TEMPORAL PATTERNS OF HUMPBACK WHALE, *MEGAPTERA NOVAEANGLIAE*, NON-SONG CALLS ON THEIR NEWFOUNDLAND FORAGING GROUNDS

By

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Thesis Abstract

Animal signals convey information intra- and interspecifically, but their adaptive importance is often unknown. The humpback whale (*Megaptera novaeangliae*) is a widespread, highly vocal cetacean known to produce both songs and non-song calls, the latter of which has been less-studied. While associations between non-song calls and behaviour have been examined throughout their range, additional investigations into their temporal patterns in understudied regions may further provide information as to their behavioural context. Using continuous 24-h passive acoustic monitoring and aural/visual surveys of recordings, I investigated the temporal patterns in non-song call activity within three broad classes (low frequency, high frequency and pulsed) on a diel and daily scale across three summers (July-August, 2015-2017) at a foraging site on the northeast coast of Newfoundland, Canada. Low frequency calls were the dominant call class (43-75%) across all time scales relative to high frequency (9-17%) and pulsed calls (8-40%), suggesting low frequency calls are vital for communication among humpback whales on the foraging grounds, as observed throughout their range. Non-song call activity in all call classes was higher during light relative to dark or twilight periods, suggesting individuals are inactive, not engaged in behaviours requiring acoustic communication, and/or remain silent to minimize predator detection. Call activity peaked when humpback whales arrived into the study area and subsequently decreased, suggesting calls are more important in mediating social interactions during movement into the area, but less-so as whales disperse to forage throughout the area. Lastly, call activity varied among years with 2016 having double the call activity of the other years, which was also associated with the highest estimated humpback whale abundance but lowest prey (capelin, *Mallotus villosus*) biomass, suggesting call activity may indicate humpback whale abundance. Overall, temporal call activity patterns suggest that non-song calls may be important for conspecific communication and mediating social interactions rather than for foraging; however, more research is required to further elucidate their behavioural context in Newfoundland.

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Dedication

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Chapter 1

General Introduction

Animal communication systems have evolved over evolutionary time resulting in the production of signals, enabling animals to convey information (i.e. the ‘signalers’) to conspecifics and heterospecifics regarding their abiotic (e.g., rain, storms) and biotic environment (e.g., predators, prey), as well as their own biological condition (e.g., reproductive status, health, toxicity; Seyfarth and Cheney 2003, Alcock 2013). Indeed, signals may enable both intra- and interspecific communication (e.g. via eavesdropping) allowing animals to develop a more complete picture of their surroundings to inform decision-making processes (Marler 1967, Alcock 2013). For signals to evolve, there must be a signaler, receiver, and a pre-existing sensory mechanism from which new signals can be produced and detected, known as ‘sensory exploitation’ (Marler 1967, Green and Marler 1979, Seyfarth and Cheney 2003, Alcock 2013). Signals must also be propagated effectively through the signaler’s respective environment whilst retaining all necessary information to the receiver (Marler 1967, Green and Marler 1979, Alcock 2013, Kaplan 2014). Finally, the receiver must respond to the signal, whereby the response maximizes the fitness of the receiver and/or the producer (Green and Marler 1979, Alcock, 2013, Kaplan 2014). Indeed, animal communication systems, and their respective signals, will only persist and be maintained over time if they are well-conserved (i.e. stable over time) and possess adaptive value (Alcock 2013). In many cases, however, the adaptive values and purpose of signals produced by animals are unclear.

Animals use a variety of signals to communicate and convey information intra- and interspecifically within their respective environments, where the production of these signals is ubiquitous in the animal kingdom across both terrestrial and aquatic taxa. Some of the most effective and commonly produced signals across numerous taxa include olfactory, visual, acoustic, electrical, and physical (i.e. touch) signals, which can occur individually or in combination (Alcock 2013). For instance, olfactory communication can attract mates or signal readiness to mate in insects (Colwell et al. 1978, Meer et al. 1998, Fors et al. 2015) and mammals (Kean et al. 2011). Olfactory signals can also be used for dominance and hierarchy discernments within a social structure and/or system, such as with female hyena (*Crocuta crocuta*) pseudopenis inspections for dominance (East et al. 1993, Alcock 2013). Visual signals are among the most prolific and prevalent in the animal kingdom and can signal aggression (e.g., red-winged damselfly, *Mnesarete pudica*: Guillermo-Ferreira et al. 2015; Tzabcan rattlesnakes, *Crotalus tzabcan:* Carbajal-Márquez et al. 2018), such as by using colour patterns or dancing (e.g. birds of paradise: Soma and Garamszegi 2015, Stavenga et al. 2015, Scholes et al. 2017, Ligon et al. 2018); toxicity to deter predation (e.g., monarchs, *Danaus plexippus*: Parsons 1965; poison dart frogs, Dendrobatidae: Summers and Clough 2001, Santos and Cannatella 2011); and predator presence, such as posture to warn conspecifics of impending predation danger (e.g., erect posture and aggression in Eastern grey squirrels, *Sciurus carolinensis*: Jayne et al. 2015). Additionally, movements, such as the honey bee dance within a hive, may indicate the identity and location of prey (Von Frisch 1967, Von Frisch 1973; *Apis mellifera*: Dornhaus and Chittka 2004). Lastly, acoustic signals are also commonly employed in social systems and are used to indicate prey presence and availability, as well as locate prey and other nearby and feeding conspecifics (e.g. bats: Simmons et al. 1979, Obrist 1995, Schnitzler and Kalko 2001), and warn conspecifics of predator presence (e.g. birds: Fallow and Magrath 2010). Acoustic signals are also thought to follow ‘motivational-structural’ rules ("MS" concept; Morton 1977). Specifically, the MS concept stipulates that the structure of acoustic signals across numerous taxa has converged, whereby animals produce structurally-similar sounds during high-arousal (e.g., hostile, aggressive, appeasement, fearful, affiliative) or low-arousal (e.g., friendly, non-affiliative) situations, resulting in variations of a call type depending on the signaler’s state (Morton 1977). Acoustic communication has not been as extensively studied in aquatic relative to terrestrial environments and, thus, less is known regarding both the modes of signal production and behavioural functions of acoustic signals in aquatic species.

Marine mammals, specifically cetaceans, typically depend upon acoustic signals for conspecific interactions and communication within their environment due to greater signal propagation and fidelity over time and space relative to visual and other signals (Tyack 1997, Dudzinski et al. 2007, Dunlop et al. 2007, Weilgart 2007, Risch et al. 2013, Zapetis and Szesciorka 2018). Cetaceans produce a variety of vocalizations, such as songs, non-song calls and cries, which are highly variable in their structure (i.e., physical call characteristics and appearance) and characteristics within and among species (Edds-Walton 1997, Cerchio and Dahlheim 2001, Dunlop et al. 2007, Mellinger et al. 2007, Riesch and Deecke 2011). While the exact functions and/or behavioural contexts of cetacean vocalizations are often unknown, a few studies have inferred a variety of potential functions in recent years. For example, cetacean sounds may function for indicating distress (bottlenose dolphins, *Tursiops truncatus*: Lilly 1963; humpback whales, *Megaptera novaeangliae*: Tellechea et al. 2017), searching for prey (e.g., echolocation to locate prey in killer whales, *Orcinus orca*: Simon et al. 2007; harbour porpoises, *Phocoena phocoena*: Deruiter et al. 2009; attracting con- and heterospecifics to prey sources, (in)directly: pilot whales, *Globicephala melas*: Cure et al. 2012), capturing prey (e.g., sperm whales, *Physeter macrocephalus*: Miller et al. 2004; coordination of feeding attacks in killer whales: Riesch and Deecke 2011), avoiding predators (sperm whale antipredator strategy: Cure et al. 2013), communicating with conspecifics (e.g. social and/or contact calls: Dunlop et al. 2008, Wild and

Gabriele 2014, Dunlop 2017), breeding and/or mating (fin whales, *Balaenoptera physalus*: Croll et al. 2002; humpback whales: Smith et al. 2008, Herman 2017), aggression (bottlenose dolphins: McCowan and Reiss 1995; killer whales: Graham and Noonan 2010), and navigation (bowhead whales, *Balaena mysticetus*: George et al. 1989; finless porpoises, *Neophocaena phocaenoides*: Akamatsu et al. 2005, Zapetis and Szesciorka 2018).

Study species

Perhaps one of the most notable and well-studied examples of marine mammal acoustic signals and its associated behavioural function occurs in humpback whales, *Megaptera novaeangliae*. Male humpback whales produce songs that seem to occur mostly on their breeding grounds, which appear to serve as a mating call (Payne and McVay 1971, Smith et al. 2008). Songs are typically characterized by long, repeatable units and are highly structured and stable over time (Payne and McVay 1971), but also undergo annual or bi-annual ‘cultural revolutions’ (Eriksen et al. 2005, Garland et al. 2011, Allen et al. 2018). In contrast, non-song vocalizations are shorter bouts of sound that may be produced individually or in a series with other non-song call types (Cerchio and Dahlheim 2001, Rekdahl et al. 2015) and exhibit higher structural stability over time (Rekdahl et al. 2013, Fournet et al. 2018a, Epp 2019). Despite some knowledge regarding the behavioural context of some non-song call types, only limited information is available regarding their function. Dunlop (2017) suggested humpback whale non-song calls follow MS rules, whereby more stereotyped humpback whale non-song calls may contain specific information, such as signaling the location of prey or predators and/or coordinating feeding (i.e. signalling specific behaviours). In contrast, more graded call types are dynamic and may contain motivational information, such as signalling the amounts and types of prey or predators, as well as indicating the caller’s state, arousal level, sex, size, and/or behavioural context. Additionally, Fournet et al. (2018c) uncovered that at least five non-song call types of humpback whales are shared and commonly produced between two allopatric, genetically distinct populations of humpback whales of the North Pacific (Southeast Alaska) and North Atlantic (Massachusetts Bay) oceans. The widespread nature of these non-song calls suggest that they are critical components of humpback whale acoustics and/or communication (Dunlop et al. 2007, Stimpert et al. 2011, Rekdahl et al. 2013, Fournet et al. 2018c, 2018a).

Humpback whales are a unique cetacean species in that they exhibit a large vocal repertoire with great variability within their songs on the breeding grounds, as well as in their non-song call types during migration (Thompson et al. 1986, Dunlop et al. 2007, Stimpert et al. 2007, 2011, Rekdahl et al. 2013, Parks et al. 2014, Fournet et al. 2015). Due to the high vocal flexibility of humpback whales, the function and behavioural importance of their non-song calls has not been well characterized (Stimpert et al. 2011, Rekdahl et al. 2013). During migration, some calls appear to be important for social interactions, such as maintaining contact with conspecifics and/or mediate fission-fusion (i.e. affiliations) between migrating social groups (Dunlop et al. 2008, Dunlop 2017). On the foraging grounds, humpback whale non-song calls have been associated with foraging, suggesting that certain call types might be associated with certain prey types (D’Vincent et al. 1985, Cerchio and Dahlheim 2001, Stimpert et al. 2007, Parks et al. 2014, Fournet et al. 2015). Additionally, a novel acoustic signal was described for tagged humpback whales in their North Atlantic foraging grounds (specifically in the Gulf of Maine), termed the “megapclick” (Stimpert et al. 2007). The “megapclick” is similar in structure to odontocete echolocation click trains and appears to share a similar function in nighttime foraging (Stimpert et al. 2007). Similarly, humpback whales also produce a ‘paired burst’ sound while foraging for sand lance (*Ammodytes* spp.), which may influence prey behaviour but may also function as a communicative signal to coordinate foraging activity as it is produced almost exclusively in the presence of conspecifics in dim light conditions during bottom feeding (Parks et al. 2014). Humpback whales are known to produce ‘feeding cries’ on their Alaskan foraging grounds while engaged in coordinated foraging on Pacific herring (*Clupea pallasii*; D’Vincent et al. 1985, Cerchio and Dahlheim 2001, Fournet et al. 2015, 2018b). Finally, the non-song vocalizations of migrating humpback whales may function for both intra- and intergroup communication by potentially mediating and/or facilitating contact, fusion, and splitting of individuals between and within the different migratory social groups (Dunlop et al. 2007, Wild and Gabriele 2014, Dunlop 2017), and/or in mother-calf communication (Zoidis et al. 2008, Indeck et al. 2020).

Even less is known about the temporal (i.e., diel, daily, annual) patterns in non-song call activity of humpback whales on their foraging grounds, although some temporal patterns have been described elsewhere during other parts of their annual cycle (Wild and Gabriele 2014, Huang et al. 2016, Kowarski et al. 2018). Temporal (diel, seasonal) patterns in call types have been observed in numerous other cetacean species, such as blue whales (Stafford et al. 2005, Wiggins et al. 2005, Leroy et al. 2016, Shabangu et al. 2019), minke whales (*Balaenoptera acutorostrata*: Risch et al. 2013, 2019, *Balaenoptera bonaerensis*: Dominello and Sirovic 2016, Shabangu et al. 2020), and right whales (Mellinger et al. 2007, Munger et al. 2008, Mussoline et al. 2012, Matthews et al. 2014, Bort et al. 2015), some of which are in relation to diel variation in prey availability and accessibility. Humpback whale songs exhibit diel variation in their Hawaii breeding grounds, whereby singing increases at nighttime, possibly to attract potential mates (Au et al. 2000). Other studies uncovered diel patterns in humpback whale non-song vocalizations, whereby non-song calls were minimally detected during the day but prevalent at night (Huang et al. 2016, Kowarski et al. 2018), indicating a potential function for nighttime communication and/or foraging on Atlantic herring (*Clupea harengus*: Huang et al. 2016). Additionally, diel foraging patterns of humpback whales have been examined, but these observations were not paired with acoustic recordings. For instance, tagged humpback whales in Antarctic waters exhibited diel foraging behaviour consistent with krill (*Euphausia superba*) diel vertical movement patterns, whereby whales did not feed during the daytime when krill reside in dense clusters deep in the water column, but instead fed extensively once krill migrated into surface waters at night where they reside in less dense aggregations (Friedlaender et al. 2016). Nighttime foraging on these surface aggregations of prey is thought to maximize foraging efficiency whilst decreasing energetically costly behaviours of diving and searching for prey (Friedlaender et al. 2016). Similarly, tagged humpback whales off the Gulf of Maine display diel feeding behaviour in relation to sand lance (*Ammodytes* spp.) prey availability, whereby humpback whales predominantly fed near the surface during the daytime, when sand lance was abundant near the surface, but fed near the seabed during nighttime, when sand lance were closer to, and in the process of, burying in substrate (Friedlaender et al. 2009). Although diel shifts in humpback whale foraging behaviour mirror changes in prey behaviour, it is unclear whether humpback whale call activity exhibits similar diel variation in most regions throughout their range.

