

ALCID COMMUNICATION AT SEA: VOCAL REPERTOIRE AND INDIVIDUAL CHICK

SIGNATURES

By

Katrina Wilcox

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Thesis Abstract

Seabirds are highly vocal at breeding colonies, and although they spend most of their life at sea, our understanding of their vocal behaviour away from breeding colonies is limited. Seabird vocalisations are uniquely adapted to communicate both within dense breeding colonies and at sea, but vocalisations likely serve distinct functions and experience different environmental conditions that influence propagation within these distinct contexts. Here, we investigated the vocal behaviour in alcid seabirds (Family Alcidae) on the northeastern coast of Newfoundland, Canada. In Chapter 2, we identified and quantitatively described vocalisations emitted by common murre (*Uria aalge*) while foraging at sea and qualitatively compared these calls to colony-based repertoires. Four call types were described ('eng', 'arg', 'crow', 'eur') and call type assignments were validated using supervised multivariate analyses (random forest) and observer agreement. Three of these call types visually resembled call types previously described at murre colonies with one exhibiting high temporal variation that appeared to grade between different call types. The fourth call type was novel and may only be emitted at sea. Finally, we postulated functions of these four call types at sea based on the behavioural and social contexts in which they were emitted. In Chapter 3, we investigated the presence and ontogeny of individual-specific signatures in razorbill (*Alca torda*) chick vocalisations used in parent-chick communication at sea. We quantitatively described the individual signatures encoded within 'departure' calls of six razorbill chicks during early (3-5 days old) and late (15-19 days old) nestling stages. Calls were reliably assigned to individuals in both stages with similar classification success (early: 66.7%, late: 69.4%), but classification varied considerably among chicks. Temporal attributes had the strongest potential of individual coding ($PIC > 1$) and the potential to encode identity increased across nestling development, suggesting their importance

in signalling identity during fledging and at sea. These findings provide insight into alcid ecology at sea by highlighting the diversity of acoustic signals used by seabirds in this understudied environment and increasing understanding of the acoustic adaptations to specific ecological pressures experienced away from breeding colonies.

Contribution of Authors

Katrina Wilcox conducted all field work, data collection and processing, and wrote the thesis.

Gail Davoren (advisor) acquired project funding. Katrina Wilcox and Gail Davoren were both involved in determining appropriate data analyses, manuscript structure, and editing and revising the manuscript.

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Thesis Format

This thesis is presented in a grouped manuscript format. Chapters 2 and 3 are independent, with their own introduction, methods, results, discussion, conclusions and reference sections. These chapters are accompanied by a general introductory chapter (Chapter 1) to provide the theoretical background information of both chapters, and a concluding chapter (Chapter 4) to integrate the findings of both chapters and recommend areas for future research. The data collection, analysis, and writing were performed by myself, Katrina Wilcox, with guidance and input from my thesis advisor and committee members.

Chapter One: Introductory Chapter

In animal communication systems, evolutionary theory predicts that signals have evolved for producers and/or receivers to maximize their fitness (Alcock 2013). Individuals maximize their fitness when the communication ensures that a signal reaches and is interpreted correctly by its intended receiver (Endler 1993). Therefore, the scientific study of acoustic communication (or ‘bioacoustics’) is fundamental to the understanding of a species’ ecology (Todt and Naguib 2000). Vocal communication in birds has been widely studied, with vocal use linked to breeding and foraging success (e.g., Lengagne *et al.* 2004, Choi *et al.* 2017), individual recognition (Falls 1982), and response to environmental change (e.g. Warrington *et al.* 2018). Acoustic communication systems are often well-described in birds, although most studies focus on the song systems of passerine birds (Todt and Naguib 2000, Marler 2004, Benedict and Krakauer 2013). In contrast, call-based systems (often shorter, monosyllabic, and less complex than songs) are historically understudied, despite their importance to meet the ecological demands of both passerine and non-passerine species (Marler 2004, Benedict and Krakauer 2013).

A vocal repertoire, where all vocalisations of a species are quantitatively described, provides baseline information for addressing questions related to a species’ ecology. Repertoire size is a powerful indicator of a species’ communication complexity and response to ecological pressures (Kershenbaum *et al.* 2015, Leighton and Birmingham 2021). Based on the social complexity hypothesis (Freeberg *et al.* 2012), highly social animals may develop complex vocal repertoires (i.e. many different signals; Griesser 2008, Grieves *et al.* 2015); however, persistently noisy environments may mask vocalisations, leading to constrained repertoire size, and species may instead exhibit few vocalisation types (Freeberg *et al.* 2012, Leighton and Birmingham

2021). Once vocalisation types are defined in a vocal repertoire, acoustic parameters can be used to infer their functions and better understand the species' vocal communication. For instance, calls of longer duration and lower frequency increase the probability of the signal being received and, thus, may have evolved for long-distance communication, relative to calls of a short duration and high frequency that attenuate over shorter distances (Wiley and Richards 1978).

Within call types, variation in acoustic parameters of calls (or 'call signatures') may also function to indicate individuality, thereby allowing recognition between individuals with repeated contact (Wiley and Richards 1978). Individual signatures held within call types reduce confusion regarding conspecific interactions and, consequently, may minimize energy expenditure during these interactions. For instance, individual recognition resulting from past experiences can optimize interactions, such as territorial species discriminating between mates, neighbors and strangers, and modifying their behavioural response accordingly (Carlson *et al.* 2020). Another example may be vocal signatures in calls made by offspring that are used by adults to recognise and direct parental care towards their own young (e.g., Schommer and Tschanz 1975, Jones *et al.* 1987). Individual vocal signatures can be more adaptive than visual cues when the visual field is busy, such as in dense foraging aggregations and breeding colonies, and when individuals within a group show little variation in morphological characteristics (e.g., monomorphic species; Falls 1982).

Vocal individuality may be represented through modulations in spectral, temporal, and other attributes, and the relative variation in call structure is indicative of the features most important in individual recognition. The attributes used to signal individual identity may also indicate the ecological pressures and constraints in a species' life history (Falls 1982). For example, selection may favour individual call signatures of chicks from non-nest building birds

to ensure parental care is focused on their own offspring, but may be less favoured in birds that build discrete nest sites, indicating different environmental pressures (Favaro *et al.* 2015). Within a call type, the parameters necessary for a call to be detected, and potentially localised, by the intended receiver must be preserved. Therefore, there is a trade-off between a signal reaching and being interpreted correctly by its receiver, and modulating call parameters to signal identity. The broadcast distance used in signalling individual recognition is an important factor, and may select for finer spectral characteristics in close-range interactions, and temporal variation when communicating identity across longer distances (Falls 1982).

Studies examining vocal behaviour in seabirds have largely been limited to breeding colonies, although they spend most of their time at sea and only come on land to breed. During the breeding season, seabirds also spend considerable time away from the colonies to forage at sea (Cairns *et al.* 1987). While at sea, seabirds may use vocalisations that serve a variety of functions. For instance, vocalisations may facilitate locating prey over large spatial scales, or may manage close contact interactions, such as during foraging with conspecifics, as recently described in penguins and gannets (Choi *et al.* 2017, Thiebault *et al.* 2019a, McInnes *et al.* 2020). Species foraging on patchily distributed prey often travel long distances and may use several behavioural strategies to minimize energy expenditure while locating prey. For species that forage on predictably located prey aggregations, they may simply rely on previous experience (e.g. memory) to minimize prey searching activities (Bairos-Novak *et al.* 2015). When prey cannot be predictably located, seabirds are known to use visual cues of foraging conspecifics to detect high density prey patches (i.e. local enhancement), resulting in high density seabird aggregations (Thiebault *et al.* 2014, Bairos-Novak *et al.* 2015). Vocalisations at sea may act as auditory cues of foraging conspecifics in a similar manner, but this has not been

studied. As local enhancement results in high conspecific densities at foraging sites, close contact interactions between conspecifics often occurs during foraging activities. When foraging at high conspecific densities, seabirds may benefit from coordinating foraging (e.g., herding prey); however, benefits may only increase up to a threshold density, after which competitive interactions increase (Götmark *et al.* 1986, Thiebault *et al.* 2016b, Maynard *et al.* 2019). Therefore, vocalisations in foraging aggregations may also function to manage close contact interactions (e.g. avoiding collisions in plunge-diving seabirds, Thiebault *et al.* 2019b). Surprisingly, there are few studies that have described seabird vocalisation use at sea (Choi *et al.* 2017, Thiebault *et al.* 2019b). Overall, the use of acoustic communication in seabirds while at sea is not well understood and the study of their bioacoustics can provide important insight into seabird ecology.

On the northeast coast of Newfoundland, Canada, seabirds gather to feed on capelin (*Mallotus villosus*), a patchily distributed forage fish species. Capelin shoals move inshore in the spring and spawn at intertidal and subtidal sites, and the subtidal spawning sites are seasonally and annually persistent foraging hotspots for seabirds and other predators (Davoren 2013, Davoren *et al.* 2025). The common murre (*Uria aalge*; hereafter “murre”) is the numerically dominant seabird in these dense multi-species foraging aggregations (Davoren *et al.* 2025). Murres use their wings to propel themselves underwater to pursue and capture capelin (Ainley *et al.* 2021). Murres have the highest wing loading (mass per unit area) of all flying birds (Thaxter *et al.* 2010), and consequently have high energetic costs associated with flight (Elliott *et al.* 2013). As travel required to search for patchily distributed prey is energetically costly, murres appear to use strategies to minimize these high energy demands. For instance, murres use local enhancement to locate capelin patches (Bairos-Novak *et al.* 2015) and may similarly use

vocalisations of foraging conspecifics as cues to locate prey patches. Once in these high-density aggregations, vocalisations may function to manage conspecific interactions. Murre vocalisations at sea have not been characterised, although a colony-based vocal repertoire was recently described (Smith *et al.* 2023), based on similarity to call types characterised of the closely related thick-billed murre (*Uria lomvia*; Lefevre *et al.* 2001). It is possible that murrees may use these same call types while at sea, but this is unknown. Overall, the roles of seabird vocalisations at sea are unclear, and a better understanding of at-sea call types and associated social and behavioural contexts are warranted.

Seabirds may also vocalise to signal identity, as they forage in large aggregations and breed in dense colonies, where the visual field is busy. At breeding colonies, some seabird species have developed vocalisations used specifically for parent-offspring recognition (e.g., Ingold 1973, Harris 1983, Jones *et al.* 1987, Jouventin *et al.* 1999, Insley *et al.* 2003, Klenova *et al.* 2011). The adaptive significance of parent-offspring recognition and when it develops varies among seabird species and appears to have evolved differently in species with divergent nestling development strategies. In particular, alcids (Family Alcidae), a diverse family of 22 extant species, exhibit extreme variation in nestling development strategies (Sealy 1973). The majority of alcids are semi-precocial, being cared for at the nest site until they reach 50-100% adult body weight before fledging unaccompanied by adults, and chicks exhibit little vocal individuality (Kolesnikova and Klenova 2011, Klenova 2015). Conversely, precocial alcids (*Synthliboramphus* spp.) are provisioned at sea by both parents after fledging the colony two days post-hatch, and mutual recognition between parents and chicks develops almost immediately after hatching (Jones *et al.* 1987). Unique among alcids, razorbills (*Alca torda*) and murrees (*Uria* spp.) have ‘intermediate’ development strategies, with chicks receiving biparental care at the nest site before

fledging at approximately 30% adult body mass, where they are dependent on the male parent for provisioning at sea (Gaston and Jones 1998). Playback experiments have shown mutual parent-offspring vocal recognition in razorbills (Ingold 1973, Insley *et al.* 2003) and murre (Schommer and Tschanz 1975) at colonies when near fledging and at sea.

Species with ‘intermediate’ development strategies vary in the developmental timing of individual chick call signatures, which has likely evolved to minimize the probability of misidentification at certain parts of the developmental period (Falls 1982). Murres appear to use vocal recognition within days of hatching and chicks can recognize their parents’ “luring” call heard before hatching (Schommer and Tschanz 1975). In comparison, razorbills appear to exhibit mutual vocal recognition only when nearing the chick departure date (Ingold 1973, Insley *et al.* 2003). Breeding murres do not build a nest per se, but instead lay a single egg on flat ground or ledges in densely packed conspecific colonies. Razorbills also nest in dense conspecific colonies, but nest sites are in rock crevices that are often separated by > 30 cm (Gaston and Jones 1998). Thus, the probability of chick misidentification is likely higher in murres than razorbills throughout the nestling period. For both species, chicks leave their nest site alone after a 16-22 day nestling period and reunite with their male parent on the water nearby the colony, increasing selection pressures for individual recognition in razorbills near fledging (Lefevre *et al.* 1998, Lavers *et al.* 2020). Both murre and razorbill chicks vocalise during colony departure, and this call type (‘departure call’) appears to be individually distinct (Lefevre *et al.* 2001). Playback experiments have shown that these calls appear to help reunite parents and chicks at sea (razorbill, Ingold 1973, Insley *et al.* 2003; murre, Schommer and Tschanz 1975, Lefevre *et al.* 1998). Interestingly, vocal recognition near fledging in razorbill parents appears to be male-

biased and likely functions to maintain contact at sea and is suggested to develop when chicks are nearing fledging (Insley *et al.* 2003).

Objectives

The overall objective of my thesis was to investigate the at-sea vocal behaviour in alcid seabirds during the breeding season to increase understanding of their ecology in this understudied environment. The objectives of Chapter 2 were to compile a repertoire of vocalisations emitted by common murrelets at sea and qualitatively compare call types to those previously characterised for common and thick-billed murrelets at breeding colonies (Lefevre *et al.* 2001, Smith *et al.* 2023). I expected that vocalisations would differ from those emitted at colonies, as murrelet vocalisations at sea are emitted under different environmental conditions that influence propagation and may have unique functions related to foraging. As the colony-based calls were noted to have intermediate forms between discrete call types (Lefevre *et al.* 2001), I also expected to observe graded call types, which may be related to the motivational state of a signaller. Additionally, I described the behavioural and social contexts of vocalising murrelets to postulate call functions at sea. The objectives of Chapter 3 were to investigate the acoustic features important in signalling identity in razorbill chick departure calls, and how these features develop throughout the nestling period. I first aimed to investigate the ontogeny of these call signatures while at the colony and hypothesized that departure calls would exhibit higher individuality closer to fledging relative to earlier in development. I predicted that classification of departure calls to individual chicks, based on acoustic parameters, would be higher nearing fledging compared to earlier in the nestling period. Next, I aimed to investigate the acoustic parameters used to communicate identity. I hypothesized that chick departure call signatures are adapted for long-distance communication and localisation by adults, as they appear to function in

reuniting parents and offspring during fledging and provisioning at sea. Thus, I predicted that temporal call features would exhibit higher between-individual variation relative to within-individual variation, as temporal modulations persist over longer distances and in environments with high background noise.

