001–100,000 hr, or g) 100,001–860,000 hr.
	Number of species targeted	Number of species or aim was to capture "all present". If one species was targeted, but other species are noted (not included in results figures, tables, etc.), then considered 1 target species.
	Species described	Common species name.
	Data collection platform	Coded as autonomous (near) bottom-mounted, over the side (dipping), tag, fixed buoy, drift buoy, towed array, multiple platforms, or other/unclear.
1000 hr +	Research question	Coded as occurrence (spatial, temporal, or diel), characterization (of song or non-song vocalizations in terms of characteristics, patterns, or comparisons across time, space, or populations), occurrence and characterization, or other.
	Percent of data manually analyzed	Where applicable, reported amount described in article and converted to percent of data volume if not already done.
	Method to select subset of data for manual analysis	Reported description from article.
	Diel analysis	Coded as Yes or No, and methods described.
	Metrics to describe detector performance	Each metric or lack thereof recorded where applicable.
	Presentation of occurrence results	Coded as inapplicable, using presence, or using number of vocalizations/detections and described.
	Temporal breadth of data	Coded as <1, 1–2, 2–4, 4–6, 6–8, and 8–10 years
	Terminology used to desribe methodology	Each applicable term recorded.

TABLE A-4. Variables utilized and approach to explore each literature review question.

Literature review question	Variables utilized and approach
Did data collection platforms and data analysis methods vary with data volume for PAM data?	Summarize data collection platforms and data analysis methods utilized across studies with varying data volumes.
For large PAM data sets, how did data analysis methods vary depending how many species were targeted?	For studies with more than 1000 hr of acoustic data, describe data analysis methods including all applicable variables (e.g., percent of data manually analyzed, the method to select subset of data for manual analysis, and presentation of results) for a) studies targeting 1–2 species b) studies targeting all species acoustically present in data
For large PAM data sets, how did data analysis methods vary depending on the research question of the study?	For studies with more than 1000 hr of acoustic data, summarize the temporal breadth of data and data analysis methods including all applicable variables (e.g., percent of data manually analyzed, the method to select subset of data for manual analysis, presentation of results, and/or diel analysis) separately for each research question.
For large PAM data sets, what metrics were presented to describe automated detector performance?	For studies with more than 1000 hr of acoustic data that utilized automated detection techniques, summarize the metrics used to describe automated detector performance.
For large PAM data sets, what terminology was used to describe data analysis methods?	For studies with more than 1000 hr of acoustic data, summarize the terminology used to describe data analysis methods.
What data analysis methods, detector performance metrics, and terminology should be utilized in future baleen whale PAM studies?	Discuss consistency and inconsistency in variables collected and recommend methods for future research.

A.1 Results

TABLE A-5. Summary of methodologies for big PAM data characterization papers targeting 1–2 baleen whale species including full manual (FM), partial manual (PM), and a combination of manual and automated (M&A) methods. Both non-song (NS) and song (S) vocalizations (Voc. type) were characterized. The percent of data reviewed (%) was at times unclear (Unc.).

Voc. type	Method	Review protocol (% data reviewed)	Study
NS	FM	All acoustic data (100).	Fournet et al. (2018a)
NS	PM	Randomly selected 60 hr known to contain vocalizations (3.0).	Fournet et al. (2018b)
NS	PM	4 hr of every 24 (16.7).	Jacobs et al. (2019)
NS	PM	Randomly selected 20% of hr (20).	Stafford and Moore (2005)
NS	M&A	All automated detections (Unc.).	Rekdahl et al. (2017)
S	FM	All acoustic data (100).	Miksis-Olds et al. (2008b), Garland et al. (2015), Johnson et al. (2015), Cholewiak et al. (2018), Mercado (2018), Miksis-Olds et al. (2018)
S	PM	Selected 1–2 days/month (5.0).	Oleson et al. (2014)
S	PM	Selected 2 days/month (6.6).	Širović et al. (2017)
S	M&A	All automated detections for 2 of 3 years; randomly selected high-quality recordings for 1 of 3 years (Unc.).	Magnúsdóttir et al. (2015)
S	M&A	Automated detector identified songs; randomly selected subset of suitable songs for analysis (Unc.).	Delarue et al. (2009)

TABLE A-6. Summary of methodologies, including the percent of data manually analyzed, for full and partial manual analysis techniques for all occurrence papers with 1000 hr or more of data that target 1–2 baleen whale species.