While humpback whale non-song calls in the Northwest Atlantic (Maine: Stimpert et al. 2007) and Pacific (D’Vincent et al. 1985, Fournet et al. 2015, 2018b) foraging grounds have begun to be described in relation to foraging, this has not been assessed on the coastal Newfoundland foraging grounds. The annual return of humpback whales to coastal Newfoundland coincides with the annual inshore spawning migration of large numbers of capelin, *Mallotus villosus*, from offshore overwintering areas during June-July (Whitehead and Carscadden 1985, Piatt et al. 1989, Davoren 2013, Crook et al. 2017, Johnson 2018). Capelin is a primary forage fish species, which most top predators on the Newfoundland shelf consume (e.g., baleen whales, seabirds, large predatory fish). Unsurprisingly, capelin are thought to be the main prey species of humpback whales in coastal Newfoundland (Whitehead and Carscadden 1985, Piatt and Methven 1992, Davoren 2013), which was recently confirmed (Johnson 2018). Capelin spawn in cool, deeper water (15–40 m; subtidal) and warm beach (intertidal) sites (Davoren 2013). Deeper water spawning sites of capelin act as a predictable and highly abundant food source and, thus, attract high abundances of multiple marine predators, including humpback whales (Davoren 2013). Pre-spawning and spawning capelin exhibit distinct diel behaviour, whereby capelin move up in the water column at night and disperse and then migrate to deeper water and form dense shoals during the day (Davoren et al. 2006). Following spawning events, capelin either die or migrate away from coastal areas out to the shelf break, resulting in a decrease in capelin biomass within coastal areas (Crook et al. 2017).

Thesis Objectives

The overarching objective of my thesis was to contribute to the current, limited knowledge regarding temporal patterns in call activity of humpback whale non-song calls throughout their range. My specific objective was to investigate the temporal patterns in non-song call activity of humpback whales on their Newfoundland foraging grounds, in relation to conspecific and prey abundance (Chapter 1). To do this, I aurally and visually surveyed passive acoustic monitoring recordings of humpback whales across three summers (July-August, 2015-2017) to quantify diel, daily, and inter-annual patterns in total call activity as well as the call activity of three previously defined non-song call classes (i.e., high frequency, low frequency, pulsed; Epp 2019).

Additionally, I qualitatively assessed whether inter-annual differences in diel and/or daily patterns were associated with estimates of humpback whale abundance as well as the biomass of their main prey (capelin). By elucidating temporal patterns of humpback whale call activity in an understudied foraging ground, this study will provide insight into the behavioural contexts of broad non-song call classes of humpback whales and, thus, act as a step toward understanding their function.

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Chapter One: Temporal patterns of humpback whale, *Megaptera novaeangliae,* non-song calls on their Newfoundland foraging grounds

Introduction

Mammals communicate intra- and interspecifically via visual, olfactory, gustatory, acoustic and tactile cues. A species' primary method of communication, however, is influenced by the intended purpose of the cue, proximity of the receiver, ecological and/or environmental factors (e.g., visibility, soundscape), social relationships, and life history stages (Marler 1967, Green and Marler 1979, Seyfarth and Cheney 2003, Dudzinski et al. 2007, Kaplan 2014). In oceanic environments, marine mammals primarily depend on acoustic signals (hereafter, sounds) to communicate underwater due to greater propagation and fidelity of sound over time and space relative to alternative signal types (Tyack 1997, Dunlop et al. 2007, Weilgart 2007, Risch et al. 2013, Zapetis and Szesciorka 2018). Specifically, cetaceans produce a variety of sounds that serve many functions, including indicating distress (Lilly 1963, Tellechea et al. 2017), foraging (Miller et al. 2004, Simon et al. 2007, Deruiter et al. 2009, Riesch and Deecke 2011, Cure et al. 2012), avoiding predators (Cure et al. 2013), communicating with conspecifics (Weilgart and Whitehead 1993, Edds-Walton 1997, Thomsen et al. 2002, Dunlop et al. 2008, Dunlop 2017), reproduction (Croll et al. 2002, Herman 2017), aggression (McCowan and Reiss 1995, Graham and Noonan 2010), and navigation (George et al. 1989, Akamatsu et al. 2005, Zapetis and Szesciorka 2018). Cetacean sounds are highly variable in their structure and characteristics within and among species, ranging from low to high frequency sounds of variable duration and bandwidth (Edds-Walton 1997, Cerchio and Dahlheim 2001, Dunlop et al. 2007, Mellinger et al. 2007, Riesch and Deecke 2011).

Acoustic communication has been especially well-studied in humpback whales (*Megaptera novaeangliae*). Humpback whales are unique among cetaceans in that they exhibit a large and highly variable vocal repertoire, which can be broadly classified into two vocalization types: songs and non-song calls (Dunlop et al. 2007, Stimpert et al. 2011, Gong et al. 2014, Fournet et al. 2015). Male humpback whales produce long, highly structured songs where sound units are combined into a 'phrase' and multiple 'phrases' are subsequently arranged into 'themes' which occur in a stereotyped, predictable pattern (Payne and McVay 1971, Winn and Winn 1978). Songs are produced by males primarily on low-latitude winter breeding grounds but have also been detected during migration and on their high-latitude summer feeding grounds (Payne and McVay 1971, Winn and Winn 1978, Tyack 1981, Mattila et al. 1987, Darling and Berube 2001, Clark and Clapham 2004, Darling et al. 2006, Smith et al. 2008, Herman et al. 2013). Song structure is stable among individuals in the breeding area within a single year but undergoes a 'cultural revolution,' rapidly changing every few years within the population (Payne and Payne 1985, Eriksen et al. 2005, Garland et al. 2011, Allen et al. 2018). Although the exact function of song is unknown, songs may directly and/or indirectly function for males in attracting a mate (Payne and McVay 1971, Winn and Winn 1978, Tyack 1981, Parsons et al. 2008, Herman 2017), facilitating intrasexual interactions (e.g. establish dominance and/or cooperation among males: Darling and Berube 2001, Darling et al. 2006, Herman 2017), and/or attracting other singing males, potentially to form a lek thereby increasing the intensity of the 'song' stimulus in attracting females (Cholewiak 2008, Smith et al. 2008, Herman 2017). In contrast, 'non-song' calls are individual sound units that are not found in highly structured, repeating phrases or themes (Tyack 1983, Silber 1986, Stimpert et al. 2007, Dunlop et al. 2008, Kowarski et al. 2018), but rather are highly variable calls produced individually or in a 'series' with other non-song call types (Cerchio and Dahlheim

2001, Rekdahl et al. 2015). Non-song calls are produced by both sexes and all age classes throughout their range (Silber 1986, Zoidis et al. 2008, Rekdahl et al. 2015) and while some are ephemeral within the humpback whale repertoire, others exhibit higher structural stability over time (Rekdahl et al. 2013, Fournet et al. 2018c, 2018a, Epp 2019).

A number of non-song call types have been defined and classified in the humpback whale repertoire; however, humpback whales are known to produce a multitude of different non-song call types which fall along a continuum (Dunlop et al. 2007, Stimpert et al. 2007, 2011, Rekdahl et al. 2013, Fournet 2014, Parks et al. 2014, Fournet et al. 2015, Dunlop 2017, Epp 2019). These flexible, or ‘graded’, calls are difficult to classify into discrete call types, as evidenced by high misclassification rates, but there is higher classification success within a broader call class (Fournet 2014, Fournet et al. 2015, Epp 2019). This broad classification may indicate that graded calls do not have a discrete ‘function’, but rather may have multiple meanings based on the caller’s state or environmental conditions (e.g. proximity to conspecifics). For instance, graded call types may result from calls containing additional information to inform receivers of the signaler’s motivation and/or state, which may follow “motivation-structural” rules ("MS"; Morton 1977, Dunlop 2017). Dunlop (2017) suggested more stereotyped humpback whale non-song calls may contain specific information, such as signalling location for prey and predators, or coordinating feeding behaviours. In contrast, more graded call types are dynamic and may contain motivational information, such as signalling quantity and types of prey and/or predators, or indicating the caller’s sex, size, arousal level, and/or behavioural context. Indeed, migrating humpback whales produced calls that were structurally similar to those produced by terrestrial animals in either aversive, aggressive, or competitive contexts (i.e., sounds at a single high frequency, or noisy sounds at multiple low or high frequencies) during high-arousal group settings when males competed to act as the primary escort of females and/or were common among affiliating humpback whale groups. In contrast, short low frequency calls with a terminal upsweep (i.e. sound where frequency increases from low to high), were typically produced in low-arousal, non-affiliative situations containing 1-2 adults or mother-calf pairs (Dunlop 2017) and were previously considered a contact call (Dunlop et al. 2008).

Calls of humpback whales may also vary within a year and throughout their range due to varying environmental and/or ecological factors affecting their arousal state (i.e. breeding versus foraging versus migrating). For example, in low-aggression environments, such as on the foraging grounds where intraspecific competition is low and prey abundance is high, more low-arousal sounds may be expected, such as those produced during positive interactions among individuals where individuals are affiliating (Dunlop, 2017). Alternatively, large numbers of individuals migrating into foraging grounds may increase interactions among individuals from different groups, resulting in a heightened arousal state of humpback whales and, thus, high-arousal sounds may be primarily expected (Dunlop 2017). Alternatively, low frequency calls may simply serve to transmit signals over longer distances relative to high frequency calls, thereby allowing communication with conspecifics outside of their visual range; while the high frequency calls could function over shorter distances, thereby limiting communication to close-contact interactions. Overall, given the graded nature of humpback whale non-song calls, it may be more useful to categorize calls sharing similar basic acoustic properties into broad classes to initially assess call patterns and function, as function may be contained within general call structure instead of discrete call types (Fournet 2014, Fournet et al. 2015, Dunlop 2017).

Some non-song call types are shared between allopatric, genetically distinct populations of humpback whales (Southeast Alaska versus Massachusetts Bay: Fournet et al. 2018c;

Newfoundland versus Hawaii: Epp 2019). Some calls within populations also are stable across time (Rekdahl et al. 2013, Fournet et al. 2018a), possibly because they are important for foraging and/or social interactions. Non-song calls appear to serve multiple functions as they are produced during foraging activities (Stimpert et al. 2007, Parks et al. 2014, Fournet et al. 2018b), aggression (Silber 1986, Dunlop 2017) and/or social interactions (Dunlop et al. 2007, 2008, Zoidis et al. 2008, Rekdahl et al. 2013, 2015, Wild and Gabriele 2014, Dunlop 2017, Indeck et al. 2020). Specifically, three call types have been associated with foraging and have been heard primarily on feeding grounds. First, Stimpert et al. (2007) first described broadband clicks and terminal buzzes in humpback whales, termed “megapclicks”, which are typically found in call bouts during nighttime foraging, possibly on Atlantic herring (*Clupea harengus*), and believed to share a similar function as odontocete click trains. Second, “paired-burst” sounds are short, paired broadband pulsive sounds produced while foraging on sand lance (*Ammodytes* spp.) under low-light conditions exclusively in the presence of conspecifics and, thus, may be produced to influence prey behaviour or coordinate foraging activity among conspecifics during bottom feeding (Parks et al. 2014). Third, stereotyped, tonal ‘feeding cries’ have been documented in their Alaskan foraging grounds and are associated with feeding on Pacific herring (*Clupea pallasii*; D’Vincent et al. 1985, Cerchio and Dahlheim 2001, Fournet et al. 2015, 2018b). This suggests that specific call types might be associated with feeding on particular prey types at certain times of the day. Despite some knowledge regarding the behavioural context of some non-song call types (D’Vincent et al. 1985, Dunlop et al. 2008, Zoidis et al. 2008, Wild and Gabriele 2014, Dunlop 2017, Fournet et al. 2018b, Indeck et al. 2020), only limited information is available regarding their function.

Numerous taxa exhibit diel patterns in call activity which may be related to foraging, predator avoidance, mate attraction, social activities, and/or environmental conditions. Examples of diel call activity patterns include the evening calls of insects and amphibians (Gerhardt and Huber 2002) and increased calling during dawn in birds (Brown and Handford 2003, Burt and Vehrencamp 2005). These diel patterns in call activity have often led to a better understanding or inference of call function. Although few studies regarding cetacean diel call activity exist, diel variation has been found for some species, such as blue whales (*Balaenoptera musculus*: Stafford et al. 2005, Wiggins et al. 2005, Leroy et al. 2016, Shabangu et al. 2019), minke whales (*Balaenoptera acutorostrata*: Risch et al. 2013, 2019; *Balaenoptera bonaerensis*: Dominello and Sirovic 2016, Shabangu et al. 2020), humpback whales (Au et al. 2000, Wild and Gabriele 2014, Huang et al. 2016, Kowarski et al. 2018, 2019), and right whales (*Eubalaena glacialis*: Mellinger et al. 2007, Munger et al. 2008, Mussoline et al. 2012, Matthews et al. 2014, Bort et al. 2015). Specifically, humpback whale non-song call activity was higher during dark periods on the Gulf of Maine foraging grounds (during fall: Huang et al. 2016) and during fall-winter-spring migration off of Nova Scotia (Kowarski et al. 2018), indicating a potential function for nighttime communication and/or foraging (Huang et al. 2016). As humpback whales show diel foraging behaviour whereby tagged whales feed extensively when prey migrate into surface waters during the night (krill, *Euphausia superba*, in Antarctic waters: Friedlaender et al. 2016) or day (sand lance in the Gulf of Maine: Friedlaender et al. 2009), but also feed when prey are closer to the seabed at night (sand lance in the Gulf of Maine: Friedlaender et al. 2009), calls associated with foraging are expected to be higher when their primary prey are more available, as previously shown (Stimpert et al. 2007, Parks et al. 2014).