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Chapter Two. Vocal repertoire of the common murre (*Uria aalge*) at sea

Abstract

In animal communication systems, evolutionary theory predicts that acoustic signals have evolved for producers and/or receivers to maximize their fitness. Seabirds often form dense aggregations to forage on patchily distributed prey, and acoustic signals may assist in finding patches and managing conspecific interactions within aggregations. Unfortunately, seabird vocal behaviour has been predominantly studied at breeding colonies, although they spend most of their time at sea. We aimed to create a vocal repertoire of common murres foraging at sea during the breeding season (July-August), in 2022 and 2023. We recorded ~18 hours of calls from a small boat using a handheld parabolic microphone and recorder at persistent foraging areas on the northeast coast of Newfoundland, Canada, and recorded behavior when vocalising. During an aural and visual (AV) survey of spectrograms, 2789 calls were assigned a call type based on qualitative comparisons to previously described colony-based thick-billed and common murre calls or was assigned a new call type. Acoustic variables (e.g., duration, peak frequency) were measured on 155 high-quality calls (i.e., signal to noise ratio > 15 dB above ambient noise) and a supervised multivariate classification analysis (random forest) was used to discern whether call types were discrete or graded. The AV survey revealed four call types ('eng', 'crow', 'eur', 'arg'), with one previously undescribed ('eur'). The random forest model trained on 15 acoustic parameters (e.g., duration, peak frequency, amplitude modulation) had a high classification success for 'eng' (93%) and 'crow' (96%) call types, while the other two call types had lower classification success ('arg' = 62%, 'eur' = 50%), with an 80% overall classification success. In general, there were higher misclassification rates for call types with intermediate duration. These results, paired with the behavioural and social contexts of vocalising common murres, provided

insight into their ecology at sea. These findings represent the first quantitative vocal repertoire of murre foraging at sea, allowing for future research to test call functions through playback experiments and passive acoustic monitoring of murre presence to inform marine spatial management decisions.

Introduction

A vocal repertoire, where all vocalisations of a species are quantitatively described, provides baseline information for addressing questions related to a species' ecology. Repertoire size is a powerful indicator of a species' communication complexity and response to evolutionary pressures (Kershenbaum *et al.* 2015, Leighton and Birmingham 2021). Based on the social complexity hypothesis (Freeberg *et al.* 2012), highly social animals may develop complex vocal repertoires (i.e. many different signals; Griesser 2008, Grieves *et al.* 2015); however, persistently noisy environments may mask vocalisations, leading to constrained repertoire size, and species may instead exhibit few vocalisation types (Freeberg *et al.* 2012, Leighton and Birmingham 2021). Within and between these vocalisation types, variation in acoustic parameters (e.g., duration, peak frequency) may convey additional contextual information, such as expressing how an emitter responds to a stimulus (e.g., motivational state; Briefer 2020, G  mard *et al.* 2021). Following the creation of a vocal repertoire, the acoustic parameters of defined vocalisation types can be used to infer their functions to better understand the species' vocal communication. For instance, calls of longer relative duration and lower frequency increase the probability of the signal being received and, thus, may have evolved for long-distance communication, relative to calls of a short duration and high frequency that attenuate over shorter distances (Wiley and Richards 1978). Acoustic communication systems are often well-described in birds, although most studies focus on the song systems of passerine birds (Todt and Naguib 2000, Marler 2004, Benedict and Krakauer 2013). In contrast, call-based systems (often shorter, monosyllabic, and less complex than songs) are historically understudied, despite their importance to meet the ecological demands of both passerine and non-passerine species (Marler 2004, Benedict and Krakauer 2013).

Seabird calls have been studied when they come to land and breed in high density, multi-species colonies, after spending the remainder of their annual cycle at sea. These breeding colonies are typically very noisy and, thus, seabirds have likely evolved vocal systems to efficiently communicate under these conditions. Although vocal communication systems in seabird species are often understudied, calls at breeding colonies appear to establish and maintain pair bonds (Tschanz 1968), communicate identity (Aubin *et al.* 2000, Favaro *et al.* 2015, Bowmaker-Falconer *et al.* 2022), and manage chick-rearing duties (Harris 1983, Lefevre *et al.* 1998, Klenova 2015, Osiecka *et al.* 2024). Species within the Family Alcidae (hereafter, ‘alcids’) are wing-propelled pursuit divers that typically breed in extremely high-density colonies (Ainley *et al.* 2021). The common murre (*Uria aalge*; hereafter “murre”) is a highly vocal alcid that only recently had their vocal repertoire described at a colony (Smith *et al.* 2023), based on visual similarity of call types described for the closely related thick-billed murre (*Uria lomvia*; Lefevre *et al.* 2001). Common and thick-billed murres exhibit similar vocal behaviour and are ecologically similar (Ainley *et al.* 2021), thus, qualitative descriptions of vocal behaviour are often grouped together. Murres appear to use the same discrete call types in a variety of behavioural contexts across parent-chick, mate, and conspecific interactions at colonies, although intermediate calls were noted between discrete call types (Lefevre *et al.* 2001). Their vocal behaviour at sea has not been described, however, even though they spend over half of their time away from colonies during the breeding season to forage at sea (Cairns *et al.* 1987).

On the northeastern coast of Newfoundland, Canada, murres gather in large multi-species foraging aggregations to capture capelin (*Mallotus villosus*), a patchily distributed forage fish species (Davoren 2024). Capelin migrate inshore to spawn in the summer, resulting in a dramatic increase in the inshore prey biomass, and form high-density shoals at seasonally and annually

persistent spawning sites. Prior to capelin spawning, the inshore prey biomass is much lower near seabird breeding colonies and the small, ephemeral shoaling fish (primarily sand lance, *Ammodytes* spp.) are less predictably found (Gulka and Davoren 2019, Staudinger *et al.* 2020). Murres have the highest wing-loading (body mass to wing area ratio) of all flying birds (Thaxter *et al.* 2010), which makes flying to search for prey extremely energetically costly (Elliott *et al.* 2013). Therefore, murres use several strategies to minimize costly searching behaviour (Davoren *et al.* 2003a, Bairos-Novak *et al.* 2015) during their often-long distance travel from the colony to foraging locations (Montevecchi *et al.* 2019, Gulka *et al.* 2020). During capelin spawning, murres appear to primarily rely on previous experience (e.g. memory) to locate persistent spawning sites (Davoren *et al.* 2003a, Bairos-Novak *et al.* 2015). Prior to capelin arriving inshore, murres show increased foraging effort and consumption of a higher diversity of prey types relative to during spawning (Davoren 2024). To reduce energetically costly search efforts under these conditions, at-sea experiments revealed that murres visually cue to foraging conspecifics to locate high density prey patches (i.e. local enhancement; Dall *et al.* 2005, Bairos-Novak *et al.* 2015). As local enhancement is often investigated through a visual lens (Haney *et al.* 1992, Thiebault *et al.* 2014, Bairos-Novak *et al.* 2015), it is unclear whether auditory cues of foraging conspecifics and heterospecifics play a role in locating prey patches. Indeed, vocalisations emitted by foraging conspecifics may act as cues, possibly along with other sensory cues (e.g., olfactory; Bastos *et al.* 2020), to allow for coarse-level local enhancement (Pöysä 1992, Putland *et al.* 2016, Monier 2024), which may be especially adaptive when foraging under sub-optimal visual conditions (e.g., dark, foggy and stormy seas, Regular *et al.* 2011).

Within these large multi-species foraging aggregations, murres are the numerically dominant species (Davoren 2013) and, although diving in close contact with conspecifics may

benefit from coordinating foraging (e.g., herding prey), these benefits may become offset at a threshold density, leading to increased competitive interactions among individuals (Götmark *et al.* 1986, Thiebault *et al.* 2014, Maynard *et al.* 2019). At high-density, persistent capelin spawning sites, murre maintain loose aggregations (~250 m spacing, Davoren *et al.* 2003b) and primarily forage solitarily on individual capelin found just outside of the shoal boundary, which may require less effort to catch than shoaling fish due to decreased predator confusion (Crook and Davoren 2014). When foraging on ephemeral shoals of various prey species (e.g., sand lance) prior to the inshore arrival of capelin, cooperative foraging may be used. Therefore, vocalisations may be used in close contact interactions and to manage optimal spacing and agonistic interactions (Choi *et al.* 2017, Thiebault *et al.* 2019), and/or facilitate group foraging efforts (McInnes *et al.* 2020). As few studies have described the vocal behaviour of seabirds at sea, the vocalisations produced by murre during foraging are not understood and, thus, the functions of at-sea vocalisations are unclear.

Objectives

The overall objective of this chapter is to investigate the at-sea vocal behaviour of common murre to increase understanding of their ecology in this understudied environment. Specifically, we aimed to create a repertoire of vocalisations emitted by common murre at sea, and to qualitatively compare call types to those previously characterised for common and thick-billed murre at breeding colonies (Lefevre *et al.* 2001, Smith *et al.* 2023). As murre vocalisations at sea are emitted under different environmental conditions that influence propagation, and may have unique functions related to foraging, we expected that these vocalisations differ from those emitted at colonies. As the colony-based calls were noted to have intermediate forms between discrete call types (Lefevre *et al.* 2001), we also expected to observe

graded call types, which may be related to the motivational state of a signaller. Additionally, we described the behavioural and social contexts of vocalising murres to postulate call functions at sea.

Methods

Sound recordings

To create a vocal repertoire of common murres at sea, we visited an annually persistent capelin spawning area (Crook *et al.* 2017), over which high abundances of multiple predator species aggregate to forage on the northeast Newfoundland coast during July-August 2022 and 2023 (Davoren 2013). Within this 5-10 km² multi-species hotspot (N49.24988, W53.43214), we approached a group of murres in a small speed boat (5 m length) until they were within 300 m of the boat. The boat engine was turned off, and we waited 2-5 min for birds to adjust to the presence of the boat before recording. From the boat, we recorded calls of a focal group of murres using a handheld parabolic microphone (Telinga Pro-X V.2) and recorder (Zoom H4N Pro). Recordings were conducted in stereo mode, using a sampling frequency of 48 kHz and 24-bit depth, and were saved as uncompressed WAV files. Although murres were numerically dominant within the hotspot, other seabird species were often present nearby, primarily sooty and great shearwaters (*Ardenna grisea*, *A. gravis*; Davoren 2007, 2013), and, thus, their vocalisations were present in the acoustic recordings. We recorded vocalisations from small groups of only murres and only shearwater species, which allowed us to distinguish among species-specific calls and isolate calls of murres.

At the start and end of recording sessions, we used a dictation microphone to record the species composition of the focal group, along with the number of individuals in the group and

approximate recording distance from the group. Murres in small focal groups (up to 10 individuals) were counted but total numbers were estimated in larger groups due to the difficulty of counting more birds when individuals were moving and diving. The presence of other seabirds and marine predators (e.g., humpback whales) were dictated opportunistically during recording sessions to add contextual information. In 2022, when focal groups were within 100 m of the boat during a recording session, the group size, estimated distance between individuals, and ethogram-based behaviours (Table S2.1) of the focal group were recorded continuously to describe the behavioural context of vocalising murres. For focal groups > 100 m from the boat, the predominant behaviours (e.g., foraging, flying, resting) were determined using binoculars and dictated at the start and end of recording sessions and mid-session when new groups joined the focal group or when we switched focal groups. In 2023, the predominant behaviours (e.g., foraging, flying, resting) were determined for focal groups both > 100 m and < 100 m because acoustic recordings were primarily collected to increase sample sizes of high-quality calls for repertoire analysis. Recording sessions lasted up to 20 min, after which we changed locations within the larger hotspot to decrease resampling the same individuals.

Aural and visual survey

Acoustic files were examined by a single observer (K.W.) in *Raven Pro 1.6* (K. Lisa Yang Center for Conservation Bioacoustics at the Cornell Lab of Ornithology 2022) and calls were manually identified during an aural and visual (AV) examination of spectrograms. To visualize the spectrograms, we used a sliding window of 10 s with a Hann window of 512 samples. The frequency grid was configured using a Discrete Fourier Transform (DFT) of 16384 samples, resulting in frequency spacing of 2.93 Hz. The time grid overlap was 50%, resulting in a hop size of 256 samples. These settings were chosen to maximize the temporal resolution of call

parameters, which were expected to be critical for communication at sea, while retaining reasonable spectral (i.e. frequency-related) resolution for varying call durations.

To focus processing effort on acoustic recordings with high-quality calls suitable for defining the repertoire, each recording was inspected visually to determine if environmental noise (i.e., wind and wave action) greatly affected call quality throughout the file. If noise greatly affected call quality, the file was not used for repertoire analysis. In 2022, all discernable calls were selected and annotated with a species identifier during the AV survey of each low-noise acoustic file. The species identifier was based on reference calls recorded of single-species groups comprised of murre or shearwaters to ensure only murre vocalisations were included in the repertoire analysis. When available, behaviours of the vocalising murre were also annotated with the call selection based on the time-stamped continuous behavioural dictations. For murre vocalisations, selection boxes were manually placed around a call to capture the entire visual frequency range and duration of the call, including a minimum of 25% of the cells within the selection box without the focal signal. This ensured accurate signal-to-noise ratio (SNR) measurements (Mellinger and Bradbury 2007). Selection boxes were only placed around a call if it did not overlap with other calls or non-biological sound (e.g., wave or boat noise). As the recordings were conducted in stereo format, individual calls were selected in the channel that appeared to have a higher SNR. Each selection was assigned a call type based on qualitative comparison to previously described colony-based calls of thick-billed and common murre (Lefevre *et al.* 2001, Smith *et al.* 2023). For murre calls not previously described, the selected calls were assigned a new call type with a name that phonetically resembled the call. In 2023, only murre vocalisations presumed to have high SNR were selected and assigned a call type to increase sample sizes within each call type.

Measurement of acoustic parameters

A total of 24 acoustic parameters, and SNR, were measured using the Noise-Resistant Feature Set (NRFS) within the *Acoustat* package in MATLAB (The Mathworks Inc. 2022), developed by Mellinger and Bradbury (2007; Table 2.1). The NRFS is based on work by Fristrup and Watkins (1993) and automates drawing a smaller feature box within each manually drawn selection box during the AV survey (in *Raven*). The bounds of the feature box are calculated by ranking and summing the energy within the selection box such that the loudest parts of the sound have the most impact on the acoustic parameter measurements and, thus, these measurements are more robust to differences in user-drawn selection box placement, varying signal amplitude, and environmental noise across recording sessions (Fristrup and Watkins 1993). Although this package was developed for classification of marine mammal vocalisations emitted underwater, recordings of aerial vocalisations at sea exhibit similar challenges (i.e., high environmental noise and varying recording distances resulting in low SNR; Mellinger and Bradbury 2007). Therefore, the *Acoustat* package is ideal for such conditions while providing standard acoustic parameter measurements to compare with previously defined repertoires. A bandstop filter of 0-500 Hz was applied to all recordings before measurement of acoustic parameters to reduce the effects of constant low-frequency environmental noise (i.e. wind, waves) on feature box placement. Although this filter excluded parts of each selected call below 500 Hz, we expect that call features at these frequencies do not impart biologically relevant information to receivers due to their near-constant masking by environmental noise at sea. In support, recent work has demonstrated that common murres are most sensitive to sound from ~ 1 to 3 kHz (Smith *et al.* 2023). Calls with an SNR lower than 15 dB above ambient noise were removed from the

repertoire analysis to maximize the precision of acoustic parameter measurements (Araya-Salas *et al.* 2019), while retaining as many high-quality calls as possible (Fig S2.1).

Statistical analysis

Before multivariate analyses, the 24 acoustic parameters were tested for multicollinearity at a level of 0.9 (Fig S2.2), and several parameters were excluded (Table 2.1) to limit potential overestimation of importance values of highly correlated parameters in call classification (Nicodemus *et al.* 2010). A total of 15 acoustic parameters were maintained in analyses (Table 2.2) based on their ease of interpretation and previous use in defining repertoires to maximize comparability with other publications.