Overall analysis method	Review protocol	%	Study
Full manual	Every hr to determine presence per hr	100	Samaran et al. (2010)
	Every 225 s file to determine presence per file	100	Wright et al. (2018)
	Every day until a vocalization was observed to reveal daily presence	100	Murray et al. (2014)
	All data to get occurrence of each vocalization	100	Sciacca et al. (2015)
	Long-term spectral averages to determine presence	100	Munger et al. (2012), Soldevilla et al. (2014), Širović et al. (2015a)
Partial manual	Random sample of six 1-min periods from each hr	10	Charif et al. (2013)
	Randomly selected 24-hr periods from each week	14	Matthews et al. (2014)
	All data not considered masked	67	Paniagua-Mendoza et al. (2017)
	340 of every 990 s	44	Rannankari et al. (2018)

TABLE A-7. Summary of manual review protocol, including the percent of data manually analyzed, for big passive acoustic monitoring data occurrence studies (targeting 1–2 baleen whale species) with the intent to determine some aspect of automated detector performance, optimize automated detectors, or create ROC curves. Protocols are summarized for those that additionally reviewed all automated detections (Y) and those that did not (N). The percent of data reviewed (%) was at times unclear (Unc.).

Reviewed all detections (Y/N)	Review protocol	%	Study
Y	Randomly selected 1 day/month.	0.2	Balcazar et al. (2015)
Y	Selected 26 days of varying ambient levels.	0.5	Mussoline et al. (2012)
Y	Randomly selected 20 days from each location.	2.0	Hodge et al. (2015)
Y	Subset across varying number of detections per file.	8.0	Kowarski et al. (2018)
Y	Randomly selected 10% of files.	10	Lammers et al. (2011)
Y	Randomly selected 20% of data.	20	Buchan et al. (2018)
Y	Every third day.[a]	33[a]	Davis et al. (2017)
Y	Spot-checked days without detections.	Unc.	Tripovich et al. (2015)
Y	Manually selected vocalizations from different time periods.	Unc.	Širović et al. (2015b)
N	5 min to get characteristics for automated detector and create ROC curve.	>0.001	Tsujii et al. (2016)
N	Randomly selected 100 files with low numbers of detections.	1.0	Širović et al. (2004)
N	Randomly selected 10 days from each location.	7.0	Risch et al. (2019)
N	Randomly selected subset.	Unc.	Gavrilov and McCauley (2013)
N	Low detection counts.	Unc.	Samaran et al. (2013)
N	Spot-checking.	Unc.	Thomisch et al. (2016)
N	Unclear (created ROC curve).	Unc.	Español-Jiménez and van der Schaar (2018)
N	Unclear.	Unc.	Wiggins et al. (2005)
N	Unclear.	Unc.	Nieukirk et al. (2012)
N	Unclear.	Unc.	Simon et al. (2010)

[a] Protocol and % for one of many recording sites, unclear of protocol at other sites and the resulting % for entire study.

TABLE A-8. Summary of how baleen whale occurrence results were presented in big PAM data studies that targeted 1–2 baleen whale species including the descriptive unit and how the unit was presented in the results of the study.

Unit	Presentation of results	Study
Number of vocalizations or automated detections	Per hr	Gavrilov et al. (2018)
	Per day	Munger et al. (2008), Matsuo et al. (2013), Risch et al. (2014a), Sciacca et al. (2015), Tripovich et al. (2015), Paniagua-Mendoza et al. (2017), Wright et al. (2018)
	Per week	Gavrilov and McCauley (2013)
	Per 8 days	Širović et al. (2009)
	Per month	Širović et al. (2004), Stafford et al. (2004), Stafford et al. (2005), Širović et al. (2009), Stafford et al. (2011), (2012a), Samaran et al. (2013), Bort et al. (2015), Buchan et al. (2018)
	Per season	Wright et al. (2018)
	Per year	Leroy et al. (2016) Wright et al. (2018)
	Daily average per minute	Thomisch et al. (2016)
	Weekly average per hr	Wiggins et al. (2005)
	Monthly average per day	Bort et al. (2015), Buchan et al. (2015)
	Average (across locations) per day	Mussoline et al. (2012), Charif et al. (2013)
	Median (unclear of what) per month	Balcazar et al. (2015)
Presence	Hourly	Širović et al. (2015a)
	Daily	Murray et al. (2014), Salisbury et al. (2016)
	15 min	Rannankari et al. (2018)
	# (or %) 30–32 s recordings per day	Munger et al. (2012), Español-Jiménez and van der Schaar (2018)
	# min per day	Soldevilla et al. (2014)
	% 225 s segments per day	Wright et al. (2018)
	% half hr per day	Tsujii et al. (2016)
	# (or %) hr per day	Mellinger et al. (2007a), Matthews et al. (2014), Kowarski et al. (2018) Risch et al. (2019)
	# days per week	Davis et al. (2017)
	% 30 s recordings per month	Lammers et al. (2011)
	% hr per month	Samaran et al. (2010), Risch et al. (2014a)
	# (or %) days per month	Whitt et al. (2013) Morano et al. (2012a), Hodge et al. (2015)
	Average daily hr per week	Kerosky et al. (2012)