Humpback whales return annually in the summer to foraging grounds in coastal Newfoundland in large numbers, which coincides with the annual inshore spawning migration of large numbers of capelin, *Mallotus villosus*, from offshore overwintering areas during June-July

(Whitehead and Carscadden 1985, Piatt et al. 1989, Davoren 2013, Crook et al. 2017). Humpback whales form groups of two to more than 10 individuals, with no apparent consistency in companions aside from mother-calf pairs (Whitehead et al. 1982, Whitehead 1983). Larger groups are more ephemeral relative to smaller groups of 2-3 individuals (Whitehead 1983), and relatedness of individuals in these groups is unknown. Non-feeding whales are often observed in pairs, whereas feeding whales are found in groups, whereby the size of the group is related to the size of the prey aggregation (Whitehead 1983). Capelin is the primary forage fish species in coastal Newfoundland during the summer, where they aggregate at predictable locations in high abundance (Davoren et al. 2006), thereby attracting multiple top marine predators (e.g., baleen whales, seabirds, large predatory fish), including humpback whales (Davoren 2013, Johnson 2018). Specifically, humpback whales first arrive on the southeast coast of Newfoundland with the inshore arrival of capelin at the beginning of the summer, and then continually move northward in aggregations along the coast to coincide with the later arrival of capelin inshore farther north (Johnson 2018). Unsurprisingly, capelin are believed to be the main prey species of humpback whales in coastal Newfoundland (Whitehead and Carscadden 1985, Piatt et al. 1989, Piatt and Methven 1992, Davoren 2013), which was recently confirmed (Johnson 2018). Similar to the widespread phenomenon of diel vertical migration in fish and zooplankton (Haney 1988, Davoren et al. 2006), capelin exhibit distinct diel behaviour, whereby capelin move up into the water column at night and disperse, then migrate to deep water and form dense shoals during the day (Davoren et al. 2006, 2010, Regular et al. 2010). Although the call repertoire was recently characterized on the northeast Newfoundland coast (Epp 2019), it is unknown whether humpback whale call activity exhibits diel patterns that reflect diel behaviour of their primary prey type in coastal Newfoundland. Although foraging-associated calls have been described in their Atlantic (Maine:

Stimpert et al. 2007, Parks et al. 2014, Huang et al. 2016) and Pacific (Alaska: Cerchio and Dahlheim 2001, Fournet et al. 2015, 2018b) foraging grounds, diel patterns in non-song calls have been described in select foraging areas during non-peak feeding seasons (Huang et al. 2016, Kowarski et al. 2018), and diel shifts in humpback whale foraging behaviour appear to mirror diel prey movements (Maine: Friedlaender et al. 2009; Antarctic: Friedlaender et al. 2016), it is unclear whether humpback whales on their Newfoundland summer foraging grounds exhibit similar diel variation in call activity, or if calling is instead associated more with maintaining contact with conspecifics, such as during migration.

Objectives

The objective of my chapter is to investigate temporal patterns in non-song call (hereafter, "call") activity of humpback whales within and across three summers (July-August, 2015-2017) on their foraging grounds on the northeast coast of Newfoundland as a first step to investigate call function. Specifically, I hypothesize that the number of occurrences of humpback whale calls within three call classes (i.e., high frequency (HF), pulsed (P), low frequency (LF)), as well as total call activity, will vary across multiple temporal scales, including diel, daily, and annual (**H1**) due to varying behavioural contexts of these call classes. Indeed, calls can be reliably classified into these three broad classes (Epp 2019), which may have different functions based on their acoustic properties, such as propagation distances for conspecific communication, and/or 'motivational-structure' encoded within the general call class structure. If calling is important to maintain contact with conspecifics, I predict that both total call activity and activity within specific call classes will be highest on days that humpback whales initially migrate into the study area (**P1**).

Additionally, I predict that each call class will exhibit a distinct and consistent diel pattern within and across years (**P2**). In particular, the higher frequency call class (HF) is predicted to be most frequent during light (rather than twilight or dark) periods across all years, to communicate with conspecifics within visual range, possibly in high-arousal situations (e.g. close-contact group formation and dissolution). In contrast, low frequency calls (LF) are predicted to be most frequent during dark periods as their acoustic properties enable reliable signal transmission to maintain contact with conspecifics at longer and/or unknown distances. Alternatively, if calls are associated with foraging, as previously found (D'Vincent et al. 1985, Stimpert et al. 2007, Parks et al. 2014, Fournet et al. 2015, 2018b), I predict call activity would be limited to dark periods during which humpback whales may concentrate foraging on surface aggregations of capelin, as previously observed elsewhere on other prey types (Friedlaender et al. 2009, 2016). Furthermore, if calls are related to conspecific communication and/or foraging, then variation in call class activity among years may be associated with interannual variation in the biomass of their main prey species (i.e. capelin), and/or humpback whale abundance estimates in the area. As acoustic data are available for three years, this relationship was investigated qualitatively. Elucidating the behavioural context of calls is important as changes in call production could indicate shifts in their environment (e.g., differences in conspecific density, prey type).

Methods

Study design

During 2015-2017, hydroacoustic recordings of humpback whale calls were made continuously over consecutive 24-hour periods per day from mid-July to mid-August (2015: July 27-August 17; 2016 and 2017: July 14-August 16) on the northeast coast of Newfoundland (Notre

Dame Bay), Canada (Fig. 1). Specifically, recordings were made at the same capelin spawning site (49.20° N, 54.20° W), which is centrally located in the study area (Fig. 1). From previous research in the study area during my study period (Table 1; Johnson 2018, Carvalho and Davoren 2019, Gulka et al. 2019), I assembled the following information to compare call activity among years of this study (2015-2017): date of capelin spawning, peak capelin biomass (g m^{-2}), date of humpback whale arrival, and estimated humpback whale abundance, which were collected using previously described research monitoring methods. In brief, trained observers regularly monitored all known capelin spawning (Johnson 2018) sites in the study area every 1-4 days throughout July-August (Fig. 1; see methods in Crook et al. 2017) to determine the date of capelin arrival (i.e. capelin presence) and date of first spawning (i.e. capelin eggs adhered to spawning sediment) in the study area. Capelin biomass was measured approximately weekly (2-7 days) during July and August by conducting a hydroacoustic survey (15 km) covering a cluster of four annually persistent capelin spawning sites (i.e. hydrophone deployment site; Fig. 1; Penton and Davoren 2012), to which aggregations of capelin and foraging humpback whales annually return (Davoren 2013). During each survey, an echosounding system (BioSonics DTX 6000 operated through a 70 kHz split-beam transducer; BioSonics Inc., Seattle, Washington) continuously measured capelin biomass (g m^{-2}) in the water column (see Gulka et al. 2019 for details). Humpback whale arrival was defined as the date where aggregations (i.e. $\geq$ 10 individuals) were first observed in the study area, as determined by boat-based surveys and other anecdotal observations during research activities (see Johnson 2018 for details). Mark-recapture techniques were used to estimate humpback whale abundance in Notre Dame Bay, where humpback whales were photo-identified within 10 km of the capelin biomass survey route (see Johnson 2018 for details) and compared to a long-term catalogue (2003-2017). While the detection range of the hydrophone is unknown, vocalizations of humpback whale aggregations present ≥ 10 km away are not detected on the hydrophone.

Acoustic Data Collection and Classification

Continuous hydroacoustic recordings were made with a *Wildlife Acoustics* Song Meter (SM2M) marine recorder with a standard hydrophone (model HTI-96; recording bandwidth: 2Hz-48kHz; sensitivity -165dB re: 1V/µPa; Wildlife Acoustics Inc. 2013; Epp 2019). Acoustics were recorded using a 24 kHz sampling rate, 12 dB continuous recording amplification (i.e. 12 dB gain), 3 Hz high pass filter, and 16-bit sample resolution (Epp 2019). The sampling rate was chosen to record at a frequency two times higher than the described maximum frequency of humpback whales (Nyquist 1928), which varies from ~30 Hz to 10 kHz for humpback whale song and calls (Silber 1986, Stimpert et al. 2011, Fournet et al. 2015). The number of calls determined from passive acoustic monitoring (PAM) does not explicitly indicate the number of humpback whales present and/or calling in an area, but rather indicates humpback whale call activity in the area because it is uncertain whether multiple different calls occurring within a brief period are produced by a single or multiple individuals.

Acoustic recordings were analyzed using *Raven Pro 1.5* (Cornell Laboratory of Ornithology; hereafter, "*Raven*") only on days when humpback whales were known to be present in the study area. Therefore, a total of 8, 19, and 15 days were processed acoustically to detect humpback whale calls in 2015, 2016, and 2017. All recording days underwent an aural and visual survey where spectrograms were viewed using a Discrete Fourier Transform (DFT) with 2048 samples, 75% overlap, and a Hann window. A minimum of two passes through all files was done for call class identification. Each humpback whale call was classified into three call classes: high frequency (HF), low frequency (LF), and pulsed (P). These call classes were decided upon as they were previously characterized for humpback whales in Newfoundland across two years (2015, 2016) using the same hydrophone recordings as in this study, whereby three, seven, and five call types were identified within the HF, LF, and P call classes, respectively (refer to Epp 2019 for a detailed description of each call class, which were similarly characterized elsewhere throughout their range: Dunlop et al. 2007, Dunlop et al. 2008, Fournet et al. 2018). While there is some subjectivity in manual call classification, humpback whale calls can be reliably classified into these three broad call classes which also have distinct characteristics (as shown in Epp 2019). HF calls were generally identified based on their short duration (range of averages for 2015-2016: 0.3-0.4 s) and high start frequency (> 0.5 kHz) relative to other classes, reaching an average maximum frequency of 1.5-2.1 kHz (Fig. 2; Epp 2019). The majority of LF calls were identified based on their longer duration (0.7-0.9 s), distinct low-frequency component (0.05 kHz) and lower maximum frequency (0.3-0.4 kHz) relative to other classes, and sometimes had an upsweep at the end (Fig. 3; Epp 2019). Some LF calls in 2015 and 2016 were longer in duration (1.5-2.7 s) and had a higher maximum frequency (0.5-1.2 kHz) than average (Epp 2019). Pulsed calls were quickly upsweeping calls with minimal or no low frequency component, had an average frequency range of 0.1-0.7 kHz, and were shorter in duration relative to other classes (0.2-0.3 s; Fig. 4; see Appendix Table A1 and Epp 2019 for details). Although calls were often produced singly (i.e. as a ‘unit’ – the smallest individual sound visible in the spectrogram), they also appeared as multiple calls of the same or differing types occurring in rapid succession (i.e. ‘series’). When a series was encountered, I considered each unit in the series a different, independent call as it was difficult to define a call bout due to variation in the number of repeated units and types of units, and because it is not possible to determine whether the series was produced by a single or multiple individuals.

Additionally, any overlapping calls, either belonging to the same or a differing call class, were selected and identified individually if the observer was confident that they were two separate calls; otherwise, the observer was conservative and only selected a single call for identification.

In the first, coarse-level aural and visual survey of the acoustic files, any sounds thought to potentially be humpback whale were point-selected to identify all possible occurrences of humpback whale calls (Table 2). Calls were annotated with additional comments regarding its call class, the quality of the call relative to background noise, as well as the observer's confidence in call class identification. During the second, fine-scale survey, all selected calls that were possibly humpback whale calls were assessed one to multiple times (depending on the degree of call identification uncertainty) to confidently assign calls into one of the three call classes (Table 1; Table 2). This was done with the assistance of a trained call-identification observer (M. Epp). If calls could not initially be assigned to a call class, they were assessed up to three more times. If the humpback whale call's identity was still uncertain following these subsequent reviews, the call was excluded from analysis to ensure the final dataset consisted of calls with a high degree of call identification certainty. A total of approximately 1%, 18%, and 33% of possible humpback whale calls per year (2015, 2016, and 2017, respectively) were excluded from final analyses as they could not be classified with certainty during the second fine-scale survey (Table 2). A signal-to-noise ratio (SNR) was not used as a cut-off in this study to ensure calls that could be identified into a class were included in the final dataset. The approximate percentage of calls with poor-moderate SNR (i.e. < 10 dB; Dunlop 2017) was determined manually in *Raven* (http://ravensoundsoftware.com/knowledge-base/signal-to-noise-ratio-snr/) in the final dataset by quantifying SNR of 30 randomly selected calls per class in each year (Table 2). Manually determining SNR in *Raven* involved creating a 'selection box' around each call and creating an identical selection box nearby in an area with minimal background noise (i.e. no calls) and using the ‘Inband Power (dB)’ measurement of both boxes to calculate SNR. In the final dataset, each call was associated with a call class, year, date, and time.