To determine if calls could be correctly classified into call types assigned during the AV survey based on acoustic parameters, thereby representing distinct call types, we used a supervised random forest (RF). We used the *randomForest* package (Liaw and Wiener 2002) within R 4.2.3 software (R Core Team 2023). Repertoire studies commonly use supervised multivariate classification techniques, in particular RFs, due to their ability to handle common challenges in acoustic datasets (i.e., non-normal distributions, non-independent data, highly multidimensional, unbalanced categories and outliers; Valletta *et al.* 2017, Keen *et al.* 2021). A RF analysis also determines the parameters most important in dividing calls into separate call types (Valletta *et al.* 2017).

The RF algorithm is based on the classification and regression tree algorithm (Breiman *et al.* 1984), where a decision tree is grown by repeatedly splitting the dataset into two subsets based on the parameters with the smallest splitting error. The RF algorithm adds two levels of randomization; by growing many trees via bootstrapping (random sampling with replacement)

and using a random subset of acoustic parameters to split at each node, which both reduce overfitting of the model (Breiman 2001). The random sample of data left out of the bootstrap data (~30%), termed ‘out-of-bag data’ (OOB data), are then used to predict the misclassification rate (i.e., OOB error) per call type. The number of trees to be grown (i.e., *ntree*) was chosen in an iterative process, where the number of trees was increased by 1000 until the OOB error was minimized consistently (*ntree* = 3000). The number of acoustic parameters to be randomly chosen to split each node (i.e., *mtry*) was chosen in an iterative process, with *mtry* set from 1 to 10 with a standard 1000 trees per model, and the *mtry* used in the model with the smallest OOB error was selected (*mtry* = 3).

The accuracy of the overall model and each grouping were then calculated as a proportion of the correct classifications within each call type. To determine whether the RF classified call types better than by chance, we calculated the percentage of correct classifications by chance by dividing the number of calls within each call type by the total number of calls in the analysis, similar to Thiebault *et al.* (2019). We then divided the classification success by this percentage by chance per call type to assess the improvement of classification success by the RF. The acoustic parameters were also ranked in order of importance, where importance was assessed by the mean decrease in accuracy (MDA) of the model if the acoustic parameter was removed.

To test whether key acoustic parameters differed among call types, we ran linear mixed effects models using the *lmer()* function from the *lme4* package (Bates *et al.* 2015) on four response variables: call duration, amplitude modulation, lower frequency, and peak frequency. These response variables were selected based on their importance in the RF model (in the top 5 variables) and/or their use in describing previous colony-based repertoires. Call type was the

fixed predictor variable and recording ID was a random effect to deal with the potential lack of independence of calls within recording sessions (i.e. repeated calls from the same individual). The significance of the fixed factor (call type) was determined using the *Anova()* function (Fox and Weisberg 2019), and when significant, post-hoc tests were run to determine the significance of pairwise comparisons using the *emmeans()* function (Lenth 2024). We also assessed whether response variables met parametric assumptions by visually assessing quantile-quantile plots and histograms of the residuals.

Call types with lower classification success (see below) were then assessed by a novice observer (G.K.D.) to evaluate whether these call types could be classified accurately with minimal training based on AV characteristics. The novice observer was given a set of unlabeled call clips containing a random subset of each call type with low agreement (all calls if $n < 25$ calls or 70% of the call type if $n > 25$ calls), and a similar-sized random subset of the call type it was commonly misclassified as. The AV classification agreement between the two observers was then assessed as above, and if agreement was high, the call type was considered discrete and included in the vocal repertoire.

Results

In 2022, we recorded a total of 10 h 55 m 17 s of sound data over 12 days from July 12 to August 4 and omitted 1 h 14 m 53 s due to high noise. From the remaining files, we selected all murre call types in 3 h 42 m 2 s of sound data to determine how often each call type was heard ($n = 2789$ for all murre call types). Due to a high number of overlapping calls in the other recordings, we only selected high-quality murre calls in these other files for repertoire analysis. In 2023, we recorded a total of 6 h 39 m 26 s sound data over 7 days from July 14 to August 4,

from which an additional 101 high-quality murre calls were selected to increase sample sizes of each call type for repertoire analysis.

From both 2022 and 2023 recordings, a total of 155 calls were high enough quality (SNR > 15 dB) and did not overlap with other vocalisations to be retained for acoustic parameter measurement and repertoire analysis. These calls were qualitatively divided into four call types based on AV characteristics: ‘eng’ (n = 74), ‘crow’ (n = 25), ‘arg’ (n = 34), and ‘eur’ (n = 22) (see Fig. 2.1). Sample sizes of these call types do not represent how often they were heard during the at-sea recordings, but rather the number of high-quality calls. In particular, ‘crow’ calls were recorded at sea often; however, their long duration resulted in higher occurrences of these calls overlapping with other calls and noise.

Classification success

Across all call types, the RF showed a classification success of 80%. Of all included calls (n = 155), 96% and 93% were correctly assigned to ‘crow’ and ‘eng’ types, respectively. This classification success using the RF model trained on the acoustic parameters of each call type was 2 times (‘eng’) and 6 times (‘crow’) better than expected by chance (Table 2.3). For ‘arg’ and ‘eur’ calls, 62% and 50% were correctly assigned to their type, respectively, which was 2.8 and 2.5 times better than expected by chance (Table 2.3). This improvement in classification success was largely attributed to differences in call duration across call types, as removing call duration resulted in the highest mean decrease in classification accuracy relative to other parameters (Fig. 2.3). In general, there were higher misclassification rates for call types of intermediate duration.

Across all call types, mean call duration ranged from 0.19 to 1.40 s and mean lower and upper frequency ranged from ~ 0.5 to 2.6 kHz (Fig. 2.1b, Table 2.2). Call duration differed across call types ($\chi^2_3 = 359.92, p < 0.0001$), with ‘crow’ calls being significantly longer than all other call types (p -values < 0.0001), and ‘arg’ calls longer than ‘eng’ calls ($p = 0.01$; Fig. 2.1b). Amplitude modulation also differed across call types ($\chi^2_3 = 53.91, p < 0.0001$), and ‘eng’ calls had lower amplitude modulation compared to ‘crow’ and ‘arg’ calls (p -values < 0.0001). Lower frequency also differed among call types ($\chi^2_3 = 31.44, p < 0.0001$), and this acoustic parameter was higher in ‘eur’ calls compared to other call types (‘eng’ and ‘arg’, p -values < 0.0001 ; ‘crow’, $p = 0.0005$; Fig. 2.1b). There was no difference in peak frequency across call types ($\chi^2_3 = 2.15, p > 0.5$).

Due to lower agreement between AV assignment and the RF, a subset of call clips was evaluated by a novice observer (G.K.D.), including the ‘arg’ ($n = 24$), ‘eur’ ($n = 24$), and ‘eng’ ($n = 22$) call types classified in the first AV survey. The experienced (K.W.) and novice observer had a 92% agreement for ‘eng’ calls, 96% for ‘arg’ calls, and 45% for ‘eur’ calls. ‘Eur’ call clips were originally provided to the novice observer as a single call (as in Fig. 2.1a), but the call was often heard repetitively within recordings (as in Fig. 2.4). When the novice observer was provided call clips containing more than one ‘eur’ call, agreement between the novice observer and experienced observer increased ($> 95\%$).

Call types

Eng

This call type was very short and monosyllabic with the lowest peak frequency of all call types, along with the lowest amplitude modulation throughout the call (Fig. 2.1, Table 2.2).

There was also a slight increase and decrease in frequency throughout the call and many harmonics were expressed with energy concentrated in the lower harmonics of the call (Fig. 2.1a). The short duration and little amplitude modulation separated ‘eng’ calls from other call types (Fig. 2.1, Table 2.2). These calls were occasionally misclassified as ‘arg’ calls (5/74, < 7%). Within the acoustic recordings where all at-sea murre calls were selected (n = 2789 calls), ‘eng’ was the most frequently heard call type (90.2%). When this call was emitted, the vocalising murre would crane its neck downwards and forwards while opening its beak slightly. This call type was frequently heard in conspecific and multispecies aggregations of smaller (< 10 individuals) and larger group sizes, where individuals typically repeated ‘eng’ calls several times within a recording session (Fig. 2.4). ‘Eng’ calls were frequently heard when groups of murrees would encounter each other, form into larger groups, and disperse repeatedly into smaller groups. This call type was also heard when individuals engaged in pecking behaviour while in groups with low inter-individual spacing (< 0.5 m) on the water. On two occasions, ‘eng’ and ‘arg’ calls were frequently heard when ~50 murrees were tightly aggregated (< 0.5 m between individuals) in a line. This call type was not emitted by solitary murrees or when a solitary murre was observed in a multi-species seabird aggregation without other murrees present.

Arg

This call type was structurally similar to ‘eng’ call types, with a rapid increase and decrease in frequency, although ‘arg’ calls were typically longer and higher in frequency (Fig 2.1). Within this call type, calls were highly variable in both spectral and temporal domains (Table 2.2, Fig. 2.1, Fig. 2.2). ‘Arg’ calls were characterised by irregular frequency and amplitude modulations, and occasionally included two syllables (i.e. a break within the call on a spectrogram; Fig. 2.2). For these multisyllable calls, the break in call parts occurred between the

increase and decrease in frequency and some of these calls were visually similar to shorter ‘crow’ calls (see below). The intermediate duration (between ‘eng’ and ‘crow’ call types) and high amplitude modulation separated ‘arg’ calls from other call types (Fig. 2.1, Table 2.2). These calls were often misclassified as ‘eng’ calls (8/34) and occasionally as ‘crow’ (2/34) and ‘eur’ call types (3/34). Although the ‘arg’ call type was recorded less frequently (2.3%) than ‘eng’ calls, ‘arg’ calls were associated with similar behaviours and social contexts and both call types were frequently heard together within the same recording sessions (Fig. 2.4).

Eur

‘Eur’ calls were comprised of two or three syllables at higher frequencies relative to other call types, and most of the energy of the call was heavily concentrated around the peak frequency (Fig 2.1a). The lower frequency acoustic parameter was higher in ‘eur’ calls than other call types (Fig 2.1b, Table 2.2). These calls were often misclassified as ‘arg’ (7/22) and ‘eng’ (4/22) call types. The ‘eur’ call type was not recorded frequently (3.5% of calls) and was unique as it was only recorded from flying murrets (Fig. 2.4). This call was emitted repeatedly from flying individuals, and the start of the call appeared to coincide with the downbeat of wings and end when wings were expanded backwards during sustained flight. When emitting this call, the bill of a flying individual was slightly open, although silent murrets would also occasionally fly with their bill open. This call was also occasionally recorded from flying individuals while they held a fish in their bill. Both murrets flying solitarily and within conspecific groups made this call type, and occasionally multiple individuals would repeat this call asynchronously from within a flying group.

Crow

This call type was visually similar to ‘crow’ call types previously described at colonies (Lefevre *et al.* 2001, Smith *et al.* 2023), thus we used the same name. ‘Crow’ calls were long, loud calls that ascend and then descend in frequency with rapid frequency and amplitude modulation (Fig 2.1a). Most of the energy was highly concentrated within the middle of the call, before descending in frequency and amplitude (Fig. 2.1a). The longer duration of ‘crow’ calls allowed for separation from the other call types, although duration was highly variable within the call type (Fig 2.1, Fig 2.2, Table 2.2). A small percentage of crow calls were misclassified as ‘arg’ call types (1/25). The ‘crow’ call type represented 4% of all calls. Individual murrets emitting ‘crow’ calls were never directly observed in focal groups within 100 m and, thus, the exact behaviour associated with this call type at sea could not be described. These calls, however, were typically heard within large conspecific and multispecies groups (Fig. 2.4), and occasionally other contexts, including when only flying murrets were observed or when small groups (2-15 individuals) were present and were repeatedly forming and separating into smaller groups with larger inter-individual spacing (50-100 m). For another project, we also often heard crow calls emitted from flying murrets while stationed on a boat within 200 m of a breeding colony (Funk Island; N49.759253°, W53.176346°) during the chick-fledging period.

Discussion

In this study, we identified and quantitatively described the repertoire of common murrets while at sea. Four call types were identified; three were supported by RF, and one was supported by high classification agreement between observers (‘eur’). Of the three call types supported by RF, ‘arg’ calls were highly variable and appeared to grade between the more discrete ‘eng’ and ‘crow’ call types. These three call types visually resembled call types previously described at murre breeding colonies (Lefevre *et al.* 2001, Smith *et al.* 2023; Table 2.4), while the ‘eur’ call

type was not. These similarities were not expected due to the different behaviours displayed and soundscape attributes in these two contexts. Comparisons of our at-sea call types with those previously described at murre colonies are limited, however, as we could not quantitatively compare the calls and the at-colony studies did not provide a description of variation within call types (i.e., multiple spectrograms or sound clips). These studies, however, showed that the parameters of these calls varied within discrete call types, particularly in the number and inflection of syllables, duration, and peak frequency, and intermediate calls between types were noted but not described (Lefevre *et al.* 2001). We also found considerable gradation in the vocalisations emitted at sea, as expected, and described a graded call type that varied within and between other types.

‘Eng’ calls emitted from within foraging aggregations at sea likely function to manage close-contact interactions, as the short duration and higher frequencies of this call likely restrict propagation in the ocean environment (i.e., scattered by wind turbulence and wave action; Morton 1975, Wiley and Richards 1978). This call type is visually similar to the ‘coo’ call type described for murrelets at the colony by Smith *et al.* (2023), which was estimated to be detectable by murrelets at a maximum of 1 - 6 m under several soundscape scenarios. In support, the ‘eng’ call type could not be heard by observers when murrelets were > 50 m from the boat without the use of our highly sensitive recording equipment. The craning of the neck down and forward while emitting the ‘eng’ call at sea was similar to the posture associated with ‘nod’ calls of thick-billed murrelets (Tschanz 1968, Lefevre *et al.* 2001). Although ‘eng’ calls were shorter than ‘nod’ calls, both were emitted under similar contexts; ‘eng’ calls occurred in groups with low inter-individual spacing (< 0.5 m) where pecking was observed when individuals collided, and ‘nod’ calls occurred during conspecific fights at the colony (Lefevre *et al.* 2001). As most of our recordings

were conducted within high-density and persistent capelin spawning sites, where murrens forage solitarily and often maintain ~250 m spacing (Davoren *et al.* 2003c), ‘eng’ calls may be important to maintain this inter-individual spacing and manage interactions when this spacing is not maintained. As visual contact for murrens may be limited under certain conditions (e.g., foggy, high seas) and while foraging at night (Regular *et al.* 2011), vocal behaviour may be especially important to manage these interactions under these conditions. Similar short, low frequency calls emitted by seabirds at sea have been described in other seabird species. Indeed, gentoo penguins (*Pygoscelis papua*) use short ‘contact’ calls while forming groups during foraging trips (Choi *et al.* 2017), and similar vocalisations emitted by Cape gannets (*Morus capensis*) rafting on the water were hypothesized to maintain group cohesion and manage agonistic interactions when in close contact (Thiebault *et al.* 2016a, 2019).