TABLE A-9. Summary of how diel variation in vocalization behaviour was explored across big PAM data studies including whether the full data set was included in the diel analysis, the number of light regimes per 24-hr day, the unit used to compare light regimes, and whether nautical twilight based on angle of the sun was used to define light regimes.

Full data set (Y/N)	**# of light regimes**	**Units to compare light regimes**	**Nautical twilight (Y/N)**	**Study**
Y	48	Visualized only.	Unclear	Simon et al. (2010)
N	24	Total number of vocalizations in each hr.	N	Morano et al. (2012a)
Y	24	Average number of vocalizations per hr.	N	Bort et al. (2015)
Y	24	Hourly mean adjusted number of vocalizations per hr.	Y	Wiggins et al. (2005)
Y	5	Hourly mean adjusted number of vocalizations per hr.	Y	Munger et al. (2008)
N	4	Average number of vocalizations events per hr.	Y	Matthews et al. (2014)
Y	4	Hourly mean adjusted hr with calls presence	Y	Kowarski et al. (2018) Kowarski et al. (2019)
N	3	Hourly mean adjusted number of vocalizations per hr.	Y	Stafford et al. (2005) Risch et al. (2013)
Y	3	Hourly mean adjusted number of vocalizations per hr.	Y	Mussoline et al. (2012)
Y	3	Percent 32 s segments with vocalizations present.	Y	Español-Jiménez and van der Schaar (2018)
Y	3	Average number of vocalizations per hr.	Y	Wright et al. (2018)
Y	2	Ratio of vocalizations at night/day.	N	Gavrilov and McCauley (2013)
Y	2	Average minutes per hr with vocalizations present.	Y	Soldevilla et al. (2014)
N	Unclear	Diel cycle index.	Y	Risch et al. (2019)

TABLE A-10. Summary of methodologies for big PAM data papers that explored both occurrence and characterization of vocalizations and targeted 1–2 baleen whale species. Methodologies included full manual (FM), partial manual (PM), and a combination of manual and automated (M&A). The percent of data reviewed (%) was at times unclear (Unc.).

Occurrence analysis			**Characterization analysis**			**Study**
Method	**Review protocol**	**%**	**Method**	**Review protocol**	**%**	
FM	All acoustic data.	100	**FM**	All seen during occurrence analysis.	Unc.	Stafford et al. (2007b), Leroy et al. (2017)
FM	All acoustic data.	100	**PM**	Selection of high SNR vocalizations.	Unc.	Stafford et al. (2001), Morano et al. (2012b)
FM	All acoustic data.	100	**M&A**	Random selection of 10% of hr.	10	Stafford et al. (2012)
FM	All acoustic data.	100	**M&A**	Selection of high SNR vocalizations.	Unc.	Gavrilov et al. (2012)
PM	Portion of every file.	5	**PM**	Selection of high SNR vocalizations.	Unc.	Kowarski et al. (2019)
PM	Every fourth day.	25	**PM**	All seen during occurrence analysis.	Unc.	Heimlich et al. (2005)
PM	15 1-min files for each hr.	25	**PM**	All seen during occurrence analysis.	Unc.	Rice et al. (2014)
M&A	1 hr from every 18 days.	1.0	**PM**	Selected 32 hr.	1.9	Clark et al. (2002)
M&A	All automated detections.	Unc.	**PM**	Selected 44 days.	3.4	Risch et al. (2013)
M&A	8 hr from 1 day.	0.004	**PM**	Selected 1 hr/day.	4.2	Oswald et al. (2011)
M&A	All automated detections.	Unc.	**PM**	Randomly selected 6 days/month.	11	Vu et al. (2012)
M&A	All automated detections.	Unc.	**PM**	Selection of high SNR vocalizations.	Unc.	Castellote et al. (2012a)
M&A	Portion of every file.	5.0	**PM**	Selection of high SNR vocalizations.	Unc.	Delarue et al. (2013)
M&A	All automated detections.	Unc.	**M&A**	All high SNR seen during occurrence analysis.	Unc.	Jolliffe et al. (2019)
M&A	All automated detections.	Unc.	**M&A**	All seen during occurrence analysis.	Unc.	Mellinger et al. (2004)

TABLE A-11. Summary of occurrence methodologies for big PAM data papers that targeted all baleen whale species present in acoustic data. Methodologies included full manual (FM), partial manual (PM), automated (A), and a combination of manual and automated (M&A). The percent of data reviewed (%), analysis method, and review protocol was at times unclear (Unc.). Number of species found to be present in the data (# species) only refers to baleen whale species, though many of the studies also described odontocetes.