Statistical Analysis

To examine whether higher call activity was associated with the migration of whales into the study area (**P1**), I determined local maxima (i.e. ‘peaks’) in total call activity across days within each year using a peak analysis test (function: findpeaks) with default settings using the *pracma* package in R. This function examined a 3-day window and a peak was identified when the value on the middle day was greater than each day on their sides. The proportion of calls within each call class per day and per year, along with patterns in total call and class-specific activity across days within years, were qualitatively compared among years in the context of peak capelin biomass, timing of capelin and humpback whale arrival, as well as humpback whale abundance.

To assess humpback whale diel call activity within and across years (**P2**), I partitioned each day into four non-overlapping time periods (i.e. diel cycle) representing different light conditions. The four day periods include dawn, light, dusk and dark, as in previous studies (Wiggins et al. 2005, Matthews et al. 2014, Leroy et al. 2016). ‘Dawn’ was defined as the period when the sun was 12° below the horizon and ceased when it is 0° on the horizon (i.e. sunrise). ‘Dusk’ was defined as the period when the sun was below the horizon (< 0°; ‘sunset’) and ceased when it is 12° below the horizon. ‘Light’ was defined as the period between sunrise and sunset and ‘dark’ as the period between dusk and dawn. All daily twilight start and end times were obtained for Gander, Newfoundland (48.95° N, 54.61° W) from https://www.timeanddate.com as this location is approximately the same latitude as the study area. To determine diel call activity, I counted the total number of calls occurring over all classes and per class during each day period on each day. As the day periods within the diel cycle varied in duration, and the duration of each day period varied across days in the year, I calculated the average number of calls per day period (per class and overall) for each day by dividing the total number of calls during the day period by its exact length (in hours) for that day. As the number of total and class-specific calls varied considerably across days, I calculated a z-score of call activity for each day by subtracting the average number of calls across all day periods for a single day from the average number of calls for a single day period within that day, and then divided by the standard deviation of that day. Similar to other studies (Wiggins et al. 2005, Matthews et al. 2014, Leroy et al. 2016), diel pattern analysis was conducted only on days where at least one call per call class was present during the day (Table 2).

Diagnostic plots (i.e. Normal Q-Q plots), along with tests for normality (Shapiro-Wilks test) and homogeneity of variance (Levene's test; Fligner-Killeen's test) indicated that the standardized data satisfied the homogeneity of variance assumption but did not meet the underlying normality assumption for parametric statistics. To verify the robustness of ANOVAs to these assumption violations, I conducted a Kruskal-Wallis non-parametric test and an unbalanced one-way ANOVA to assess diel call activity across all call classes (separately) within a single year, as well as an unbalanced Two-Way ANOVA to assess diel call class activity (separately) among years. All statistical tests yielded similar results for all call classes and, thus, I used parametric statistics to allow inclusion of multiple predictor variables within one model. This was further justified as ANOVAs are considered fairly robust to non-normality (Blanca et al. 2017). A two-way ANOVA was used to test for differences in mean call activity among day periods and years as well as whether diel patterns were consistent across years. A Tukey's HSD test was used for pairwise comparisons among day periods across years. I conducted the same analysis again (i.e., two-way ANOVA, Tukey's HSD test) to test for differences in mean proportions of calls per call class among day periods and years. The proportions for each call class were arcsine transformed prior to analysis to meet the assumptions of parametric statistics (Quinn and Keough 2002). All statistical analyses were conducted in R v. 3.5.1.

Results

Call activity patterns varied across days within years, where call activity was typically highest near the estimated date of humpback arrival (Table 1; Fig. 5) into the study area but subsequently decreased thereafter. A total of two, five, and three local maxima in call activity were identified within the time series for 2015, 2016, and 2017, respectively (Fig. 5). In 2015 and 2016 the highest local maximum (i.e. peak call activity) occurred immediately following the arrival of humpback whales into the study area (July 17 and Aug. 1, respectively) but decreased shortly after and remained consistently low until the end of the recording period (Table 1; Fig. 5). In 2017, the highest local maximum (i.e. peak call activity) occurred much later after humpback whales arrived in the study area relative to 2015 and 2016 (Table 1; Fig. 5). While call activity within call classes varied across days, LF was the dominant call class for most days in all years, followed by pulsed and then HF in two of the three years (Fig. 5). Humpback whales arrived later during 2016 (July 31) and even later in 2017 (August 4) relative to 2015 (July 17), corresponding to later capelin arrival in the study area during both years relative to 2015 (Table 1).

Total call activity was similar during 2015 and 2017 (~2000 identified calls) and both were associated with a similar estimated abundance of humpback whales in the study area (~1000 whales), despite approximately double the capelin biomass in 2015 than 2017 (Table 1). In contrast, 2016 had the highest call activity, with approximately double the calls of the other years, which was also associated with the highest estimated humpback whale abundance in the study area but lowest capelin biomass relative to other years (Table 1; Fig. 5). Each call class was present in all years but the proportion of call classes varied among years, where LF consistently comprised the majority of all calls in each year (43-75%), pulsed comprised nearly the same proportion of calls as LF during 2015 (40%) but were in lower proportions in the other years (8-28%), and HF calls consistently comprised a low proportion of calls (9-17%; Table 1). In 2017, the majority of calls for both the HF (> 90%) and LF (~70%) call classes appeared to be dominated by a single call type (and/or variants; Fig. 2G, Fig. 3D) and differed from those described in previous years as most calls were flat in appearance, lacked an upsweep at the end, were much shorter in duration (~0.2 s), and occasionally had harmonics.

Total call activity differed significantly among day periods (Two-Way ANOVA, $F_{3, 146}$ = 19.616, $p < 0.0001$; Fig. 6) but not among years ($F_{2, 146}$ = 0.005, $p = 0.995$), nor was there an interaction between day period and year ($F_{6, 146}$ = 1.889, $p = 0.086$). Total call activity was highest during light relative to dawn, dusk, and dark periods (Tukey's HSD test; p-values < 0.0001) but did not differ among other day periods (p-values = 0.846-0.993; Fig. 6). Similarly, HF call activity differed significantly among day periods ($F_{3, 74}$ = 57.703, $p < 0.0001$; Fig. 6) but not among years ($F_{2, 74}$ = 0.010, $p = 0.990$) and the interaction between day period and year was not significant ($F_{6, 74}$ = 0.446, $p = 0.846$). HF call activity was significantly higher during light than dawn, dusk, and dark periods (p-values < 0.0001), and also during dark than dawn or dusk periods (p-values: 0.006-0.012), while dawn and dusk ($p = 0.996$) did not differ significantly (Fig. 6). LF call activity also differed significantly among day periods ($F_{3, 146}$ = 10.365, $p < 0.0001$; Fig. 6) but not among years ($F_{2, 146}$ = 0.003, $p = 0.997$), and the interaction between day period and year was not significant ($F_{6, 146}$ = 1.174, $p = 0.323$). LF call activity was higher during light than dawn, dusk, and dark periods (p-values < 0.001) but did not differ significantly between other day periods (p-values = 0.663-0.999; Fig. 6). Pulsed call activity differed significantly among day periods ($F_{3, 130}$ = 12.027, p < 0.0001; Fig. 6) but not among years ($F_{2, 130}$ = 0.005, p = 0.995), however, the interaction between day period and year was significant ($F_{6, 130}$ = 3.158, p = 0.006). Specifically, pulsed call activity during the light period was significantly higher than dawn and dusk in 2015 (p-values: 0.004-0.007) as well as between the light period and dawn and dark in 2016 (p-values: 0.002-0.038); however, no significant differences were observed among all other day periods in 2015 (p-values: 0.114-0.999) and 2016 (p-values: 0.430-0.999), nor among any day periods in 2017 (p-values: 0.055-0.999; Fig. 6).

Similar to the daily and annual scales, the LF call class dominated across all day periods in all years, with the exception of the light period during 2015, where HF calls were present in similar proportions (Fig. 7). The mean proportion of LF calls did not differ significantly among day periods ($F_{3, 113}$ = 2.527, p = 0.061; Fig. 7) but did differ among years ($F_{2, 113}$ = 4.129, p = 0.019), and the interaction between day period and year was not significant ($F_{6, 113}$ = 1.596, p = 0.155). Specifically, the mean proportion of LF calls during 2015 was significantly lower than 2016 (p = 0.026), but proportions did not differ between 2015 and 2017 (p = 0.349) or between 2016 and 2017 (p = 0.192). The mean proportion of HF calls differed significantly among day periods ($F_{3, 113}$ = 5.057, p = 0.003; Fig. 7) and years ($F_{2, 113}$ = 7.681, p < 0.001), and the interaction between day period and year was significant ($F_{6, 113}$ = 2.256, p = 0.043). Specifically, the mean proportion of HF calls in 2015 was significantly higher during light than dark periods (p-values = 0.006; Fig. 7) but did not differ significantly among other day periods during 2015 or any of the other years (p-values = 0.216-0.999; Fig. 7). Additionally, the mean proportion of HF calls was highest during light in 2015 relative to light periods in both other years (p-values < 0.001; Fig. 7); however, no significant differences in mean HF call proportions were observed in other day periods across years (p-values ≈ 0.999; Fig. 7) as the mean proportion of HF calls consistently comprised < 10% of total calls in all day periods among years. The mean proportions of pulsed calls did not differ significantly among day periods ($F_{3, 113} = 0.458$, p = 0.712; Fig. 7) and years ($F_{2, 113} = 2.599$, p = 0.079), and the interaction between day period and year was not significant ($F_{6, 113} = 1.048$, p = 0.399). In 2015, only one day had humpback whale calls present during the dusk period and all three call classes were present this day, therefore, no standard error bars are present (Fig. 7).

Discussion

The results of this study are the first, to our knowledge, to describe inter-annual, daily, and diel patterns of three non-song call classes on the humpback whale foraging grounds in coastal Newfoundland. Humpback whale non-song calls of all three classes were detected in the study area in all years, and the proportion of calls per class remained fairly consistent across day periods, days, and years, being dominated by low frequency calls. The overall call activity and class-specific call activity, however, varied across all of these time scales. Specifically, 2016 had the highest call activity and humpback whale abundance but lowest capelin biomass of all years, while 2015 and 2017 had similar call activity and humpback whales despite higher capelin biomass in 2015. As predicted, the total and class-specific call activity peaked around the date of humpback arrival into the study area, with the exception of 2017 (**P1**), suggesting that calling (regardless of call class) may be more important for communication and mediating social interactions among humpback whales while moving into the area rather than while foraging in the study area. Additionally, with the exception of pulsed call activity during 2017, total and class-specific call activity showed distinct and fairly consistent diel patterns within and across years (**P2**), but not as initially predicted. The higher prevalence in call activity of all call classes during light periods did not support our hypothesis and predictions, and contrasts other studies in the Atlantic (Huang et al. 2016, Kowarski et al. 2018) where humpback whale non-song calls occurred primarily at night. Peak call activity during light periods suggests that both short- and long-distance acoustic communication are more important during daylight relative to dark periods. As previously described foraging-associated calls (D'Vincent et al. 1985, Stimpert et al. 2007, Parks et al. 2014, Fournet et al. 2015, 2018b) were not heard during this study, it is difficult to link foraging and foraging-associated calls to specific day periods.

Call Type Composition

The dominance of the LF call class across all time scales (i.e., diel, daily, annual), with the exception of the 2015 light period, suggests that these calls play an integral role in humpback whale communication on their coastal Newfoundland foraging grounds. The majority (> 70 %) of LF calls in our study area in 2015 and 2016 were classified as 'whups' and 'growls' (Epp 2019), which have been identified in geographically isolated populations on foraging grounds (Rekdahl et al. 2013, 2017, Fournet et al. 2015, Epp 2019), along migration routes (Dunlop et al. 2007, 2008, Dunlop 2017) and on breeding grounds (Epp 2019), as well as across decades within a region (Rekdahl et al. 2013, Fournet et al. 2018a). The production of these calls under multiple behavioural contexts (i.e., foraging, breeding, migrating) throughout the humpback whale range suggests these calls are important for general communication, possibly as a contact call to indicate an individual's position to others when outside of visual range, and/or for intra- or intergroup communication, coordination of social interactions and social integration of conspecifics (Dunlop et al. 2008, Wild and Gabriele 2014). For instance, the behavioural context of low frequency call types during migration included individuals traveling alone (typically lone males) as well as in groups (Dunlop et al. 2008), where groups consisted of mother-calf pairs either alone or with one (or more) escorting males, and also groups without mother-calf pairs (Dunlop et al. 2008). Indeed, LF calls were often made when individuals or groups joined or split from other groups (Dunlop et al. 2008). As the acoustic properties of low frequency calls enables enhanced signal propagation and fidelity across time and space, the prevalence of these calls may allow for communication at unknown and/or far distances, as suggested for the low frequency sounds of terrestrial mammals, such as elephants (Langbauer Jr. 2000, Garstang 2004). Interestingly, ‘whups’ and ‘growls’ were classified within low-arousal sound groupings of migrating humpback whales in Australia (Dunlop 2017). Low-arousal situations are likely common while foraging in coastal Newfoundland where prey is highly abundant, potentially explaining the prevalence of LF calls. Indeed, non-competitive and/or cooperative or coordinated behaviours seem more common among humpback whales on the foraging grounds, while aggressive behaviours are seldom observed and/or described in coastal Newfoundland (Whitehead 1983, Bredin 1985, Davoren pers. comm.) and elsewhere (Baker and Herman 1984, Weinrich 1991, Burrows 2017). Overall, the acoustic properties of low frequency calls likely allow whales to communicate over short and long distances, which may be adaptive to ensure cooperative foraging opportunities, maintain larger group sizes to reduce predation risk, and attract mates during breeding. The prevalence of low frequency calls throughout their global range and in a variety of social settings suggests an integral function in facilitating and/or maintaining contact with conspecifics (Wild and Gabriele 2014).