Although ‘eng’ calls may function to maintain contact and manage inter-individual spacing to reduce competitive interactions when foraging on high-density stationary prey patches, they may also allow for murrens to maintain close enough contact to observe and cue to the diving behaviour of individuals to locate and/or maintain contact with ephemeral prey patches (‘network foraging’; Wittenberger and Hunt 1985). When prey patches are ephemeral, murrens may also use vocalisations to coordinate foraging behaviour (e.g., herding). In support, common murrens found in multi-species foraging associations in other regions were tightly aggregated and performed highly synchronized dives while targeting sandeel (*Ammodytes* spp.) schools, suggesting that murrens were cooperatively herding fish into higher concentrations (Camphuysen and Webb 1999, Ainley *et al.* 2021). On two instances prior to capelin spawning, we observed murrens repeating ‘eng’ calls while evenly spaced (< 2 m) within a line of ~ 40 and ~ 100 individuals, while simultaneously diving and surfacing. Actively herding fish, and vocal

behaviour used in this coordination of activities, may be more important when foraging on less dense and ephemeral prey (Camphuysen and Webb 1999), such as what we observed outside of the capelin spawning season. In support, seabird vocalisations have previously been linked to group foraging at sea in one study; African penguins (*Spheniscus demersus*) engaging in dive bouts with conspecifics were found to vocalise more often when they encountered schooling fish compared to a single prey item (McInnes *et al.* 2020).

In contrast to the ‘eng’ call type, ‘crow’ calls were highly variable and long, and may serve in long-distance communication at sea. In support, these calls could be heard by observers when murre were > 50 m from the boat and we often heard murre emitting ‘crow’ calls before visually detecting birds on the water. This call type appeared visually similar to spectrograms of the ‘crow’ call type described at colonies and acoustic parameters (i.e., duration, peak frequency) fell within similar ranges (Table 2.4; Lefevre *et al.* 2001, Smith *et al.* 2023). At colonies, this call type is heard during agonistic interactions with neighbors and intruders (Tschantz 1968), and mates often use this individually distinct call type during colony arrival, copulation, and change-over of parental duties (Lefevre *et al.* 1998, 2001, Lengagne *et al.* 2004). Parents also use ‘crow’ calls during interactions with chicks at the colony, and male parents use this call during fledging to reunite with the chick at sea (Tschantz 1968, Ainley *et al.* 2021). As our ‘crow’ calls were recorded prior to chick fledging in the study area (early August; Davoren and Montevecchi 2003), this call type clearly serves functions outside of these previously described behaviours at sea. Indeed, ‘crow’ calls may be broadly used in many contexts, as described at murre colonies (e.g., conspecific fights and intrusions, in response to predators) but more research is needed to confirm.

It is also unknown whether the individual signatures held in this call type would be received in the at-sea environment, and if vocal recognition among adult murrees would increase fitness while foraging at sea. Vocal recognition during foraging may have evolved if specific individuals are more reliable signallers of prey quality, such as older individuals that may display specialized foraging strategies and higher foraging efficiency compared to younger individuals (Porter and Sealy 1982, Bertellotti and Yorio 2013, Riotte-Lambert and Weimerskirch 2013). There are, however, limitations to the number of individuals that a bird could reliably remember and identify (Beecher 1989, Carlson *et al.* 2020). In Cape gannets, the modification of several acoustic parameters are required for individuals to identify each other at sea, although a risk of confusion still exists (Thiebault *et al.* 2019). Within breeding colonies, vocalisations are critical for murrees to recognize mates and neighbors (Lefevre *et al.* 1998, 2001, Ainley *et al.* 2021), the latter of which are often kin (Friesen *et al.* 1996, Ibaruchi *et al.* 2011). Consequently, it may not increase fitness to recognize individuals in large, dense aggregations at sea, as suggested in Cape gannets (Thiebault *et al.* 2019), unless neighbors depart the colony and travel to similar foraging areas simultaneously (Jones *et al.* 2018, Monier 2024).

It is possible that ‘crow’ calls may inadvertently act as an auditory cue for searching birds to locate prey. Indeed, its long duration, high amplitude modulation and broadband (i.e. energy distributed over many frequencies) signal, not only increase propagation but also the ability for the receiver to locate the signaller, respectively. This call type may be especially important when the visual field is obscured, although high wind and wave action that are characteristic of the marine soundscape, likely decreases signal transmission compared to calls emitted within breeding colonies (Morton 1975, Wiley and Richards 1978, Larsen and Radford 2018). Vocal behaviour emitted within murre foraging aggregations may cue flying murrees to begin an area-

restricted search for prey if they can be detected at farther distances or used in combination with visual cues. This may allow crow calls to decrease the reaction distances and reduce search efforts, thereby maximizing novel foraging opportunities.

The ‘arg’ call type was highly variable, primarily in duration, and shared similar acoustic parameters and appeared visually similar to a number of call types defined at colonies. Single syllable ‘arg’ calls appeared similar to ‘nod’ calls at colonies, while multi-syllable ‘arg’ calls appeared to grade between ‘eng’ and ‘crow’ call types at sea, and individual calls within this gradation appeared similar to previously described ‘adow’ call types at colonies (Fig 2.2, Table 2.4; Lefevre *et al.* 2001, Smith *et al.* 2023). The presence of these calls within similar behavioural contexts as other call types (e.g., ‘eng’ and ‘crow’) also supports that ‘arg’ calls are comprised of several sub-types that form a gradient between call types. This gradation may represent the short-term affective (i.e., emotional or motivational) state of a vocalising murre as they respond to a specific stimulus, and vary based on the associated valence (i.e., positive or negative emotion) and degree of arousal (Briefer 2020a, Gémard *et al.* 2021, Osiecka *et al.* 2023). As the benefits of group foraging may be outweighed by competitive interactions at high conspecific densities (Götmark *et al.* 1986, Thiebault *et al.* 2016b, Maynard *et al.* 2019), graded calls may function to manage these interactions among densely aggregated individuals. Recently, context-dependent vocal plasticity in seabirds have been demonstrated. Blue petrels (*Halobaena caerulea*) and Antarctic prions (*Pachyptila desolata*) responding to calls outside their burrow vary their responses based on the perceived sex of the burrow visitor (Gémard *et al.* 2021). When male intruders vocalised nearby, interpreted as a competitive interaction, the responding calls were higher in frequency (in blue petrels) and number of phrases in a call (in both species), relative to calls directed towards females for courting. Graded calls have also been demonstrated

in alcids, where little auk (*Alle alle*) vocalisations between mated pairs were shorter and had higher frequency parameters compared to calls emitted in the presence of predators and human handlers (Osiecka *et al.* 2023). In murre ‘arg’ calls, acoustic variation may also communicate the emotional valence and degree of arousal within calls emitted during competitive interactions with conspecifics in dense foraging aggregations. However, as we could not always observe the behaviour of the calling individual, it is possible that the variation observed in ‘arg’ calls represent stable individual differences, such as syrinx size (Fant 1971, Favaro *et al.* 2017, 2023).

Approximately 50% of the vocalisations qualitatively assigned to the ‘eur’ call type were misclassified by the RF to ‘eng’ and ‘arg’ call types when provided to the model as individual calls. However, these calls were repeated at regular intervals by flying individuals, which was evident when we conducted the AV survey to categorize call types. The regular repetition of calls, along with other contextual information (e.g., sound of wings flapping) is likely important in discriminating ‘eur’ calls. Low classification success for the ‘eur’ call type may also result from the acoustic parameters included here not capturing the variation apparent during the AV survey, such as the timing of each frequency peak within the call, which was not available within the acoustic measurement software. Classification agreement between the novice and experienced observer increased (from 45% to > 95%) when the novice observer was provided longer clips containing repeated ‘eur’ calls, thus we considered this call type discrete.

The ‘eur’ call type emitted by flying murre does not appear visually similar to published descriptions of calls emitted at colonies, and thick-billed murre were reported to not make any vocalisations while flying above the colony (Lefevre *et al.* 2001). Therefore, it is possible this is the first description of this call type, that may be emitted only when murre fly at sea. In contrast to the other call types described, ‘eur’ calls emitted by flying murre may not be a form of

intentional vocal communication. The onset of these repeated calls appeared to coincide with wing movement during flight, and as sustained flight for murres is energetically costly (Elliott *et al.* 2013), this call type may simply be produced by air being pushed out of the lungs and vocal apparatus under pressure. The relatively higher frequencies expressed in this call also indicates the flying context in which it is used, as an elongated neck would lengthen and constrict the trachea, which may result in vocalisations of higher frequencies (Fant 1971). Similarly, vocalisations produced by flying and diving Cape gannets were at higher frequencies than calls described while they rested on the water (Thiebault *et al.* 2019). We often observed silent flying murres, and do not know whether the same individuals consistently make this call, or if this call is only emitted under certain conditions (e.g., when returning from a foraging trip with a full stomach and presumably heavier than upon colony departure). Regardless of whether this call is emitted intentionally or not, it may nevertheless signal conspecifics to the presence of a flying murre or be used to maintain spacing from the vocalising murre within a flying group.

Conclusion

In this study, we created the first quantitative description of common murre call types while within foraging aggregations at sea. We found that some vocalisations emitted at sea (i.e. ‘crow’, ‘eng’, ‘arg’) visually resembled spectrograms of call types previously described at colonies, while the ‘eur’ call type did not. We expected that different call types had evolved in these different contexts; however, our findings suggest that these ubiquitous call types impart important information across both contexts. Interestingly, the soundscape characteristics and associated evolutionary pressures may be similar at breeding colonies and dense foraging aggregations at sea, where vocal and non-vocal sounds (e.g., noise during seabird plunge-diving, whale blows) produced at these dense aggregations can potentially propagate far underwater

(Putland *et al.* 2016), and possibly in-air in the ocean environment. Rather than using multiple novel call types while at sea, murrens may instead emit graded forms within and between call types to convey context-specific information. Indeed, we found that murrens use a highly variable call type within foraging aggregations, which may be similar to graded intermediate calls noted at colonies (Lefevre *et al.* 2001). The call types and associated behavioural and social contexts described here increase our understanding of murre foraging ecology, such as the variety of cues that might play a role in minimizing energetically costly search activities for prey, along with the diversity of acoustic communication away from breeding colonies. Using the vocalisations provided by this study, autonomous recording units (ARUs) moored in coastal areas could identify areas of high murre presence to mitigate negative human-wildlife interactions without requiring costly ship-based observations and increased human disturbance. For example, murrens are hunted in the fall in coastal Newfoundland (annual ‘turr hunt’; Canadian Wildlife Service 2022), and acoustic monitoring could indicate areas where hunting pressure may be high. The specific call types emitted by murrens could also provide important information related to the behavioural states and contexts experienced by murrens at these understudied areas (Teixeira *et al.* 2019). Combining deployments of in-air recording units and marine hydrophones, such as the Rockhopper (K. Lisa Yang Center for Conservation Bioacoustics, Cornell University), should also be considered to increase understanding of the foraging hotspot soundscapes, which can be used to identify critical foraging habitat (Putland *et al.* 2016, Gasc *et al.* 2017).

Due to the lack of published variation within call types described at breeding colonies, we were unable to quantitatively compare our call types to those recorded at the colony and, thus, it is unclear whether they represent the same or different call types. We recommend that multiple spectrograms of each call type and call clips (for both discrete and graded call types)

that display their variability are provided as supplementary material in future publications, allowing for quantitative comparisons among species' repertoires and an understanding of context-specific variation. With recent advancements in miniaturized video cameras, hypotheses of specific call type functions could be tested using bird-borne recorders paired with audio clips provided in this study, through both playback experiments and observational studies (Thiebault *et al.* 2016a, 2019, Choi *et al.* 2017, McInnes *et al.* 2020).

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Tables

Table 2.1. Descriptions of call parameters measured using the Noise-Resistant Feature Set (Mellinger and Bradbury 2007). Parameters marked with a * were included in the random forest analysis, while other parameters were excluded due to high multicollinearity. The noise-resistant feature set automates a feature box placed within manually drawn selection boxes in Raven Pro 1.6. Measurements of each call were made based on the contents of the feature box. Units are provided where applicable.

Parameter	unit	Abbreviation	Description
Lower Frequency*	Hz	Lower	Lowest frequency of the call
Upper Frequency	Hz	Upper	Highest frequency of the call
Duration*	s	Dur	Length of the feature box
Bandwidth*	Hz	Band	Ratio of lower to upper frequency
Median Time	ms	TimeMed	The time at which 50% of the energy is split on either side of the time envelope
Temporal IQR	s	TimeIQR	The difference between the upper third quartile and first quartile of the time envelope
Temporal Concentration	s	TimeConc	Difference between minimum and maximum of time envelope holding 50% of energy
Temporal Asymmetry*		TimeSkew	Skewness value of the temporal inter-quartile range
Median Frequency	Hz	FreqMed	The frequency at which 50% of the energy is split on either side of the frequency spectrum
Spectral IQR*	Hz	FreqIQR	The difference between the upper third quartile and first quartile of the frequency spectrum
Spectral Concentration*	Hz	FreqConc	Difference between minimum and maximum of spectral envelope holding 50% of energy
Spectral Asymmetry*		FreqSkew	Skewness value of the spectral inter-quartile range
Time of Peak Cell Intensity	ms	PeakCellTime	The time of the cell containing the peak magnitude
Relative Time of Peak Cell Intensity	%	RelPeakCellTime	The time of the cell containing the peak magnitude, divided by duration of the feature box
Time of Peak Overall Intensity*	ms	PeakTime	The time in the feature box with the maximal energy value
Relative Time of Peak Overall Intensity	%	PeakRelTime	The time in the feature box with the maximal energy value, divided by the duration of the feature box
Frequency of Peak Cell Intensity	Hz	PeakCellFreq	The mid-frequency of the cell containing the peak magnitude
Frequency of Peak Overall Intensity*	Hz	PeakFreq	The frequency with the greatest energy within the feature box (peak frequency)
Amplitude Modulation Rate*	Hz	AmpMod	Dominant rate of amplitude modulation
Variation in AM Rate*	Hz	AmpModVar	Variation in dominant rate of amplitude modulation
Frequency Modulation Rate*	Hz	FreqMod	Dominant rate of frequency modulation

Variation in FM Rate*	Hz	FreqModVar	Variation in dominant rate of frequency modulation
Average Cepstrum Peak Width*	Hz	Harmony	The largest width of the peak frequency, averaged across the call duration
Overall Entropy*	Hz	Entropy	Measure of evenness of energy distribution across frequency spectrum

Table 2.2. Mean (SE) for each call parameter used in the random forest analysis for each call type (n indicates number of calls for each call type). Parameter abbreviations correspond to those defined in Table 2.1. The * indicates one parameter that was included in the table but not in the random forest analysis to allow comparison to other published descriptions of murre vocalisations.