# species	**Method**	**Review protocol**	**%**	**Study**
2	FM	All acoustic data.	100	Wright et al. (2019) Ryan et al. (2019a)
3	PM	Randomly selected 20% of data.	20	Stafford et al. (2007a)
5	PM	All data available that was deemed useable.	45.4	McDonald (2006)
2	A	NA	NA	Klinck et al. (2012b)
5	M&A	Portion of each file (to determine detector performance).	5.0	Hannay et al. (2013)[a]
1	M&A	20 files per species per recorder with variable detection levels (to determine detector performance).	Unc.	Frouin-Mouy et al. (2017)
6	M&A	Random selection of data when results suspected to be unreliable (e.g., high numbers of detections).	Unc.	De Vreese et al. (2018)
3	Unc.	Unc.	Unc.	Nieukirk et al. (2004)[b]

[a] Varying methods across data sets, but majority were done in this manner.

[b] Described undertaking full manual, but hours reported analyzed were only ~1/6 of total estimated data size, so could be partial

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APPENDIX B Chapter 4

B.1 Results

TABLE B-1. Average day of onset of full songs and singing for 2015 and 2016 considered independently and together.

	Average 2015	**Average 2016**	**Average 2015 and 2016**	**Difference between 2015 and 2016 (days)**
First full song	8 Oct	10 Oct	9 Oct	2
First singing	26 Sep	2 Oct	29 Sep	7
Regular full song	1 Nov	7 Nov	4 Nov	6
Regular singing	18 Oct	6 Nov	27 Oct	19

TABLE B-2. First day of full song, first day when full song became regular, the number of days between the two for each recording station and year, and the average for both year combined as well as 2015-16 and 2016-17 separately.

Station	**Year**	**First full song**	**Regular full song**	**Number days between first and regular full song**
8	2015-16	6 Oct 2015	29 Oct 2015	23
7	2015-16	23 Oct 2015	4 Nov 2015	12
	2016-17	19 Nov 2016	4 Dec 2016	15
6	2015-16	5 Oct 2015	5 Nov 2015	31
5	2015-16	20 Sep 2015	26 Oct 2015	36
	2016-17	4 Oct 2016	22 Oct 2016	18
4	2016-17	6 Sep 2016	29 Oct 2016	53
3	2015-16	10 Nov 2015	NA*	NA*
2	2015-16	7 Oct 2015	NA*	NA*
1	2015-16	6 Sep 2015	4 Nov 2015	49
Average		**9 Oct**	**4 Nov**	**26**

*Full songs never became regular

TABLE B-3. Results from Pearson's pairwise correlation as the correlation coefficient (r) and P-value (p) where the average onset day was averaged across both years. Variable values were averaged over the average onset day (d) with the exception of SSP and wind speed that were also averaged over two weeks (2w).

Variable	**First full song**		**Regular full song**		**First singing**		**Regular singing**	
	r	***p***	***r***	***p***	***r***	***p***	***r***	***p***
Light hours	-0.48	0.16	-0.38	0.35	0.02	0.96	-0.65	0.06
SSP (d)	-0.22	0.53	-0.28	0.51	0.34	0.33	-0.12	0.76
SSP (2w)	-0.20	0.57	0.45	0.26	-0.07	0.84	0.04	0.93
SST	-0.47	0.17	-0.50	0.20	-0.15	0.69	-0.49	0.18
Latitude	0.50	0.14	0.34	0.40	0.15	0.68	0.61	0.08
CHLA	-0.41	0.24	-0.04	0.92	-0.29	0.42	-0.54	0.13
Wind speed (d)	-0.08	0.84	-0.55	0.16	-0.04	0.91	-0.61	0.08
Wind speed (2w)	-0.41	0.24	-0.55	0.16	0.08	0.83	-0.34	0.38

TABLE B-4. Results from Pearson's pairwise correlation as the correlation coefficient (r) and P-value (p) where the average onset day was determined separately for each year. Variable values were averaged over the average onset day (d) with the exception of SSP and wind speed that were also averaged over two weeks (2w). Results for singing can be found in Figure 4 of the main text.