In contrast, the high attenuation of high frequency and (the upper portion of) pulsed calls likely constrain their use to short-distance communication and, thus, these calls may be reserved for specific situations instead of use in general communication. Indeed, high frequency calls in terrestrial animals are often produced in close-contact, ‘high-arousal,’ fearful and/or appeasing contexts (Morton 1977). For example, infant and adult female white-faced capuchins (*Cebus capucinus*) produce pulsed, high frequency ‘trills’ when interacting directly with conspecifics (e.g., huddling, grooming) to apparently increase an affiliation and decrease aggression (Gros-Louis et al. 2008), while adults produce ‘loud trills’ apparently as a contact call to coordinate group movements during movement (Gros-Louis et al. 2008) and high frequency ‘screams’ to apparently respond to, or initiate, aggressive interactions (Gros-Louis et al. 2008). Similarly, migrating humpback whales produce higher frequency sounds (e.g., cries, shrieks) during direct interactions with other conspecifics, such as among affiliating groups and when multiple males compete to act as primary escort to mother-calf groups during migration (Dunlop 2017). As mentioned previously, these high-arousal, close-contact situations are uncommon while foraging in coastal Newfoundland, likely explaining the lower instances of HF calls, and may be limited to migrating aggregations of humpback whales into the study area. The majority (> 80%) of pulsed calls were ‘swops’, ‘droplets’ and ‘teepees’, which have been identified in geographically isolated populations on foraging grounds, including coastal Newfoundland, and appear to be stable across decades (Rekdahl et al. 2013, Fournet et al. 2015, 2018c, 2018a, Epp 2019), suggesting these calls are important in humpback whale communication. These three pulsed call types are believed to function in short-range communication on the foraging grounds in Alaska (Fournet 2014), while other pulsed calls may mediate associations and divisions of migrating groups (Dunlop et al. 2008) and are known to be commonly produced by calves in mother-calf pairs (with/without a male escort; Zoidis et al. 2008, Indeck et al. 2020), which are often present in the study area (Johnson 2018). Further research examining the behavioural context of these call classes, however, is required to determine reasons for variation in call class proportions within coastal Newfoundland.

Diel Call Activity Patterns

Humpback whale call activity showed distinct diel patterns across years in coastal Newfoundland, where calling was highest during the light period for all call classes. One exception was the pulsed call class, where diel call activity was absent during 2017, likely due to low sample sizes. Higher call activity during daylight contrasts the diel call patterns in their Gulf of Maine foraging grounds in the fall (Huang et al. 2016) and during the fall-winter-spring migration of humpback whales off of eastern Canada (Kowarski et al. 2018), whereby non-song call activity was highest during dark periods in both studies. Discrepancies among studies may result from the study periods representing different periods within the annual cycle, as humpback whale behaviour is known to be different during migration as well as on the foraging grounds (Jurasz and Jurasz 1979, Whitehead 1983, Baker and Herman 1984, D'Vincent et al. 1985, Whitehead and Glass 1985a, Clapham 1996, Cerchio and Dahlheim 2001, Dunlop et al. 2008) when prey are less abundant (fall) relative to during the summer when prey availability peaks. Nonetheless, lower call activity across all call classes during dark periods suggests that both short- and long-distance communication among humpback whales is less important during dark relative to light periods, possibly because individuals are not engaged in behaviours requiring frequent conspecific communication. For instance, if low frequency sounds act as contact calls among conspecifics (Dunlop et al. 2008, Wild and Gabriele 2014, Dunlop 2017), then activities such as group fusion and fission may be less frequent during dark periods. Similarly, if HF and pulsed sounds are typically used in high-arousal, close-contact behavioural interactions (Dunlop et al. 2008, Dunlop 2017) or in mother-calf communication (Zoidis et al. 2008, Indeck et al. 2020), respectively, lower call activity during dark periods suggests that these situations occur less at night. Alternately, lower call production during dark by mother-calf pairs may be important to minimize acoustic detectability by predators. Indeed, although infrequent, groups of 2-5 killer whales (*Orcinus orca*) are observed in the coastal Newfoundland study area briefly (1-2 days; overlapping with dates of humpback whale presence) each year (Davoren pers. comm.; Newfoundland and Labrador: Lien et al. 1988, Mitchell and Reeves 1988). Killer whales are known to hunt and/or attack humpback whale calves and adults (Newfoundland: Whitehead and Glass 1985b, Lawson et al. 2007; South America: Florez-Gonzalez et al. 1994; Australia: Pitman et al. 2015; Alaska: Saulitis et al. 2015) and other marine mammals, sometimes during dark periods (Alaska: Barrett-Lennard et al. 1996, Deecke et al. 2005, Newman and Springer 2008, Deecke 2013; Newfoundland and Labrador: Lawson et al. 2007), and can be silent while hunting, appearing to use visual cues and/or prey-generated sounds to detect their prey (Alaska: Barrett-Lennard et al. 1996, Deecke et al. 2005, Deecke 2013). Mother-calf humpback whale pairs in Australia engage in acoustic crypsis by producing weak, whisper-like calls during deep dives which have a low active space (i.e., < 100 m, facilitating close contact), likely to maintain contact while minimizing killer whale eavesdropping and predation risk (Videsen et al. 2017), similar to southern right whales (*Eubalaena australis*: Nielsen et al. 2019).

Previously described foraging-associated calls on other foraging grounds during solitary or coordinated feeding attacks (Cerchio and Dahlheim 2001, Stimpert et al. 2007, Parks et al. 2014, Fournet et al. 2015, 2018b) were not heard in our study area. Therefore, it is not possible to determine if foraging activity was related to call activity, nor can we link foraging activity to specific day periods. Although it is possible that a form of high frequency feeding cries are used in coastal Newfoundland (see description in Fournet et al. 2015), especially because feeding calls resembling those described in Alaska were heard nearby in the Bay of Fundy (off Nova Scotia) during the fall (Kowarski et al. 2019), we did not detect these calls in our study area. Based on observed diel foraging patterns of humpback whales in other regions (Friedlaender et al. 2009, 2016), we predicted that humpback whales optimized foraging efficiency by primarily foraging during dark periods when capelin are dispersed near the ocean surface (Davoren et al. 2006, 2010, Regular et al. 2010) and, thus, are highly available to air-breathing predators. Indeed, humpback whales on their Antarctic foraging grounds are observed to follow the diel vertical migration of Antarctic krill in the water column, whereby they feed on broadly-distributed, easily accessible surface aggregations during night and instead rest during daylight when krill are found in dense, discrete prey patches at greater depths (Friedlaender et al. 2016). Although nighttime foraging has been linked to a foraging-associated call ("megapclick"; Stimpert et al. 2007), calling may not be beneficial under all circumstances or on all prey types for humpback whales. For instance, producing calls while feeding on dispersed surface aggregations of capelin at night may cause capelin to school and dive deeper in the water column, thereby increasing prey capture difficulty. Therefore, lower call activity during dark periods may be indicative of high foraging activity in humpback whales (as in killer whales: Deecke et al. 2005, Deecke 2013), regardless of calls during foraging found elsewhere (Cerchio and Dahlheim 2001, Stimpert et al. 2007, Parks et al. 2014, Fournet et al. 2018b). Such behavioural flexibility is likely, as humpback whales employ a wide variety of foraging strategies to capture different prey types among regions, such as bubble netting (Jurasz and Jurasz 1979, Leighton et al. 2007, Wiley et al. 2011), surface and sub-surface lunging (Jurasz and Jurasz 1979, Ware et al. 2011), and bottom side-roll feeding (Ware et al. 2014). It is also possible that lower call activity at night may simply be due to inactivity (e.g. sleep/logging behaviour), while high call activity during light periods may indicate high foraging activity, during which previously undescribed foraging-related calls are produced. Further research is required to ascertain diel foraging behaviour of humpback whales on their Newfoundland foraging grounds and whether foraging activity is associated with call activity.

Call Activity Patterns Across Days

Call activity varied across days within a year and this was consistent across two years of this study. As predicted, peak (overall) call activity was associated with humpback whales first arriving into the study area during 2015 and 2016, after which call activity subsequently decreased. In contrast, 2017 had a delayed peak in call activity following humpback arrival into the study area, possibly due to different movement patterns of whales into the study area, such as staggered arrival of aggregations across days or increased distance among fewer individuals upon arrival. Higher call activity during initial movement of whale aggregations into the study area during 2015 and 2016, may indicate a decrease in whale abundance as the “season” progresses; however, whales are known to remain in the area across days (Johnson 2018). Alternatively, high call activity during movement into the study area concurs with calls mediating social interactions among migrating groups at varying distances, especially given that the majority of calls were low frequency (Dunlop et al. 2008, Wild and Gabriele 2014, Dunlop 2017). Calling to maintain contact during migration may ensure humpback whales arrive in groups at foraging areas, which may be adaptive to ensure cooperative foraging opportunities and higher success during prey capture. As a similar proportion of call classes was maintained on peak call activity days, high frequency and pulsed calls also increased during initial arrival of whales into the study area, suggesting an overall higher arousal state. Indeed, migrating groups of humpback whales are known to be dynamic and transient in nature, as evidenced by frequent group formation and dissolution, and arrival and splitting of individuals from groups (Whitehead 1983, Dunlop et al. 2008, Dunlop 2017). For migrating humpback whales in Australia, arousal state increased as whales moved among groups, resulting in the production of progressively more high-arousal call types (Dunlop 2017). HF calls are nearly absent in the days following initial humpback whale migration into the study area (2015 and 2016), suggesting that these high-arousal social interactions during migration shift to primarily low-arousal interactions as whales disperse to forage throughout the study area. In support, humpback whales in coastal Newfoundland are primarily found alone or in small groups (2-4 individuals) engaged in uncoordinated foraging, although larger, more ephemeral groups (≥ 10 whales) occasionally engage in coordinated foraging (Whitehead 1983, Whitehead and Glass 1985a, Davoren pers.comm.). Humpback whales are known to gradually disperse throughout coastal Newfoundland as the season progressed, showing unstable affiliations among individuals with the exception of mother-calf pairs (Whitehead 1983, Whitehead and Glass 1985a, Davoren pers. comm). As pulsed calls were commonly produced by calves in mother-calf groups (Hawaii: Zoidis et al. 2008; Australia: Indeck et al. 2020), the higher number of pulsed calls during initial humpback arrival may highlight that these pairs are calling more to maintain contact with each other. More fine-scale measurements and information on humpback whale abundance and behaviour across days will be needed to determine whether humpback whales become less vocally active following initial movement into the area.

Interannual Variation in Call Activity

Call activity varied among years in a variety of ways. First, the highest call activity was associated with the highest whale abundance during 2016, whereas 2015 and 2017 had similar (and lower) whale abundance and total call activity. This suggests that humpback whale call activity may act as a proxy for abundance and may be used as such in future surveying efforts, as suggested for other whale species (Mcdonald and Fox 1999, Marques et al. 2011, 2013, Norris et al. 2017). Higher call activity during 2016 was also associated with the lowest capelin biomass and, thus, may reflect increased difficulty foraging, such as more frequent group splitting and/or joining during search activities for prey, and/or competition during prey capture due to the greater abundance of whales and lower prey. Alternatively, humpback whales may increase call activity during years of low prey biomass to attract conspecifics to prey aggregations to increase cooperative prey capture. Indeed, cooperative foraging (e.g. bubble-netting) has been observed on other foraging grounds (Jurasz and Jurasz 1979), implying benefits of foraging in close association with conspecifics. Second, there was much lower diversity of call types within call classes during 2017 relative to other years. Indeed, HF and LF call classes during 2017 were dominated by a single call type (and/or slight variants), whereas three HF and seven LF call types were identified on the Newfoundland foraging grounds during 2015 and 2016 using the same hydrophone recordings as this study (Epp 2019). The lower call diversity within classes, the delayed peak in call activity after humpback whale arrival in the study area, along with a break down in diel call activity patterns (in the pulsed call class) indicates differences in humpback whale behaviour in the study area related to a minimal need for diversity in conspecific communication. As reasons for these differences are unknown, we recommend the continued collection of acoustic recordings, in addition to more fine-scale measurements of humpback whale behavioural to help elucidate interannual differences in call activity.

Conclusions

In conclusion, we provide the first description of the temporal patterns in humpback whale non-song call activity on their Newfoundland foraging grounds as a first step to eventually understand the behavioural context of these calls. Call activity varied in all classes across all time scales (i.e., diel, daily, interannual) in association with varying environmental and social conditions experienced by the humpback whales. In future studies, we recommend collecting more detailed, fine-scale behavioural data along with call activity upon arrival into the study area, as well as while humpback whales are dispersed within the area to forage to help inform the behavioural context of these call classes. Studies using tags equipped with hydrophones while observing focal individuals, such as Stimpert et al. 2007 and Parks et al. 2014, as well as the opportunistic use of a portable hydrophone while recording surface-active behaviours (as in Silber 1986, Zoidis et al. 2008; similar method using moored hydrophones and behavioural observations: Dunlop 2016) would also help inform the behavioural context of these calls. Additionally, combining the previously aforementioned techniques with more detailed measurements of capelin abundance and distribution while whales are in the study area and/or foraging would further inform as to the presence of previously undescribed and/or novel foraging-associated calls (as found elsewhere: D’Vincent et al. 1985, Stimpert et al. 2007, Parks et al. 2014, Fournet et al. 2015, 2018b). Investigation and analysis of temporal patterns in cetacean calling is an important first step in informing the next steps of future research to eventually understand the functions and/or behavioural contexts of calls on previously undescribed regions and marine mammals.

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Tables and Figures

Table 1. Peak capelin biomass (g m^{-2}), dates of capelin spawning and humpback whale arrival, and estimated humpback whale abundance obtained from existing studies on the northeast Newfoundland coast study area during 2015-2017. Dates are indicated by both ordinal and Gregorian calendar date. The proportion of all call classes (high frequency, HF; pulsed, P; low frequency, LF) per year are also indicated.