Parameter	Arg (n = 34)	Crow (n = 25)	Eur (n = 22)	Eng (n = 74)
Lower	458.07 (10.64)	525.96 (48.82)	696.32 (70.92)	447.38 (12.23)
Upper*	2304.32 (111.49)	2302.98 (137.41)	2615.09 (118.25)	2447.38 (94.97)
Dur	0.38 (0.03)	1.4 (0.13)	0.24 (0.02)	0.19 (0.01)
Band	1834.79 (112.73)	1777.02 (139.7)	1918.76 (115.81)	2000 (93.62)
TimeSkew	9.14E-06 (7.18E-05)	-3.53E-04 (2.25E-03)	8.04E-04 (7.26E-04)	6.88E-05 (2.93E-05)
FreqIQR	660.93 (52.14)	389.36 (47.74)	423.2 (70.95)	615.82 (30.05)
FreqConc	685.86 (83.18)	398.3 (59.52)	375.24 (82.23)	722.25 (55.85)
FreqSkew	0.04 (0.02)	-0.01 (0.01)	0.02 (0.02)	0.02 (0.02)
PeakTime	157.93 (18.15)	166.3 (31.76)	188.45 (31.1)	137.23 (12.07)
PeakFreq	1284.11 (98.69)	1589.79 (93.45)	1466.15 (76.97)	1230.59 (61.52)
AmpMod	2.67 (0.24)	2.41 (0.4)	1.52 (0.37)	0.63 (0.16)
AmpModVar	0.28 (0.03)	0.23 (0.05)	0.16 (0.04)	0.06 (0.02)
FreqMod	2.71 (0.23)	2.09 (0.28)	1.63 (0.4)	0.63 (0.16)
FreqModVar	0.09 (0.02)	0.14 (0.02)	0.04 (0.01)	0.01 (0)
Harmony	131.19 (9.03)	138.82 (5.66)	140.1 (14.28)	146.94 (9.55)
Entropy	239.3 (10.2)	193.57 (8.72)	205.22 (14.76)	275.5 (11.72)

Table 2.3. Comparison of the classification success of call types emitted by common murre at sea obtained by chance (number of calls per type divided by all calls in the analysis) or by using a random forest model (classification success per call type). The improvement of classification success using the RF was calculated by dividing the classification success of the RF model by the classification success obtained by chance.

Call type	number of calls	Classification success (%)		Improvement of classification success with RF
		By chance	With RF	
Arg	34	21.9	61.8	2.8
Crow	25	16.1	96.0	6.0
Eur	22	14.2	50.0	3.5
Eng	74	47.7	93.2	2.0

Table 2.4. Mean (SE) acoustic parameters of at-sea call types of common murres described in this study compared to published descriptions of similar call types recorded at breeding colonies of common murres (Smith *et al.* 2023) and thick-billed murres (Lefevre *et al.* 2001). All acoustic parameters of calls from Smith *et al.* (2023) and bandwidth from Lefevre *et al.* (2001) were estimated from spectrograms and boxplots.

Call type	Acoustic Parameters				Source
	Duration (s)	Peak Frequency (kHz)	Syllables	Bandwidth (kHz)	
Eng	0.19 (0.01)	1.2 (0.06)	1	2.0 (0.9)	This study
Nod	0.51 (0.03)	0.32 (0.03)	1	~ 3	Lefevre <i>et al.</i> 2001
Nod	~ 0.75	~ 0.5	1	~ 0.5	Smith <i>et al.</i> 2023
Yuk	0.06 (0.01)	0.49 (0.23)	1	~ 4	Lefevre <i>et al.</i> 2001
Coo	~ 0.1	~ 0.4	1	~ 0.1	Smith <i>et al.</i> 2023
Crow	1.4 (0.13)	1.589 (0.09)	1	1.77 (0.1)	This study
Crow	1.00 (0.03)	0.92 (0.08)	1.1 (0.04)	~ 3.5	Lefevre <i>et al.</i> 2001
Crow	~ 1.2	~ 2.1	n/a	~ 0.6	Smith <i>et al.</i> 2023
Arg	0.38 (0.03)	1.2 (0.098)	1 or 2	1.8 (0.1)	This study
Adow	0.28 (0.02)	0.88 (0.15)	2	~ 3	Lefevre <i>et al.</i> 2001
Adow	~ 0.3	~ 2.1	n/a	~ 0.1	Smith <i>et al.</i> 2023

Figures

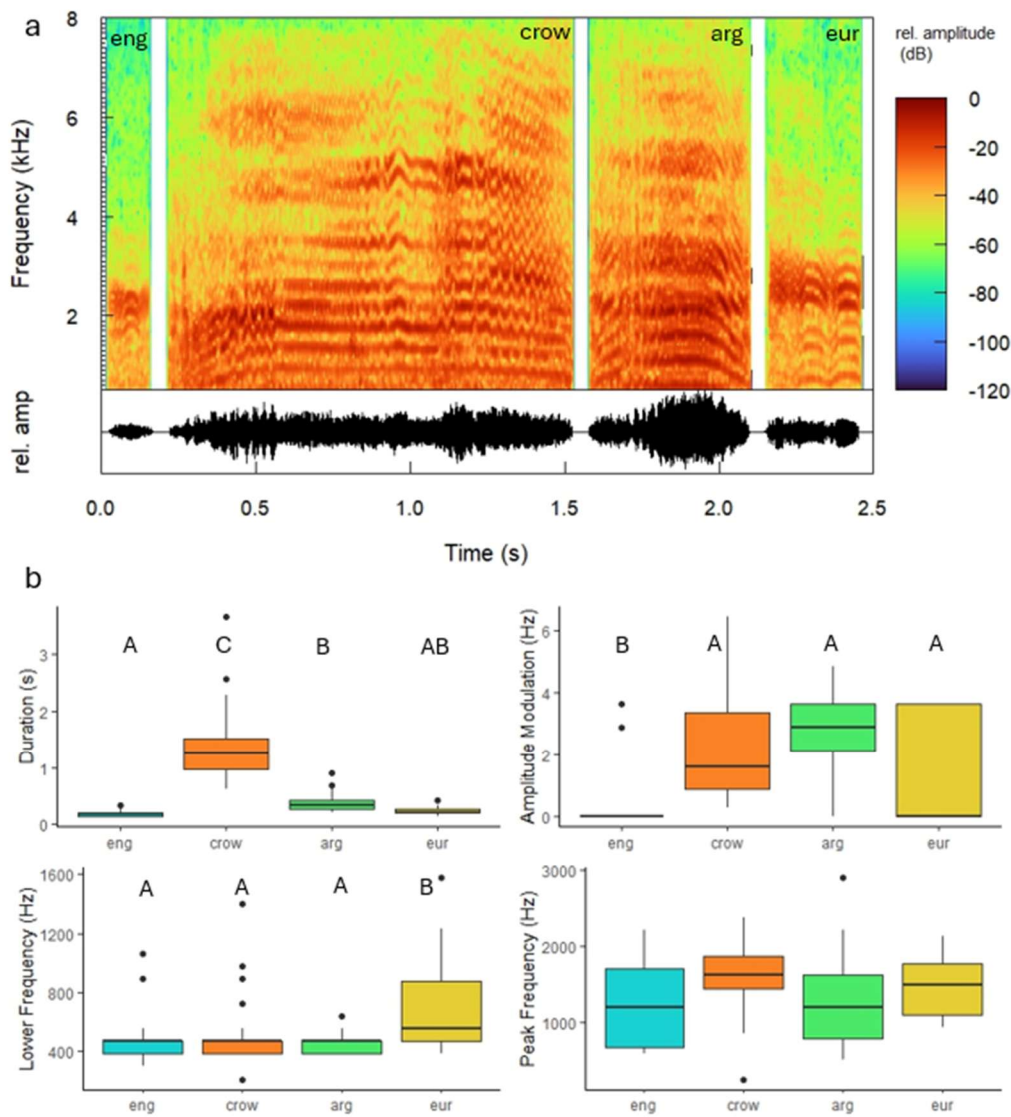


Figure 0.1. Characteristics of common murre vocalisations recorded at sea. (a) Spectrograms of the four common murre call types heard at sea, assigned during aural and visual examination in Raven Pro 1.6.1. Call types include: (a) “eng”, (b) “crow”, (c) “arg”, and (d) “eur”. Spectrograms were made using the *seewave* package in R (Hann window, 564 Discrete Fourier Transform, and 50% overlap; Sueur *et al.* 2008). (b) Comparison of key acoustic parameters for each of the four call types, with standard boxplot format (median represented by the black horizontal line, lower and upper hinges represent first and third quartiles, whiskers extend from the hinge up to 1.5 * the inter-quartile range). Call types sharing the same letter indicate that acoustic parameter did not differ significantly, while different letters indicate significant differences. Boxplots without any letters indicate that acoustic parameter did not differ significantly across all call types.

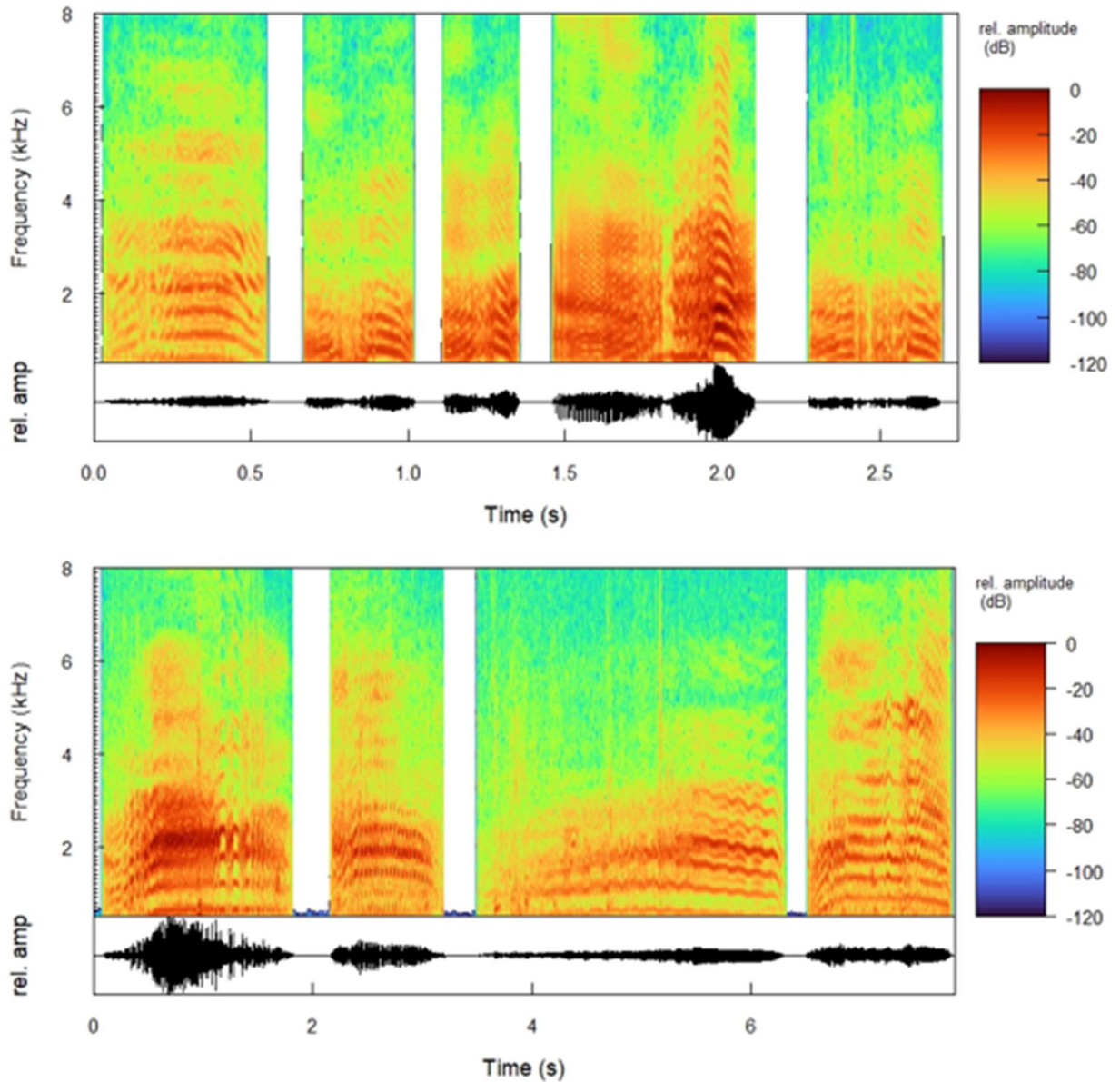


Figure 0.2. Spectrograms showing the variation within arg (top panel) and crow (bottom panel) call types of common murrelets recorded at sea. Spectrograms were made using the *seewave* package in R (Hann window and 50% overlap; Sueur *et al.* 2008).

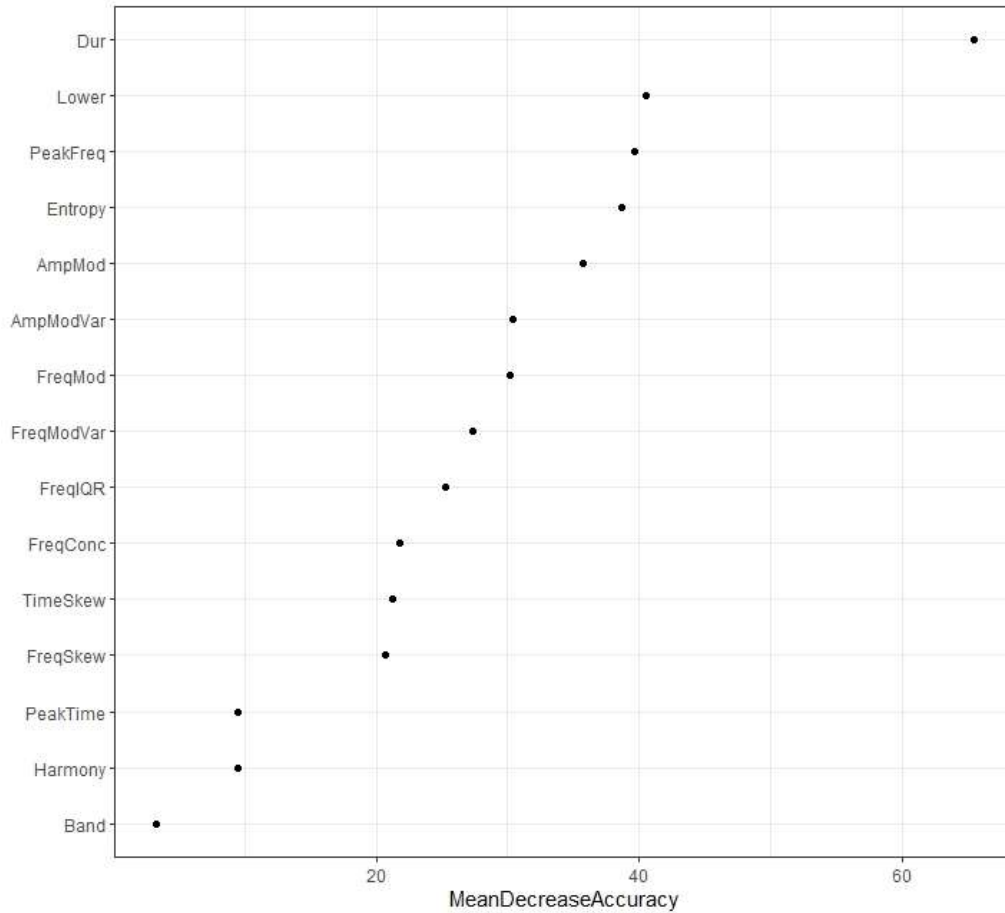


Figure 0.3. Scaled mean decrease in accuracy to classify at-sea common murre call types for each acoustic parameter used in the Random Forest model. Higher values indicate a greater contribution to the classification success of the Random Forest model. Parameter abbreviations correspond to those defined in Table 2.1.