Variable	**First full song**		**Regular full song**	
	r	***p***	***r***	***p***
Light hours	-0.32	0.35	-0.52	0.19
SSP (d)	-0.27	0.45	0.26	0.54
SSP (2w)	0.45	0.26	0.44	0.27
SST	-0.43	0.21	0.23	0.26
Latitude	-0.63	0.14	0.34	0.40
CHLA	-0.39	0.27	0.03	0.94
Wind speed (d)	0.06	0.87	-0.21	0.61
Wind speed (2w)	-0.55	0.16	-0.44	0.28

APPENDIX C Chapter 5

TABLE C-1. Description of song for each sample (represented by date) where song is described as one number (1-8) for each theme. 'Sleep' indicates the recording entered sleep mode. When samples included less than 6 songs, an indication of why song description stopped is included (e.g., singing ends or gets faint). Where there was a 'break in singing' (50-120 s) it was unclear whether the whale stopped singing temporarily or if the song temporarily got faint.

Station	Sample	Song
Cape Breton South	17 Apr 2016	7, 8, 1, 2, 3, 4, 5, 6, 7, sleep, 6, 7, 8, 1, 2, 3, 4, 5, 6 singing ends
Cape Breton South	19 Apr 2016	5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, break in singing, 5, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, overlap started
Cape Breton South	20 May 2016	2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, sleep, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, sleep, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, singing gets faint
Strait of Belle Isle	5 Dec 2016	6, 8, 1, 2, 3, 4, 5, 6, 8, 1, 2, break in singing, 5, 6, 7, 8, sleep, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 8, 1, 2, 8, sleep, 2, 3, 4, 5, 6, 7, 8, 2, 3, 4, 5, 6, 7, 8, sleep, 8, 1, 2, 8, 1, 2, 8, singing ends
Strait of Belle Isle	6 Dec 2016	8, 1, 2, 3, 4, 5, 6, 7, 8, 2, 3, 2, 3, 4, 5, 6, 7, sleep, 7, 8, 1, 2, break in singing, 5, 6, 7, 8, 1, 2, 3, 4, sleep, 7, 8, singing ends
Strait of Belle Isle	23 Dec 2016	2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, sleep, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, break in singing, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, singing ends
Cape Breton South	25 Nov 2016	6, 7, 8, 1, 2, 3, 4, break in singing, 6, 7, 8, 1, 2, sleep, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, sleep, 5, 6, 7, 8, break in singing, 5, 6, 2, 4, 5, 6, 2, 4, 5, 6, 7, sleep
Cape Breton South	16 Jan 2017	3, 4, 5, 7, 8, sleep, 7, 8 break in singing, 3, 4, 5, 7, 8, sleep, 7, 8, 1, 2, 3, 4, 5, 7, 8, singing gets faint
St. Ann's Bank	21 Nov 2016	2, 3, 1, 4, 5, 7, 1, 3, 4, 5, 7, 8, 2, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 1, sleep, 4, 5, 7, singing ends
St. Ann's Bank	27 Nov 2016	1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 7, 8, 1, sleep, 5, 3, 4, 5, 6, 7, 8, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, singing gets faint
St. Ann's Bank	29 Dec 2016	6, 7, 8, 1, 2, 3, 4, 5, 6, sleep, 6, 7, 8, 1, 2, 3, 4, 5, 6, sleep, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, sleep, 6, 7, 8, 1, 2, 3, 4, sleep, 3, 4, 5, 6, 7, 8, 1, 2, sleep, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, sleep.

Station	Sample	Song
St. Ann's Bank	9 Jan 2017	5, 6, 7, sleep, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, sleep, 3, 4, 5, 6, 7, singing gets faint
Dominican Republic	1 Jan 2017	5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8,
Dominican Republic	10 Jan 2017	7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7,
Dominican Republic	20 Jan 2017	8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7,
Dominican Republic	30 Jan 2017	7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7,
Dominican Republic	1 Mar 2017	3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8,
Dominican Republic	10 Mar 2017	5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7
Dominican Republic	20 Mar 2017	8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7,
Dominican Republic	30 Mar 2017	1, 2, 3, 5, 6, 7, 8, 1, 2, 3, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 4, 5, 6, 7, 8, 1, 2, 3, 7, 8, 1, 2,