	2015	**2016**	**2017**	**Data source**
Date of capelin spawning	201 (July 20)	197 (July 15)*	216 (August 4)	Johnson (2018)
Peak capelin biomass (g m^{-2})	0.123	0.005	0.048	Johnson (2018)
Humpback whale abundance	~ 1020 whales	~ 1800 whales	~ 1000 whales	Johnson (2018)
Date of humpback whale arrival	198 (July 17)	213 (July 31)	216 (August 4)	Johnson (2018)
Total number of identified calls	1877	4582	2198	This study
Proportion of HF calls	17%	9%	17%	This study
Proportion of P calls	40%	28%	8%	This study
Proportion of LF calls	43%	63%	75%	This study

* For 2016, day 197 (July 15) is the date when capelin were first observed at spawning sites within the study area, however, capelin spawning did not actually occur.

Table 2. Number of days per year that were examined acoustically, and during which calls within specific call classes were detected. Only these days were used for the annual (within year) diel analysis for each call class. The total number of overall calls, and calls per call class, in each year that were used in statistical analyses is given, as well as the total number of calls initially believed to be a humpback whale call. Some calls were later excluded from final analysis due to low-quality and/or uncertain call class. The percentage of 30 randomly selected calls per call class and year with poor-moderate Signal-to-Noise Ratio (SNR) is shown.

		2015	2016	2017
Total number of days examined acoustically		8	19	15
Number of days containing calls within each call class	**High frequency**	7	10	5
	Pulsed	6	19	12
	Low frequency	7	19	15
Number of calls per call class used in statistical analysis		318 **HF** 743 **P** 816 **LF**	432 **HF** 1266 **P** 2884 **LF**	375 **HF** 171 **P** 1652 **LF**
Number of calls identified to call class and used in statistical analysis		1877	4582	2198
Original number of potential calls		1892	5583	3262
Overall percentage of poor-moderate (< 10 dB) SNR calls		28%	42%	40%
Percentage of poor-moderate (< 10 dB) calls	**High frequency**	27%	63%	70%
	Pulsed	7%	23%	27%
	Low frequency	50%	40%	23%

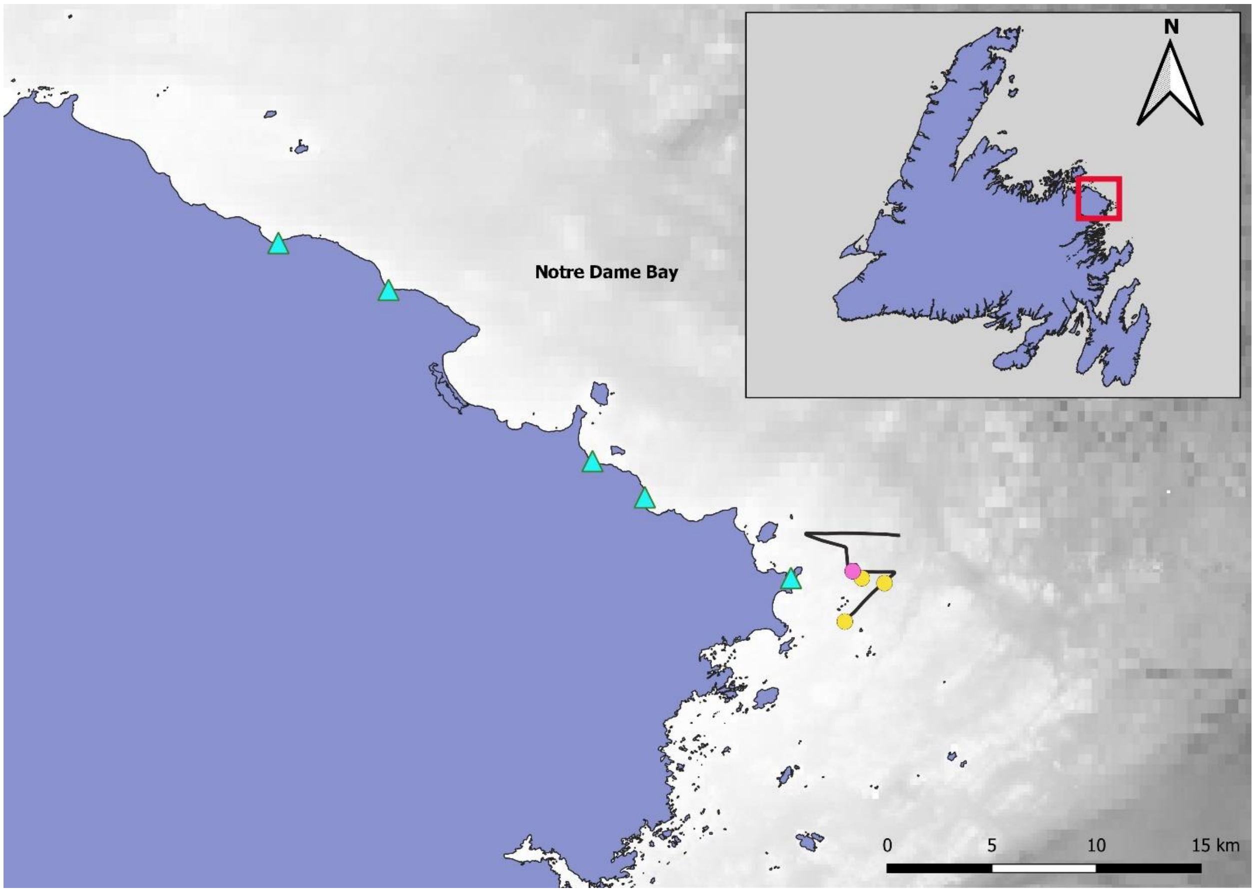

Figure 1. Location of the study area (red square) on the northeast coast of Newfoundland (Notre Dame Bay), Canada showing the beach (triangle) and four persistent deep-water (circle) capelin spawning sites monitored throughout the study area, as well as the hydroacoustic survey track (black line) to determine capelin biomass. The hydrophone was deployed at the same persistent deep-water capelin spawning site in all years (pink circle).

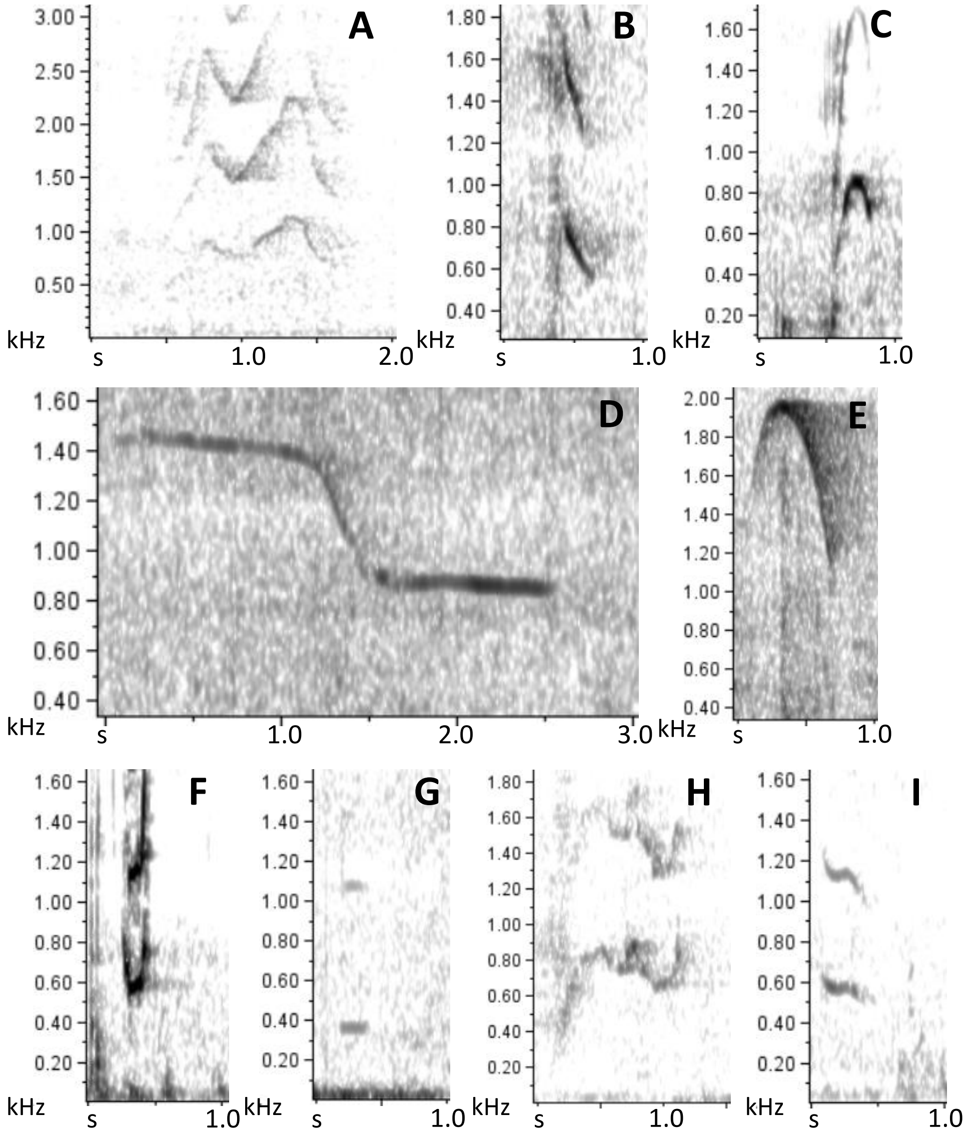

Figure 2. Spectrograms of some humpback whale calls manually classified into the high frequency call class (**A-I**) across years, 2015-2017. Specifically, **G**) was the call that dominated the high frequency call class in 2017. Note the varying y-axis scale among spectrograms.

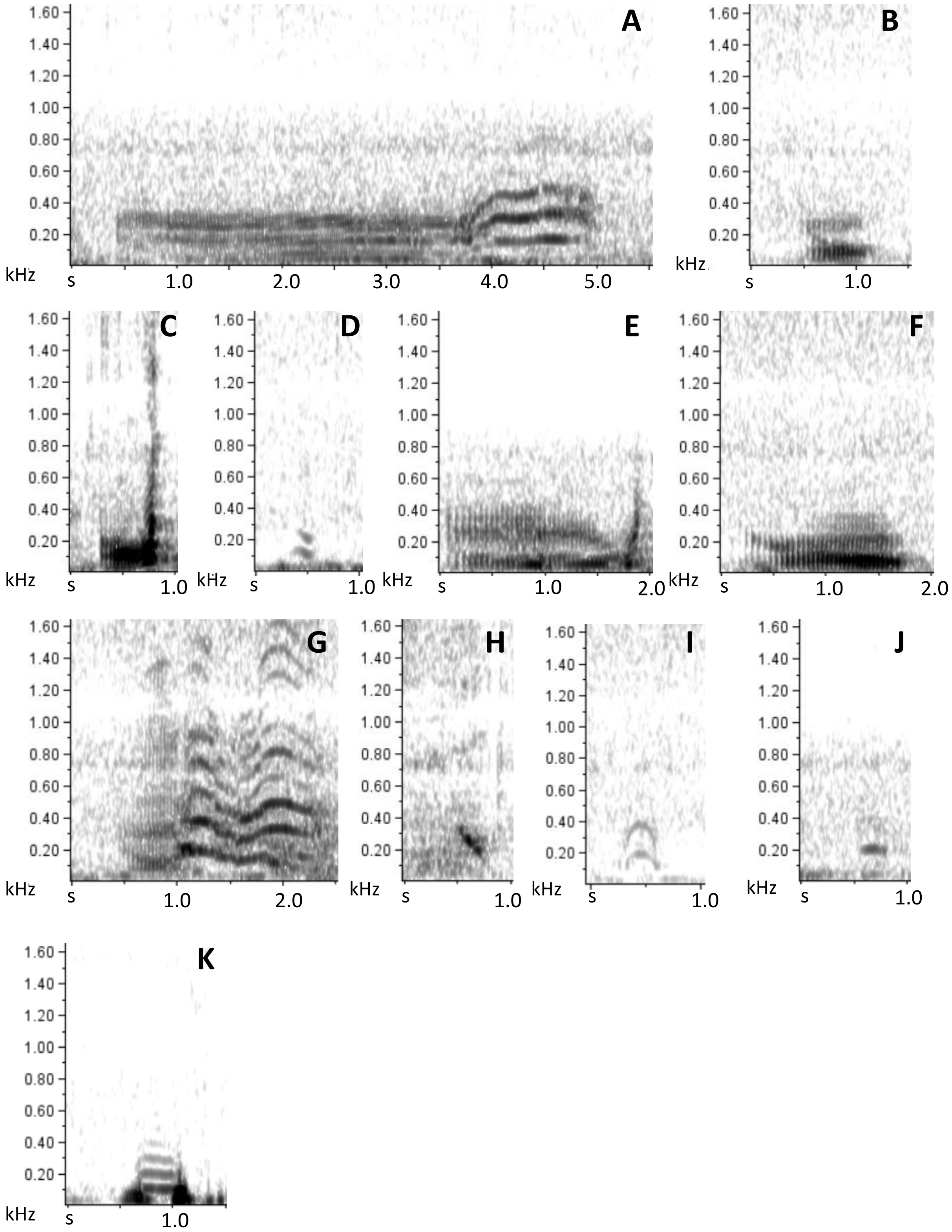

Figure 3. Spectrograms of some humpback whale calls manually classified into the low frequency call class (**A**-**K**) across years, 2015-2017. Specifically, **D**) (and/or variants) was the call that dominated the low frequency call class in 2017.