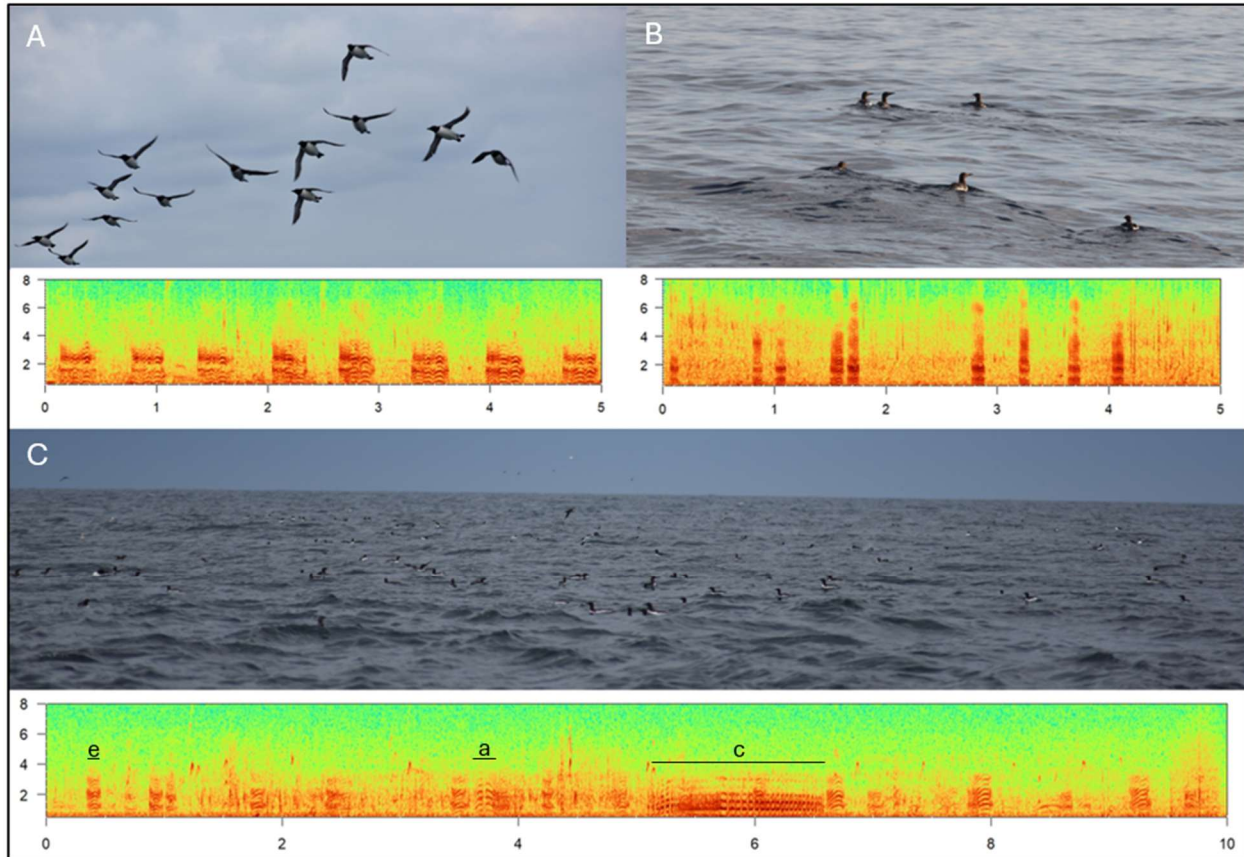


Figure 0.4. Spectrograms and associated behavioural contexts of common murre vocalisations recorded at sea. (A) Flying murre made repetitive ‘eur’ calls, (B) closely spaced (< 0.5 m) murre sitting on the water made ‘eng’ calls, and (C) murre within large multi-species foraging aggregations made ‘eng’ (e), ‘crow’ (c), and ‘arg’ (a) calls. Spectrograms were made using the spectro package in R (Hann window, 732 Discrete Fourier Transform and 50% overlap).

Supplementary materials

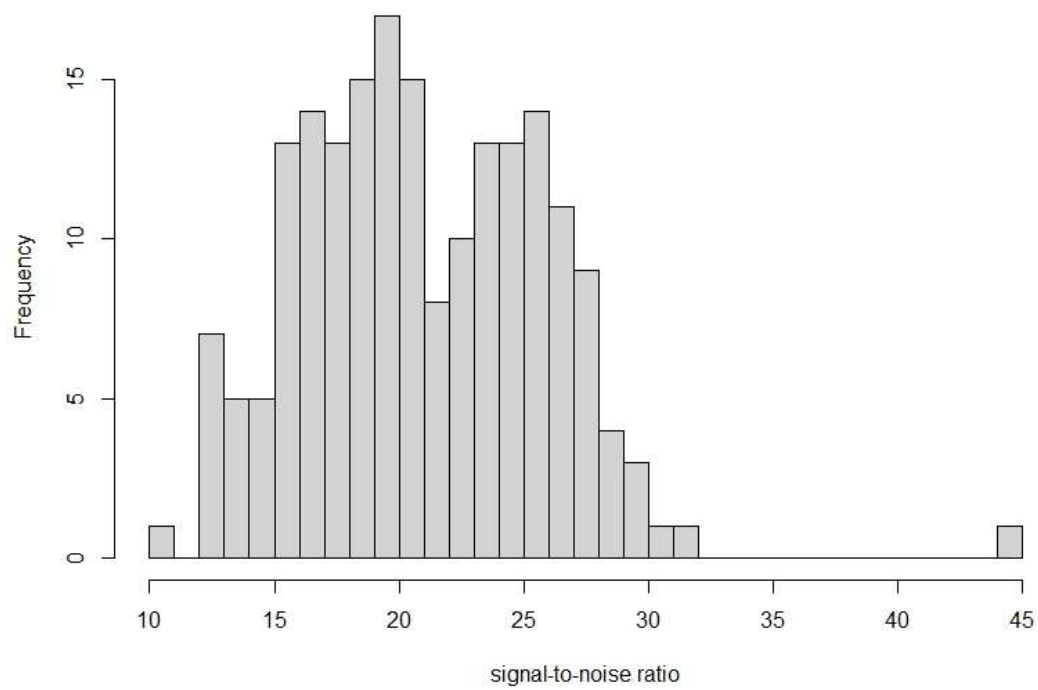


Figure S0.1. Histogram of signal-to-noise ratios (SNRs) for common murre vocalisations recorded at sea from June to August 2022 and 2023 and calls assumed to be of high SNR were measured for repertoire creation using *Acoustat* (Mellinger and Bradbury 2007).

Table S0.1. Ethogram used to define behaviour of common murre (*Uria aalge*) at sea when within 50 m of speed boat with observers. Behaviours were dictated continuously for all members of the focal group.

Behaviour	Definition
Sit	Floating on water, wings at the sides of the body and head upright.
Swim	On water, travelling with head directed forward.
Head dip	On water, head below water and body horizontal in water but not fully submerged.
Drink	Sitting with bill in water but head above water, or head dipped back to swallow water.
Land	Touching down on water, previously in air. Wings flapping and feet outstretched.
Preen	Smoothing feathers with bill
Bathe	Splashing water and ducking head into and out of water rapidly.
Dive	Head below water, wings flap before tail lifts into air, then fully submerged.
Surface flap	Wings outstretched and moving, chest pushed out but remaining on water.
Take-off	Wings outstretched and flap, body increasingly lifted out of water
Fly	In air, wings flapping, and feet tucked in
Vocalise	Beak open and sound emitted, can be during flying or while on surface of water.
Peck	Aggressive behaviour in close-proximity, one bird touches beak onto another individual (either on beak or rest of body), also dictate whether individuals move away from each other after interaction
Fight	Aggressive behaviour in close-proximity (<3 m) swooping by one bird towards another while in the air, may or may not involve physical contact. Vocalisations may occur from either individual.

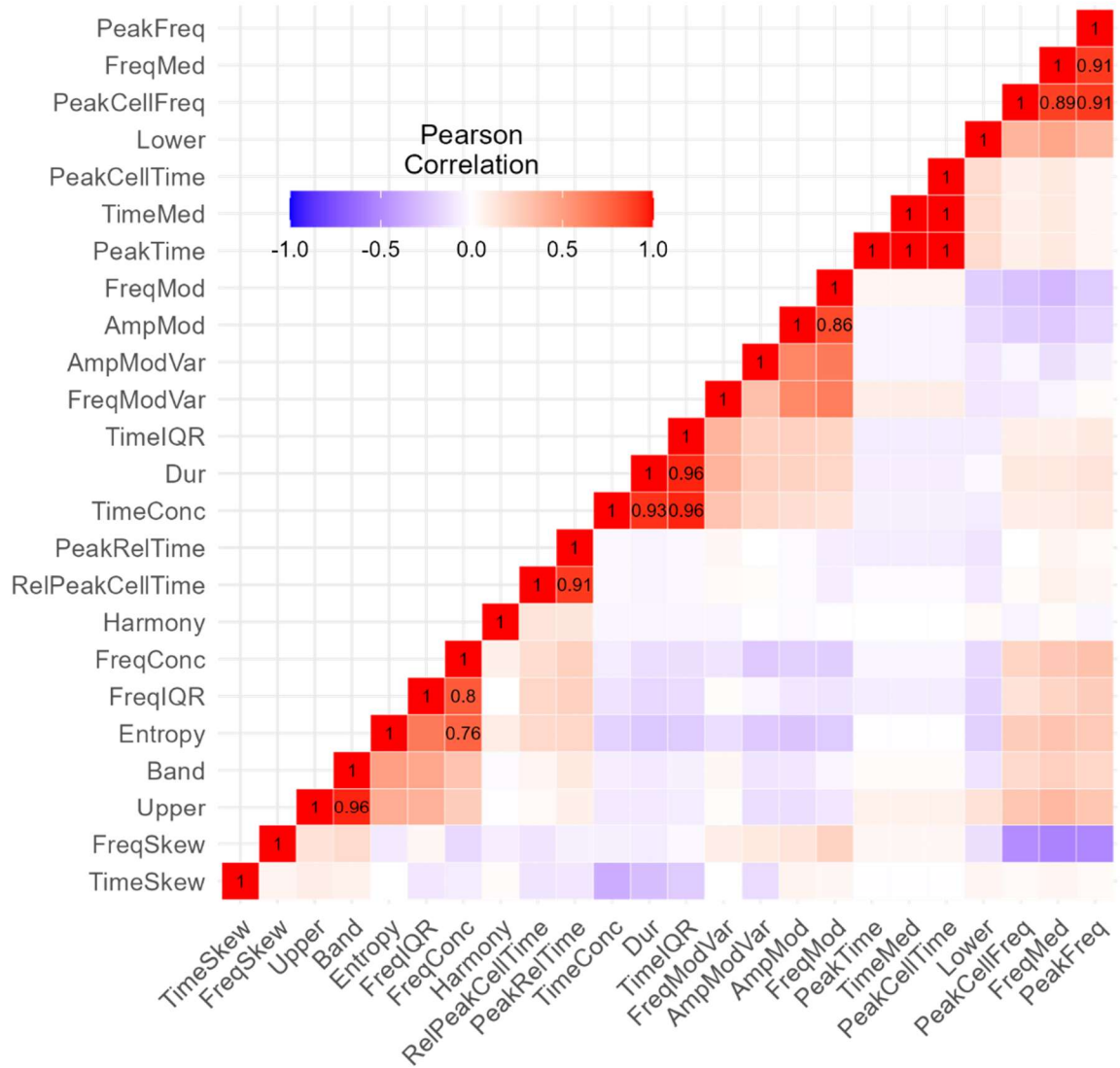


Figure S0.2. Correlation matrix of the 24 acoustic parameters evaluated for use in classifying common murre calls at sea. Acoustic parameters were measured using the Noise-Resistant Feature Set within the *Acoustat* package (Mellinger and Bradbury 2007). Correlation coefficients are calculated using Pearson’s correlation (r), and correlations with an $r > 0.7$ are displayed in the corresponding cells. Nine parameters were excluded to limit potential overestimation of importance values of highly correlated parameters in call classification. Parameter abbreviations correspond to those defined in Table 2.1. This figure was constructed using code provided at <http://www.sthda.com/english/wiki/ggplot2-quick-correlation-matrix-heatmap-r-software-and-data-visualization>

Chapter Three. Individual signatures in razorbill (*Alca torda*) chick ‘departure’ vocalisations

Abstract

Recognition of individuals with repeated contact allows for individuals to maximize their fitness, where the methods used to signal identity reflect ecological selection pressures in the environment. For some seabird species in the Family Alcidae, parents accompany and provision their chicks at sea after fledging. These species appear to develop recognition of their chicks’ calls to a greater extent when the risk of chick misidentification is high when chicks become highly mobile near fledging. Razorbills (*Alca torda*) exhibit male-biased vocal recognition of the calls of their semi-precocial chicks that appears to develop near fledging. The acoustic parameters used to signal identity and development of individual signatures across the short (16-22 d) nestling period, however, remain unclear. We aimed to investigate the acoustic parameters that encode identity in razorbill nestling ‘departure’ calls and examine the development of these individual signatures throughout the nestling period. We continuously recorded vocalisations of razorbill chicks, using miniature acoustic recorders, during two periods: early (three to five days old) and late (15 to 19 days old) nestling stages on a breeding colony on the northeast coast of Newfoundland, Canada during July-August 2023. We manually identified departure calls during eight hours of recordings for each of six chicks, with four hours during each of the early or late nestling stages. Acoustic parameters on these calls were quantified and multivariate analyses (principal component analysis, discriminant function analysis) were conducted to determine the classification success of departure calls to individuals in each stage. Calls could be assigned to individuals during both early and late nestling stages with 66.7% (early) and 69.4% (late) success, but classification success varied among chicks. Temporal features appeared to have the

highest potential of individual encoding ($PIC > 1$) in these calls, which may allow for individual signatures to propagate in long-distance communication, relative to frequency-encoded call signatures. Increased potential for temporal call features to encode identity increased across the nestling period supports the development of call signatures in communicating identity during fledging and at sea and, thus, the importance of individual recognition in maximizing fitness in razorbills.

Introduction

The ability to recognize individuals with whom one has repeated contact can maximize fitness and, thus, individual recognition has evolved multiple times across a range of taxa (Tibbetts and Dale 2007, Carlson *et al.* 2020). Individual recognition involves emitting combinations of individual-specific information ('signatures') across diverse modalities (i.e., visual, acoustic, chemical) that differ in their signaling properties (Yorzinski 2017). Individual vocal signatures may be more adaptive than visual cues when the visual field is busy, such as in dense foraging and breeding aggregations, and when individuals within a group show little variation in morphological characteristics (e.g., monomorphic species; Falls 1982). Variation in acoustic parameters of calls (or 'call signatures') may function to indicate identity, thereby allowing for individual recognition. Individual signatures held within call types can reduce confusion during interactions and, consequently, benefits individuals by minimizing energy expenditure (Wiley and Richards 1978). For instance, individual recognition can optimize interactions through past experiences, such as territorial species discriminating between mates, neighbors and strangers, and modifying their behavioural response accordingly (Carlson *et al.* 2020). Another example may be vocal signatures in calls made by offspring, used by adults to recognize and direct parental care towards their own young (e.g., Schommer and Tschanz 1975, Jones *et al.* 1987).