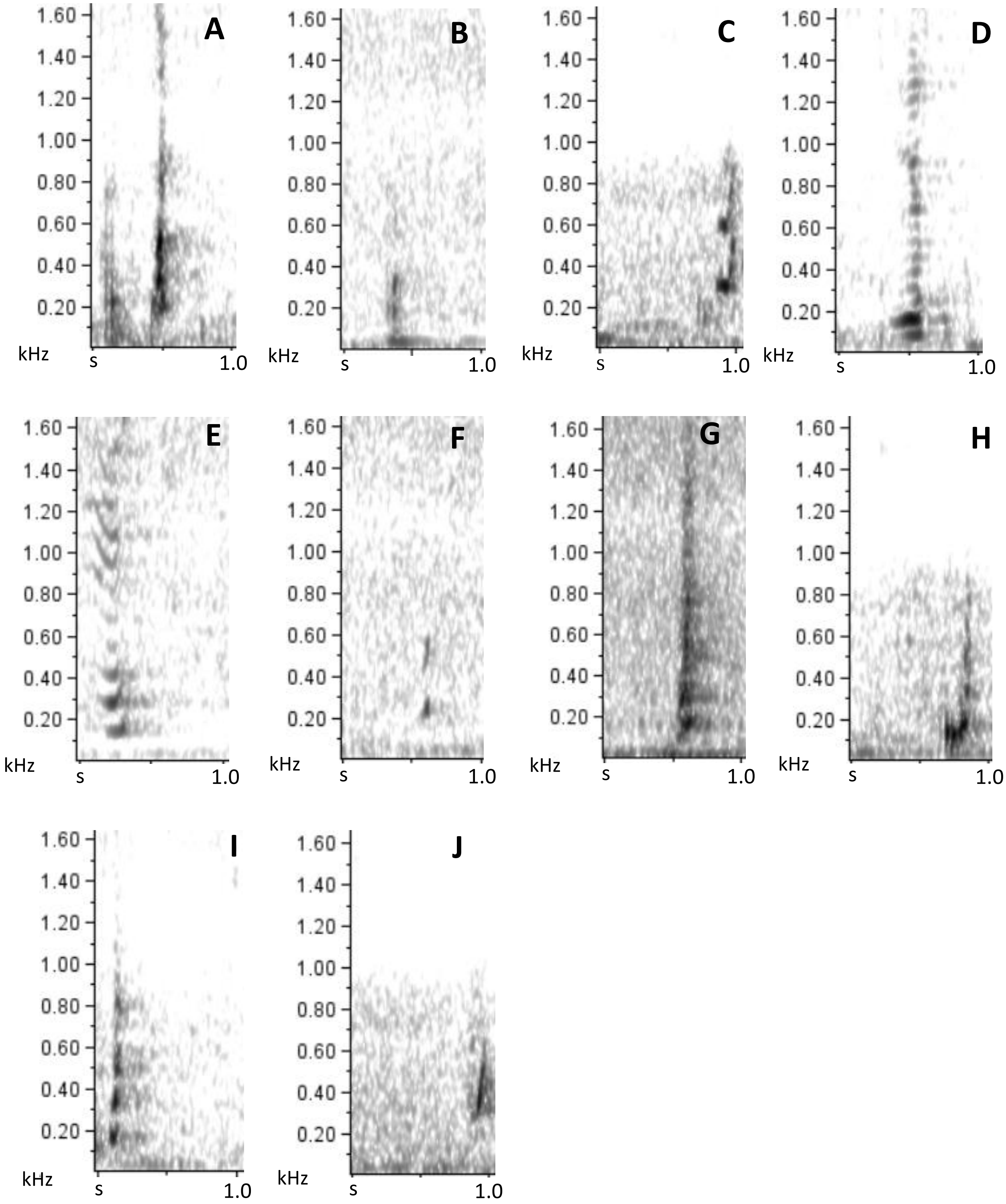

Figure 4. Spectrograms of some humpback whale calls manually classified into the pulsed call class (**A**-**J**) across years, 2015-2017.

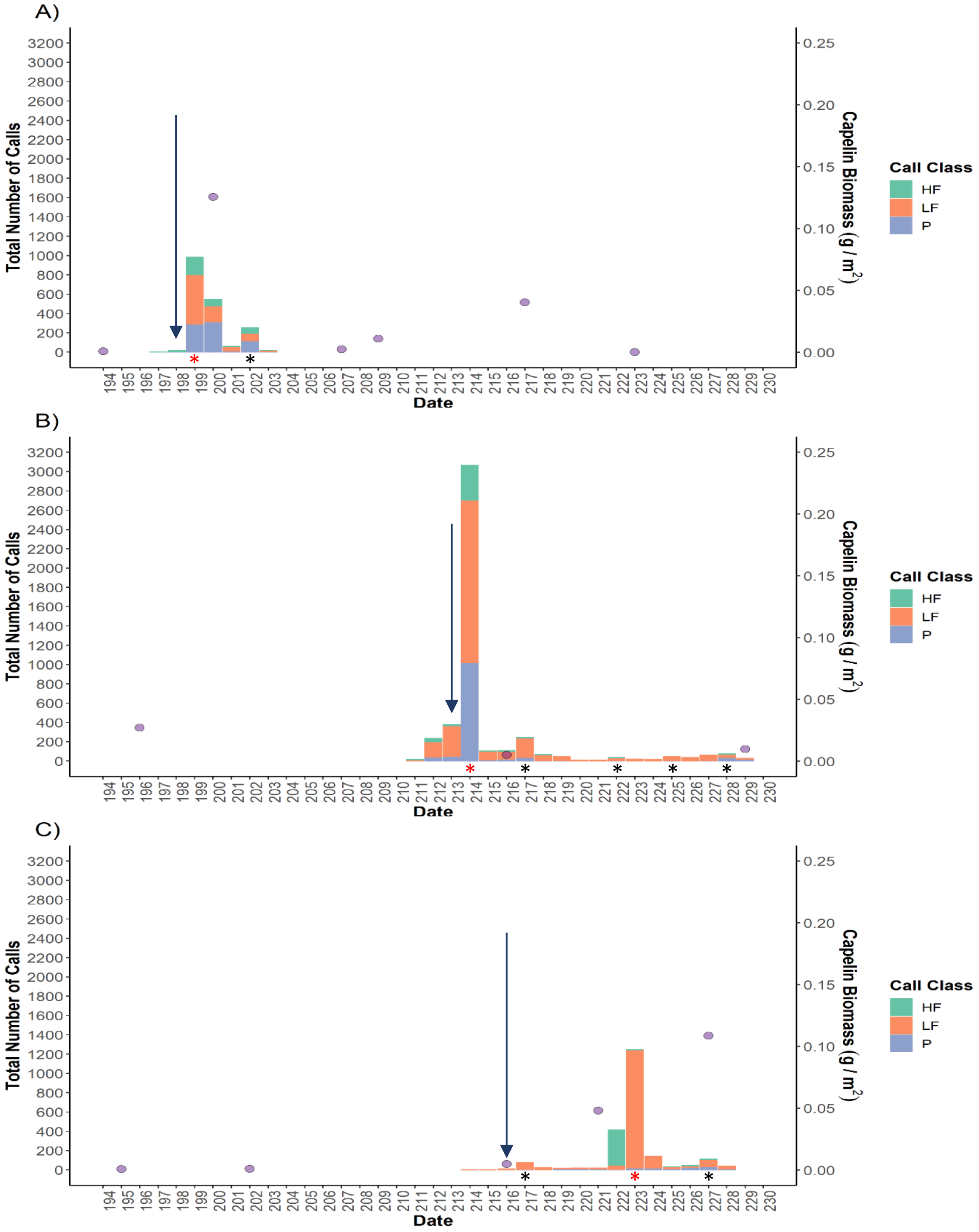

Figure 5. Daily total call, and call class, activity of humpback whales (*Megaptera novaeangliae*) and capelin biomass (circles; g m^{-2}) on their foraging grounds off the northeast coast of Newfoundland (Notre Dame Bay) from mid-July to mid-August, **A-C)** 2015-2017, respectively. The total numbers of high frequency (HF; green), low frequency (LF; orange), and pulsed (P; indigo) calls across days are indicated. Acoustic data were collected via a hydrophone moored at an annually used capelin deep-water spawning site. Ordinal date is indicated on the x-axis. Arrows indicate date of initial arrival of humpback whale aggregations (≥ 10 individuals) into the study area as determined by boat-based visual observations. Asterisks indicate dates of all detected local maxima per year, and red asterisks indicate the highest local maximum (i.e. peak call activity) within each year.

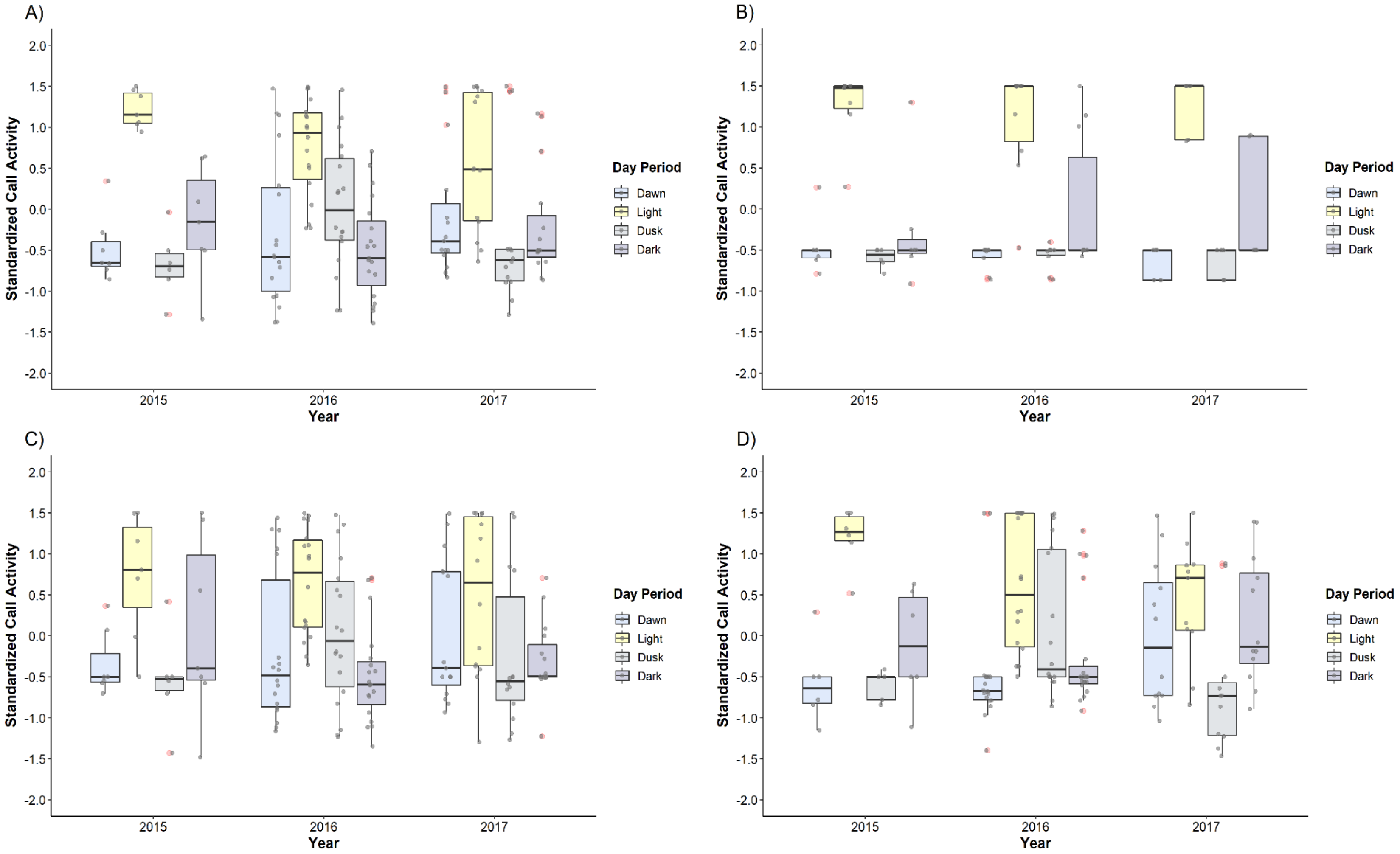

Figure 6. Boxplot indicating annual diel patterns in standardized (z-score) call activity for **A)** total calls and **B-D)** per call class (high frequency, low frequency and pulsed, respectively) across different light conditions (i.e., dawn, light, dusk, dark, respectively) in humpback whales (*Megaptera novaeangliae*) on their foraging grounds off the northeast coast of Newfoundland (Notre Dame Bay) from mid-July to mid-August, 2015-2017. Positive values indicate higher call activity than daily averages, while negative values indicate lower call activity than daily averages. Red dots indicate potential outliers, while the box indicates the minimum and maximum values along with the 25th percentile (box bottom), median (solid line), and 75th percentile (box top). Grey dots represent actual data points.