Vocal individuality may be represented through modulations in spectral, temporal, and other attributes, and the relative variation in call structure is indicative of the features most important in individual recognition. The attributes used to signal individual identity indicate the ecological selection pressures and constraints in a species' life history (Falls 1982). For example, penguins with fixed nest sites vocalise some identity information through several slightly

discriminant features (Favaro *et al.* 2015), while penguins that do not build nest sites and incubate eggs and raise young on their feet use few, but highly discriminant acoustic features, which appears to encode stronger individuality (Jouventin and Aubin 2002). Thus, selection for individual signatures held within calls of non-nest building penguins are likely stronger than those of penguins that build a nest, indicating different environmental pressures (Favaro *et al.* 2015). Within a call type, the parameters necessary for a call to be detected, and potentially localised, by the intended receiver must be preserved at a typical communication distance. Therefore, there is a trade-off between a signal reaching and being interpreted correctly by its receiver, and modulating call parameters to signal identity. The broadcast distance used in signalling individual recognition is an important factor and may select for finer spectral characteristics in close-range interactions, and temporal variation when communicating identity across longer distances (Falls 1982).

Seabirds may vocalise to signal identity, as they forage and breed in large multi-species aggregations, where the visual field is busy and individuals are typically monomorphic. At breeding colonies, some seabird species have developed vocalisations used specifically for parent-offspring recognition (e.g., Ingold 1973, Harris 1983, Jones *et al.* 1987, Jouventin *et al.* 1999, Insley *et al.* 2003, Klenova *et al.* 2011). The adaptive significance of parent-offspring recognition and when it develops varies among seabird species and appears to have evolved differently in species with divergent nestling development strategies. In particular, alcids (Family Alcidae), a diverse family of 22 extant seabird species, exhibit extreme variation in nestling development strategies (Sealy 1973). The majority of alcids are semi-precocial, being cared for at the nest site until they reach 50-100% adult body mass before fledging unaccompanied by adults, and chicks exhibit little vocal individuality (Harris 1983, Kolesnikova and Klenova 2011,

Klenova 2015). Conversely, precocial alcids (*Synthliboramphus* spp.) fledge two days post-hatch and are provisioned at sea by both parents, and mutual vocal recognition between parents and chicks develops almost immediately after hatching (Jones *et al.* 1987).

Unique among alcids, razorbills (*Alca torda*) and murres (*Uria* spp.) have ‘intermediate’ development strategies, with chicks receiving biparental care at the nest site before fledging at approximately 30% adult body mass, where they are dependent on the male parent for provisioning at sea (Gaston and Jones 1998). Playback experiments have shown mutual parent-offspring vocal recognition in razorbills (Ingold 1973, Insley *et al.* 2003) and murres (Schommer and Tschanz 1975) at colonies when near fledging and at sea. Razorbills breed in dense conspecific colonies and nest in rock crevices, where nest sites are often separated by > 30 cm (Gaston and Jones 1998). After a 16-22 day nestling period, chicks leave their nest site at dusk alone and reunite with their male parent that awaits the chick on the water nearby the colony (Gaston and Jones 1998). This intermediate development strategy appears to rely on individual recognition when chicks are highly mobile near fledging (Lefevre *et al.* 1998, Lavers *et al.* 2020), because reuniting with the male parent is crucial for chick survival (Greenwood 1964). Although chicks cannot survive without parental provisioning at sea, adult males may become separated from their chick during fledging and when diving to pursue and capture fish at sea. When separated from the chick at sea, male parents emit vocalisations and chicks call repeatedly while swimming towards their parent (Ainley *et al.* 2021).

During the nestling period, razorbill chicks emit several call types, including a long, frequency-modulated call type termed ‘departure calls’, which are also repeated often when leaving the colony during fledging and at sea (Ingold 1973, Insley *et al.* 2003, Lavers *et al.* 2020). Due to the varying characteristics of this call, and use both when in the nest and during

fledging, departure calls appear to be used in individual chick recognition. Although these calls are made shortly after hatching, historical papers using playback experiments found that adult razorbills showed minimal responses to recordings of their four-day-old chicks' departure calls (Ingold 1973). In contrast, adults approached the speaker when played recordings of their 10- and 18-day-old chick and responded to departure calls of other chicks to a lesser degree (Ingold 1973). However, Ingold's study (1973) did not identify the sexes of the parents tested, and it was later determined that only male parents develop vocal recognition of their chick (Insley *et al.* 2003). This later study showed that male parents did not respond (e.g., vocalise, approach speaker) to playbacks of their chicks' departure calls when chicks were 11 days old, but some parents began responding when chicks were within 72 h of fledging, and most parents began responding when chicks were within 48 h of fledging (Insley *et al.* 2003).

Although parent-offspring recognition was supported through playback experiments in razorbills, the acoustic parameters (e.g., duration, peak frequency) used to communicate identity in chick vocalisations is not well described. The departure calls made by chicks visually appear to be individually distinct in pitch variation and call duration (Ingold 1973). As these calls are emitted during fledging and at sea, they may have evolved to signal the chick's identity within the temporal envelope, thereby allowing signal propagation across longer distances and in high background noise (e.g., wind, wave, conspecific/heterospecific calls). Additionally, departure calls have been qualitatively described to change across the nestling period, with increasing duration, pitch variation and loudness, through aural and visual examination of recordings (Ingold 1973, Insley *et al.* 2003), potentially allowing for better identification of individual chicks with increasing age. However, only call duration, duration between call elements, and pitch variation in the departure call were investigated in these earlier studies, when the acoustic

technology limited both the temporal and frequency resolution of recordings, measurable parameters, and associated analyses (Pavan *et al.* 2022). With recent technological advances in bioacoustics, many more call parameters can be investigated for their potential role in communicating individuality. The individual signatures held within chick calls of a species that experience similar environmental conditions was recently described, and the individually distinct information of these calls were found to develop across the nestling period (little auk, *Alle Alle*; Kidawa *et al.* 2023). As individuality in razorbill calls has been postulated to be only needed near fledging (Ingold 1973, Falls 1982, Insley *et al.* 2003), razorbills provide an excellent study species to describe call parameters responsible for individual recognition and how they develop through the nestling period.

Objectives

The objective of this chapter is to investigate the acoustic features important in signalling identity in razorbill chick departure calls and how these features develop throughout the nestling period. We first aimed to investigate the ontogeny of these call signatures while at the colony, and hypothesized that departure calls would exhibit higher individuality closer to fledging relative to earlier in development. We predicted that classification of departure calls to individual chicks, based on acoustic parameters, would be higher nearing fledging compared to earlier in the nestling period. Next, we aimed to investigate the acoustic parameters used to communicate identity. We hypothesized that as chick departure call signatures are adapted for long-distance communication and localisation by adults, and appear to function in reuniting parents and offspring during fledging and provisioning at sea, individually identifying acoustic features would be those features that can propagate with distance without degrading to be unrecognisable to parents. Thus, we predicted that temporal call features would exhibit higher between-

individual variation relative to within-individual variation, as temporal modulations persist over longer distances and in environments with high background noise. Alternatively, we expected less variation in frequency and energy-related parameters among individuals.

Methods

Study site

To record razorbill chick vocalisations, we deployed nine miniature autonomous recording units (ARUs) on James Island, Newfoundland, Canada (49° 57.989' N, 53° 57.989' W) during July 2023. James Island supports ~ 2,800 breeding pairs of razorbills, which primarily breed in rock crevices on boulder banks on the south and east coastline (Jenkins *et al.* 2018). The island also has the largest population of Atlantic puffins (*Fratercula arctica*, ~17,000 pairs) in northeastern Newfoundland, and smaller populations of breeding *Larus* gulls (*L. marinus*, ~8 pairs; *L. argentatus*, ~30 pairs), leach's storm petrels (*Hydrobates leucorhous*, ~1,578 pairs) and common murrelets (~23 pairs, Jenkins *et al.* 2018).

Acoustic recording units

Miniature acoustic recorders were developed using the low-cost micro Passive Acoustic Monitor (microPAM) system with a minimalistic setup (Zimmer 2022). These microPAMs consisted of a PJRC Teensy 4.1 development board, an Adafruit 12S MEMS microphone (single channel, 24-bit, sampling range of 50Hz – 15kHz) and 3V coin cell holder. The development board, microphone and coin cell holder were soldered together following specifications outlined at micropam.com and connected to a 20000Ah battery pack via a microUSB cable. The coin cell battery allowed for the recorders to maintain their programmed clock time when switching depleted and charged battery packs. Recorders were programmed to record continuously (24 h)

and create a separate file for each ten-minute recording period. The recordings were conducted with a 48 kHz sampling frequency and were saved as 24-bit wav files. Recorders were programmed to these specifications using a .hex file written by W.M.X. Zimmer in Python language. The recorder components were placed in a sealed plastic container (16.5 cm x 10 cm x 6 cm) to waterproof the recorder and secured within the container using double-sided tape (Command brand). A small light indicating the charge on battery packs was covered using electrical tape to reduce disturbance to birds. Although ten recorders were constructed, one recorder was not deployed due to manufacturing error causing the microphone sensitivity to decrease significantly.

Prior to field recording, microphone sensitivity within the sealed plastic container was measured experimentally in the laboratory by recording multiple clips of razorbill chick vocalisations (accessed through xeno-canto.org) with the microPAM inside and outside of the sealed plastic container. The recordings showed minimal variation in frequency measurements and there was a slight reduction in the recorded amplitude after sealing the container. The recordings exhibited high amounts of noise below 500 Hz, a deficiency of the microphones that created large negative DC components in the acoustic data. This noise was not expected to affect the recording of razorbill chick departure calls, as the fundamental frequency (f_0 ; lowest frequency) of these calls are produced between ~ 3.5 and 5 kHz (Insley *et al.* 2003, Lavers *et al.* 2020).

Acoustic recorder deployment and monitoring

We monitored rock crevices occupied by breeding razorbills every second night to record nest status (i.e., egg, pipping chick, emerged chick, empty) and deploy microPAMs in the nests of young chicks. This scheduling allowed us to estimate chick age and the timing of fledging, as

well as monitor nest status and microPAM battery status. We deployed microPAMs twice during the nestling period to target recordings of the same chicks at 3-5 days old (early stage) and 15-19 days old (late stage). Nine recorders were deployed within two days of hatching, and deployments and nest checks occurred at night with red light to minimize disturbance (Rebke *et al.* 2019, Syposz *et al.* 2021). Recorders were selectively placed in larger rock crevices that allowed for unrestricted movement of razorbills in/out and within the crevice. Each recorder was placed in a separate rock crevice, and focal crevices were > 3 m away from other razorbill nest sites, when possible, to reduce the potential of recording chick calls from non-focal nests. When a focal nest was found empty within 14 days of the focal chick hatching, we assumed that the nest failed, and the microPAM was recharged and relocated to a new focal nest. When battery packs were depleted (5-9 d recording continuously), the microPAM and container were removed, battery packs charged and replaced when the focal chick was approximately 12 days old to record later development calls. Recorders were then retrieved once the nests were empty and chicks had presumably fledged, approximately 16-20 d after hatch.

Call analysis

Following methods in Chapter 2, acoustic files were examined by a single observer (KW) in *Raven Pro 1.6* (K. Lisa Yang Center for Conservation Bioacoustics at the Cornell Lab of Ornithology 2022). Acoustic files were processed when the focal chicks were 3-5 days old (early stage), and on the last two days before estimated chick fledging date (late stage; 15-19 days old). On these days, only acoustic files recorded between 0700-0900 h (Newfoundland Daylight Time, NDT) were processed to reduce the effects of varying atmospheric conditions on sound transmission (Morton 1975, Wiley and Richards 1978). Therefore, we reviewed 4 h of recordings, spread out over 2-3 days, per focal chick in early and late stages, for a total of 8 h per

chick. Razorbill departure calls were manually identified during an aural and visual examination of spectrograms, based on qualitative descriptions by Ingold (1973).

To visualise the spectrograms, we used a sliding window of 10 s with a Hann window of 1024 samples. The frequency grid was configured using a Discrete Fourier Transform (DFT) of 16384 samples, resulting in a frequency spacing of 2.93 Hz, while the time grid overlap was 50% (hop size of 512 samples). These spectrogram settings were chosen to maximise spectral resolution of the heavily frequency-modulated call, while maintaining acceptable temporal resolution. We also set the display brightness to 40 and contrast to 45 to visualise the calls without filtering out the high machine noise under 500 Hz (due to the large negative DC component in recordings).

For acoustic parameter measurement, departure calls were selected if they had low background noise, no sound clipping, and no overlap with other vocalisations, along with calls having higher amplitude and minimal distortion to reduce the probability of selecting calls from non-focal chicks. Departure calls were then analyzed using the *warbleR* package in RStudio (Araya-Salas and Smith-Vidaurre 2017) following code provided by Genes *et al.* (2023). Start and end times of selections were manually adjusted (*seltailor* function) and spectrograms of these clips were reviewed to ensure consistency in identification of departure calls among individuals (*catalog* function, *warbleR* package). We then extracted 18 acoustic parameters that are robust to varying background noise levels (*spectro_analysis* function, Table 3.1) on the departure calls, using a bandpass filter between 2 and 6 kHz to focus measurements on the fundamental frequency (f_0).

Statistical analysis

All statistical analyses were performed in R (R Core Team 2023) following the code in Osiecka *et al.* (2024). Principal component analyses (PCA) were performed on the 18 acoustic parameters (*stats* package in R) to reduce highly correlated parameters to uncorrelated principal components (PCs). A PCA was conducted on all departure calls during the early and late stage separately, and scores of the PCs with eigenvalues > 1.1 (using Kaiser's criterion) were retained for use in subsequent analyses. These retained PCs were assessed for normality (Shapiro-Wilk test) and homogeneity of variances (Levene's test) and transformed when these underlying assumptions of parametric statistics were violated.

To investigate whether the acoustic parameters of chick departure calls differed significantly among individuals and calls could be correctly classified to an individual during the early and late nestling stages, we ran discriminant function analyses (DFA) with leave-one-out cross-validation (*MASS* package; Venables and Ripley 2002). To standardize the number of departure calls included per chick in the analyses, we determined the number of departure calls from the chick with the fewest calls during each of the early and late stages (Table S3.1) and then randomly selected a subset of this number of calls from other chicks. The PC scores of these randomly selected calls were our response variables in the DFAs. As in Osiecka *et al.* (2024), we calculated the percentage of departure calls that were correctly classified to each chick in each DFA and divided that by the classification rate by chance to calculate the relative cross-classification level using the following formula:

$$\frac{\text{Correct classification (\%)}}{\text{Chance classification (\%)}}$$

$$\left(\frac{\# \text{ correctly classified}}{\text{total \# calls}} \times 100 \right) \div \left(\frac{\frac{\# \text{ calls per chick}}{\text{total \# calls}} \times \# \text{ calls per chick}}{\text{total \# calls}} \times 100 \right)$$

= Relative cross-classification level

A relative cross-classification level value > 1 indicates a classification success better than chance, while a value of 1 indicates no difference, and we qualitatively compared these values in early and late stages to indicate changes in individuality in all measured acoustic parameters from early to late stages. We also assessed whether the probability of correct classification was significantly higher than expected by chance using a Fisher test (*stats* package) for both early and late stages separately. We repeated the DFAs on ten different random subsets of calls from each individual to quantify the variation of cross-classification levels when different calls were randomly selected from individuals within each stage.