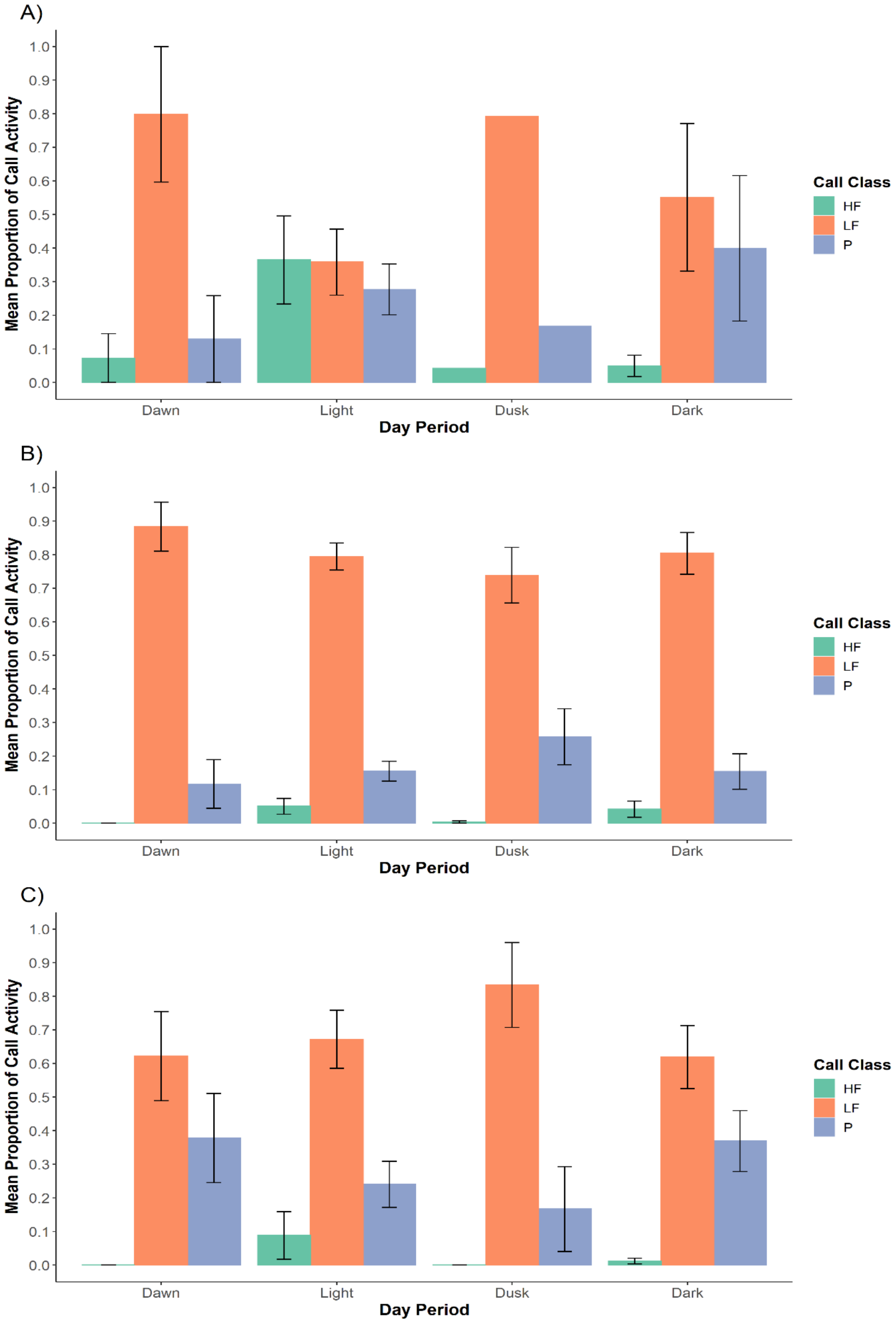

Figure 7. Mean (± standard error) proportion of humpback whale call activity for high frequency (HF; green), low frequency (LF; orange) and pulsed (P; indigo) call classes in each day period (i.e., dawn, light, dusk, dark) across all days during July-August **A)** 2015, **B)** 2016 and **C)** 2017 on their Newfoundland foraging grounds.

Appendix

Table A1. Definitions of each of the three call classes observed in all sampling years (2015-2017) detailing their duration, frequency, and harmonic presence, as well as additional comments describing any difficulties and/or oddities seen in any of the sampling years. Refer to Figures 2-4 for visuals of each of the call classes.

Call class	Typical duration (s)	Frequency spanned (kHz)	Presence of harmonics	Additional comments
High frequency (HF)	- variable, typically short in duration (range of averages for 2015-2016: 0.3-0.4s; Epp 2019) - occasionally longer duration (0.5s ≤ HF ≤ 2s)	- typically, the entire call ≥ 0.5 kHz - occasionally borderline and/or just below 0.5 kHz - average maximum frequency: 1.5-2.1 kHz (Epp 2019)	- variable	- often distinctive and obvious from other call types - nearly all HF calls in 2017 were of a single call type (i.e. little variation present in 2017) - occasionally, some calls were on the borderline between LF and HF and were primarily identified aurally (i.e. if they subjectively sounded higher in frequency, they were identified as HF) - HF was relatively common, but not as abundant as other call classes
Pulsed (P)	- short duration (0.2-0.3 s; Epp 2019)	- average frequency range: 0.1-0.7 kHz (Epp 2019) - spans low to high frequencies (up to ~1 kHz, including harmonics) - typically begins ≤ 0.3 kHz and quickly sweeps upward and/or are completely straight (i.e. vertical)	- often present - number of harmonics vary (i.e. longer vertical height in spectrogram)	- quickly upsweeping calls with minimal or no low frequency component - often quite distinctive from other classes - can sound like a drop of water in a bucket - large diversity of call types within P class - some P's can be single dots, and others are not vertical and/or upsweeping, but instead are short, horizontal lines with many harmonics spanning a wide frequency range - relatively common within years
Low frequency (LF)	- majority of calls have a longer duration (0.7-0.9s; Epp 2019) - some are longer in duration (1.5-2.7 s) - most obvious calls are 0.5s ≤ LF ≤ 1.5s - occasionally short LF's present (< 0.5s)	- distinct low frequency component (0.05 kHz; Epp 2019) - low maximum frequency (0.3-0.4 kHz; Epp 2019); occasional upsweep at the end - some longer duration calls had high maximum frequencies (0.5-1.2 kHz) - calls begin at < 0.4k Hz - for the majority of the call, most and/or all of the call is < 0.4 kHz	- variable	- often very distinctive from other call classes both aurally and visually (i.e. very obviously appear and sound low) - large diversity of call types within LF class (e.g., vary in their appearance: striated lines, straight/wavy horizontal lines, bow-shaped, downward line) - calls with terminal upsweeps identified as LF if the strongest portion of the call (and longest duration) < 0.4 kHz - some odd calls (< 0.5 s) identified as LF if entire call was < 0.4 kHz and flat and/or downward in appearance - very common within years

General Conclusion

Understanding the underlying patterns in animal vocalizations and/or acoustics in relation to time (e.g., diel cycle, across days, inter-annually), varying social and/or environmental conditions, and prey availability is a central goal unifying bioacoustics and ecology. Understanding these patterns is also an important first step in determining the behavioural contexts (i.e. function) of these vocalizations and, thus, understanding a species' vocal communication system. In this study, I found distinct diel patterns in humpback whale (*Megaptera novaeangliae*) non-song call class activity in coastal Newfoundland whereby calling was higher during light relative to dark or twilight periods, suggesting individuals are inactive, not engaged in behaviours requiring acoustic communication, and/or remain silent to minimize predator detection. Low frequency calls were the dominant call class (43-75%) across all time scales relative to high frequency (9-17%) and pulsed calls (8-40%), suggesting low frequency calls are important for communication among humpback whales on the Newfoundland foraging grounds, as observed throughout their range (Dunlop et al. 2008, Wild and Gabriele 2014, Dunlop 2017). I also determined that call activity peaked when humpback whales arrived into the study area and subsequently decreased, suggesting calls are more important in mediating social interactions during initial movement into the area, but less-so as whales disperse to forage throughout the area. Lastly, one year (2016) had double the call activity of the other years, which was also associated with the highest estimated humpback whale abundance but lowest prey (capelin, *Mallotus villosus*) biomass of all years, suggesting call activity may indicate humpback whale abundance and be useful in future survey efforts. Indeed, we provide a novel description of the diel, daily, and inter-annual patterns in non-song call activity of humpback whales on a previously understudied foraging ground. While patterns here suggest non-song calls may be important in conspecific communication during foraging and/or mediating social interactions during movement, additional research is required to further uncover the behavioural context(s) of non-song calls in coastal Newfoundland.

We used passive acoustic monitoring (PAM) to study the temporal patterns in humpback whale non-song call activity across years, and we recommend the use of PAM to continue monitoring humpback whale populations in our region and elsewhere. PAM is a valuable, non-invasive, and inexpensive technique which has been successfully employed to study acoustic communication in cetaceans across large regions and over extended periods of time (Mellinger et al. 2007, Van Parijs et al. 2009, Matthews et al. 2014). PAM has been used to monitor cetacean migration, characterize cetacean call presence and structure, as well as uncover the diel, seasonal, and geographic patterns (and occasionally, elucidating associated functions) of such calls (Au et al. 2000, Wiggins et al. 2005, Risch et al. 2013, 2014, Matthews et al. 2014, Huang et al. 2016). Additionally, PAM has proven useful in long-term monitoring of certain cetacean populations, particularly vulnerable ones (e.g. right whales: Mussoline et al. 2012, Davis et al. 2017), and has been suggested to aid in informing policy decisions by delimiting critical area and habitats for protection (Van Parijs et al. 2009, Kowarski et al. 2018). PAM may also allow for real-time monitoring of cetacean arrival into an area, thereby allowing the mitigation of threats (e.g. fishing and shipping activities; Simard et al. 2006, Van Parijs et al. 2009). Despite the increasing prevalence of PAM in marine mammal monitoring and research, knowledge gaps remain regarding the underlying mechanisms and/or associated behavioural contexts of cetacean vocalizations. Once the behavioural context of some calls is understood (e.g., stress calls, foraging-associated calls, mother-calf pair contact calls), real-time monitoring (via PAM) of cetaceans in an area could help us understand the status and health of a population, as well as whether individuals are experiencing stress (e.g., predators, fishing nets, ship strikes), or the presence and/or changes of prey in the area.

The temporal patterns of non-song calls uncovered in this study, as well as previous research on non-song calls throughout the humpback whale range (D'Vincent et al. 1985, Stimpert et al. 2007, Zoidis et al. 2008, Dunlop et al. 2008, Fournet 2014, 2018, Parks et al. 2014, Wild and Gabriele 2014, Dunlop 2017, Fournet et al. 2018, Indeck et al. 2020), allows us to speculate the potential behavioural contexts of non-song call classes in coastal Newfoundland. Specifically, non-song calls in certain regions are suggested to be important for conspecific communication, potentially acting as a contact call and/or mediating social interactions among moving groups, individuals, and/or mother-calf pairs (Dunlop et al. 2008, Zoidis et al. 2008, Wild and Gabriele 2014, Dunlop 2017, Indeck et al. 2020). As we did not record behaviour during acoustic recordings, however, we cannot provide definitive support for the behavioural context of the calls detected in Newfoundland. For instance, we were unable to link humpback whale calls with foraging in Newfoundland due to the lack of behavioural data, while other non-song calls have been associated with foraging on other foraging grounds (D'Vincent et al. 1985, Stimpert et al. 2007, Parks et al. 2014, Fournet et al. 2015). The behavioural context of non-song calls and their consistency throughout the range is not known, due to the use of PAM without paired behavioural observations (cf. Dunlop et al. 2008, Dunlop 2017, Fournet et al. 2018b, Indeck et al. 2020). To elucidate the behavioural context of these calls throughout the humpback whale range, future research could compare non-song calls in a low-arousal environment (e.g. foraging grounds) relative to a high-arousal environment (e.g., breeding grounds, migration routes) to determine whether the behavioural context is maintained or is instead context- and/or arousal-state-specific, and to determine if calls indeed follow motivational-structural rules (Morton 1977, Dunlop 2017).

This research could be accomplished by employing a variety of techniques, such as multi-sensor tags capable of recording depth, acceleration, orientation, acoustics (i.e. hydrophone), and visuals (i.e. video camera). A tag capable of collecting all of these data is ideal as it would allow us to associate vocalizations with both surface-active and submerged behaviour and movement, but also with prey density and distribution. As these tags can be prohibitively expensive, future studies could instead collect more detailed, fine-scale, frequent measurements of humpback whale abundance and surface-active behaviours during PAM when in an area to inform the behavioural context of calls. Indeed, previous studies using tags equipped with hydrophones while observing surface-active behaviours of focal individuals or groups (e.g., Parks et al., 2014, Stimpert et al., 2007), as well as the opportunistic use of a portable (dip) hydrophone (as in Silber, 1986, Zoidis et al., 2008; similarly, using hydrophones moored nearby while simultaneously observing surface-active behaviours: Dunlop, 2016), have helped to uncover some of the behavioural contexts of non-song calls. Employing the previously aforementioned techniques in addition to detailed and more frequent measurements of prey abundance, distribution (both vertical and horizontal), and movement while humpback whales are present in an area would further inform the potential presence of foraging-associated calls throughout their range and in Newfoundland.

In conclusion, this study uncovered temporal patterns in non-song call (class) activity of humpback whales on their Newfoundland foraging grounds and provides clues as to the behavioural contexts of some of these non-song calls. This study, however, highlights the need for behavioural observations simultaneous with PAM to further provide insight into the behavioural contexts of non-song calls in Newfoundland, and throughout their range. Such studies could help determine whether the behavioural contexts of non-song calls are consistent throughout the humpback whale range or vary, and may help uncover why contrasting patterns are observed among regions, such as the diel patterns in this study relative to those found elsewhere in the Atlantic (Huang et al. 2016, Kowarski et al. 2018). I recommend integrating PAM with multi-sensor tags and recording the surface-active behaviours of humpback whales in the study area. This additional and continued research would aid in further uncovering the behavioural contexts of non-song calls in their Newfoundland foraging grounds, and also reveal how and why call activity shifts in response to environmental changes (i.e. to help describe ‘different’ years like 2017). Additionally, conducting research incorporating these types of techniques throughout the humpback whale range (i.e., foraging grounds, breeding grounds, and migratory routes) would help facilitate comparisons of acoustic activity and behaviour across regions, which would assist in monitoring shifts in the health and status of humpback whales on a global scale in response to the declining health of marine environments.

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