To investigate which acoustic parameters contribute to individual signatures within departure calls, we calculated the potential of individual coding (PIC; e.g., Robisson *et al.* 1993) for each of the 18 measured acoustic parameters of all departure calls of all individuals during early and late stages separately. Following Osiecka *et al.* (2024), we first calculated the within- and between-individual coefficients of variation (CV) for each acoustic parameter, adjusting for small sample sizes using the following formula (Favaro *et al.* 2015, Linhart *et al.* 2019, Osiecka *et al.* 2024b):

$$CV = 100 \times \left(1 + \frac{1}{4N} \right) \times \frac{SD}{\text{mean}}$$

We then quantified the PIC for each acoustic parameter by dividing the mean between-individual CV for all individuals by the within-individual CV. Acoustic parameters with a PIC value ≥ 1 may be useful for individual recognition, as between-individual variation is higher than

within-individual variation, while PIC values > 2 are considered highly useful for individual recognition (Robisson *et al.* 1993).

Finally, to test the effects of the presence of recorders in nest crevices on fledging success, we used a binomial logistic regression (*lme4* package; Bates *et al.* 2015) to model the fledge success (binary response variable) of razorbill chicks with and without a recorder (predictor variable).

Results

The nine working microPAMs were originally deployed in nine nests during the 2023 breeding season, but early breeding failure of one focal chick and accidental initial placement in a nest with an older chick, resulted in deployment in a total of 11 nests. From the nine working microPAMs, we had useable data from six chicks due to overlapping calls of focal and non-focal chicks in the recordings for two nests, and due to the lack of late stage recordings from one chick that either fledged early or died at 13 days old. We found no difference in fledging success of chicks with a microPAM recorder present in the rock crevice ($n = 11$) and monitored crevices without a recorder present ($n = 35$; z -score = 0.401, $p = 0.69$).

Individual identity in departure calls

Our dataset consisted of 391 departure calls (146 in early stage, 245 in late stage) from six razorbill chicks (Table S3.1). Departure calls ranged from 2.3 to 4.7 kHz and from 0.43 to 1.9 s (Figure 3.1; Table S3.1). For early-stage chick departure calls, the first four PCs had eigenvalues > 1 and accounted for 88.1% of the cumulative variation across the 18 acoustic parameters (Table S3.2). All four PCs generally met the underlying assumptions of parametric statistics (Quinn and Keough 2002). For late-stage chick vocalisations, the first four PCs had

eigenvalues > 1 and accounted for 88.7% of the cumulative variation in measured acoustic parameters (Table S3.2). All four PCs did not meet the underlying assumptions of parametric statistics and, thus, were transformed with a boxcox transformation.

The DFAs on the combined acoustic parameters (PC1-4) revealed significant differences in acoustic characteristics among individuals in both early (approximate $F_{5,60} = 12.674$, $p < 0.0001$) and late (approximate $F_{5,102} = 18.525$, $p < 0.0001$) nestling stages (Figure 3.2). In the early stage, the overall rate of correct call assignment to individuals was 66.7% and varied from 36-91% within the chicks. Departure calls from nest B were often misclassified as other nests leading to low classification success (36%), and all other nests had classification successes $> 63\%$ (Table 3.2). Departure calls could be classified to an individual better than expected by chance (16.7%; $p < 0.001$), and the relative cross-classification level was 4. When repeated ten times with a different random subset of 11 calls from each chick, all models continued to be significant, but the relative cross-classification level varied from 3.91 to 4.72. In the late stage, the overall rate of correct call assignment to individual was 69.4% and varied from 44-100% within the chicks. Departure calls from two nests were often misclassified as each other: 33% (6/18 calls) of nest B as nest T, and 27.8% (5/18 calls) of nest T calls as nest B (Table 3.2). The percentage of correctly classified calls was stable or increased from the early to the late stage in four out of the six chicks (Table 3.2). Late-stage departure calls could be classified to an individual better than expected by chance (16.7%; $p < 0.001$) and the relative cross-classification level was 4.17. When repeated with a different random subset of 18 calls, all models were significant, and the relative cross-classification level varied from 3.56 to 4.17.

Potential for individual coding in acoustic parameters

Of the 18 measured acoustic parameters, 11 in the early stage and 14 in the late nestling stage contained a potential of individual coding ($PIC > 1$; Table 3.3). There were no acoustic parameters with high PIC values (> 2) in the early stage and four acoustic parameters with high PIC values in the late stage. Acoustic parameters with a $PIC > 1$ were spread among spectral, temporal and energy-related domains, and high PIC values were measured on the temporal spectrum. The acoustic parameter with the highest PIC was temporal energy distribution in both stages, and the individual information encoded in this parameter increased from 1.47 to 3.07 from early to late (Table 3.3).

Discussion

We quantitatively described the acoustic signatures present in razorbill chick departure calls, providing evidence that these calls can potentially be used to advertise individual identity in both the early and late nestling stages. These results support previous findings of chick acoustic recognition by male parents (Insley *et al.* 2003). In contrast to previous findings of individually discrimination of only late nestling calls (Insley *et al.* 2003), however, we found that acoustic parameters of departure calls significantly differed among individuals in both early and late stages. Within both stages, the classification success varied considerably among individuals (36-91% in the early stage, 44-100% in the late stage), indicating that chicks' departure calls were able to signal identity to varying degrees. Overlapping call signatures among individuals may be related to similar body size (Favaro *et al.* 2017), similar development of sound-producing organs (Favaro *et al.* 2015, 2023), and/or relatedness among chicks (Jones *et al.* 1987). Although we did not find strong support for an increase in the individual classification success across the nestling period as predicted, acoustic parameters with the highest PICs in the early stage increased in the potential to encode identity near fledging. As predicted, temporal call features

had the highest PIC values, which increased from the early to late stage, presumably allowing for individual signatures to be communicated over greater distances at sea. In both stages, the relative cross-classification success level varied among different random subsets of calls from each chick, suggesting that a higher number of calls per individual may be needed to better characterise the variation of individuality in departure calls between early and late nestling stages. Nevertheless, departure calls of individuals were always significantly distinguishable in all models run and relative cross-classification success values remained > 1 , indicating a classification success higher than expected by chance.

Overall, our results provide evidence that departure calls can be used to signal identity in razorbill chicks from as early as three days old. Although our findings of individual signatures in the early stage was not as predicted, our predictions were based on playback experiments that described a lack of response (e.g., vocalising, approaching speaker) of male parents to chick departure calls at 11 days old, but responses to chick calls within three days prior to fledging (Insley *et al.* 2003). The lack of response of male parents to calls of younger chicks, however, does not mean that individually distinct acoustic information is not present (Beecher 1991). For example, male parents may not discriminate between chicks until later in development because they needed time to learn the acoustic signature of their chick (Sharp *et al.* 2005). It is also possible that male parents may recognize their chick early in the nestling period but do not behaviourally respond to their acoustic signal until near fledging. Indeed, razorbills may use these signatures to reliably identify their young chick from others early in the nestling period. In support, we found that razorbill nest sites were densely aggregated at our study colony, with multiple nest sites found under one boulder with no physical separation between nest sites and multiple chicks were occasionally found in the same rock crevice. This situation resulted in

omitting the recordings of two nests, due to overlapping calls of focal and non-focal chicks. These circumstances may result in higher selection pressures for chick identification early in the nestling period compared to species that breed with little opportunity for chicks to intermingle (e.g., burrow-nesters, discrete nests with physical barriers), where adults may simply locate their young chick by returning to the same discrete nest site using geographic cues or spatial memory (Ingold 1973, Abbott *et al.* 1999, Insley *et al.* 2003).

The classification success (~ 67-69%) of razorbill departure calls throughout their nestling period appears to reflect their intermediate nesting strategy, as departure calls of 3-5-day-old razorbill chicks had stronger individual signatures than calls of semi-precocial alcids of a similar age (Kolesnikova and Klenova 2011). Indeed, only approximately half of the calls in semi-precocial alcids were correctly classified to an individual chick at 1-4 days old (42.9% in crested auklets (*Aethia cristatella*); 53% in tufted puffins (*F. cirrhata*); 40.4% in horned puffins (*F. corniculata*; Kolesnikova and Klenova 2011), whereas 66.7% could be correctly classified in 4-day-old razorbill chicks in this study. Further support for weaker selection of individual chick discrimination in semi-precocial species was shown in cross-fostering experiments of Atlantic puffins (*F. arctica*), where parents fed unrelated chicks at the same rate even when the unrelated chick was a different age (+/-8 days) than their own (Hudson 1979, Harris 1983). By contrast, calls of precocial ancient murrelet (*Synthliboramphus antiquus*) chicks at 2 to 3 days old showed high classification (84%) of acoustic signatures to individual chicks (Kolesnikova and Klenova 2011), possibly reflecting high selection for individual recognition as they fledge within three days of hatching and are provisioned at sea for at least one month (Sealy 1976, Jones *et al.* 1987, Gaston 1990). Similar to razorbills, little auks (or dovebies) have similar breeding environments and are provisioned by the male parent at sea post-fledging, and chick vocalisations held

individually distinct information within the first week post-hatch (Kidawa *et al.* 2023); however, results of cross-fostering experiments and evidence of alloparental feeding suggest a lack of strong parental discrimination of chicks in this species (Kidawa *et al.* 2023, Syposz *et al.* 2024). Although quantitative comparisons of classification success across species are likely affected by different recording and measurement methods of acoustic parameters and, thus, require cautious interpretation (Linhart *et al.* 2019, Stowell *et al.* 2019), these qualitative comparisons appear to reflect different ecological pressures for individual recognition.

Across the 18 measured parameters, 11 in the early stage and 14 in the late stage showed potential for individual coding (i.e. PIC values > 1). Based on the increasing PIC values of temporal acoustic parameters between early and late nestling stages, potential for individual coding of these temporal signals appear to become stronger over the short nestling period. Among these parameters, temporal energy distribution, duration, third quartile time and interquartile time had high PIC values (> 2) in the late stage. This finding supports the development of individual-specific temporal acoustic signatures in their departure calls, as predicted. High PIC values for temporal acoustic parameters may allow individual-specific acoustic signatures to persist across longer distances, which would be adaptive for communication and identification at sea during fledging and provisioning at sea (Morton 1975, Falls 1982, Larsen and Radford 2018). In support, signalling identity through temporal variations has been documented in chicks of ancient murrelets (Jones *et al.* 1987, Kolesnikova and Klenova 2011) and little auks (Kidawa *et al.* 2023). Selection favoring coding identity through temporal acoustic modulations has also been supported in adult seabirds (Robisson *et al.* 1993, Lefevre *et al.* 2001, Favaro *et al.* 2015, Bowmaker-Falconer *et al.* 2022), and suggested in adult razorbills (Bédard 1969). Although not quantified in this study, repetition and counter-calling observed

between razorbill chicks and male parents (Insley *et al.* 2003) presumably increases the correct identification of chicks by reducing confusion and re-affirming identity in noisy soundscapes (Shannon and Weaver 1949, Jouventin *et al.* 1999).

Although the highest PICs were measured in the temporal domain, departure calls also had the potential to encode identity information within spectral and energy-related parameters. The spreading of individual information among multiple domains may allow for redundancy in the signal under varying conditions (Shannon and Weaver 1949) and has been documented in adult African penguins (*Spheniscus demersus*; Favaro *et al.* 2015) and little auks (Osiecka *et al.* 2024b). Additionally, the parent calls of king penguin (*Aptenodytes patagonicus*) held highly redundant information in both time and frequency domains, and chicks could reliably identify their parent's call within less than 6% of the call's duration (Jouventin *et al.* 1999). As the soundscape experienced by razorbill parent-chick pairs is presumably highly variable, with calls likely refracting within rock crevices on the colony, scattered by wave action at sea, and masked by wind and other species in both environments, it may be adaptive to signal identity across several parameters to allow some identity information to persist in these different environments both in the early and late nestling stages (Morton 1975, Wiley and Richards 1978, Falls 1982, Larsen and Radford 2018). Likewise, acoustic parameters with minimal potential for encoding identity in departure calls and low within-individual variation (e.g., skewness and kurtosis; Table S3.1) may indicate morphological constraints in sound production (Favaro *et al.* 2023), and/or environmental selection pressures that maintain stereotypy across chicks in order to communicate effectively under the typically experienced range of environmental conditions (Falls 1982, Martin *et al.* 2021). Acoustic parameters that predominantly varied within individuals (e.g., mean peak frequency; Table S3.1) may signal context-specific information,

such as hunger (Rector *et al.* 2014, Klenova 2015), stress (Osiecka *et al.* 2024a), or motivational state (Briefer 2020b, Gémard *et al.* 2021, Osiecka *et al.* 2023, Kidawa *et al.* 2023), also resulting in a low potential to code identity.

Conclusion

This study provides insight into the ontogeny of individual acoustic signatures in razorbill chick departure calls, and the mechanisms encoding individual identity in the complex environments in which they live. These findings likely reflect the adaptations of acoustic signals to environmental selection pressures chicks experience at the colony, when fledging and when provisioned at sea. Although we were unable to quantify the number of chicks that may be discriminated by parents based on the variability held in departure calls, as done in other studies (e.g., Osiecka *et al.* 2024), or to quantitatively compare among chicks of different alcid species (Beecher's statistic; Linhart *et al.* 2019) due to the low number of chicks recorded, this study added to our limited understanding of seabird communication both at the colony and at sea. Our findings may be particularly relevant to mitigating the negative impacts of offshore wind energy development in coastal Canada and the USA, where razorbills and other alcids overwinter (Runnells *et al.* 2024). For example, due to the importance of chick-male parent communication at sea during the approximate one-month period of parental provisioning at sea after fledging (Lavers *et al.* 2020), noise associated with construction and operation of offshore wind turbines could be minimized during this critical period to lessen impacts on parent-chick communication and energetic demands associated with avoidance of these structures (Masden *et al.* 2010, Peschko *et al.* 2020). The long-term impacts of higher background noise associated with wind turbine operations should also be assessed, as noise emitted at a similar frequency as razorbill vocalisations may mask important communication signals (Kunc *et al.* 2016, Duarte *et al.* 2021).

More studies examining the effects of increasing noise pollution caused by turbine construction and operation on seabird communication at sea, however, are needed (Duarte *et al.* 2021).

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Tables

Table 0.1. Description of acoustic parameters measured on razorbill chick departure calls, using the warbleR package (Araya-Salas and Smith-Vidaurre 2017). Measurements of each call were made between 2 and 6 kHz. Units are provided where applicable. Measurements marked with an asterisk (*) indicate acoustic parameters that describe the calls in multiple domains (temporal, spectral, energy), and rough classifications were used to interpret the potential of individual coding across each domain (see Table 3.3).

Parameter	unit	Abbreviation	Description
Temporal			
Duration	s		Length of signal
Median Time	s	time.median	The time at which the time envelope is divided in two time intervals of equal energy
First Quartile Time	s	time.Q25	The time at which the time envelope is divided in two time intervals of 25% and 75% energy respectively
Third Quartile Time	s	time.Q75	The time at which the time envelope is divided in two time intervals of 75% and 25% energy respectively
Interquartile Time Range	s	time.IQR	Time range between 'time.Q25' and 'time.Q75'
Spectral			
Mean Frequency	kHz	meanfreq	The weighted average of the frequency spectrum (i.e. weighted by the amplitude within the supplied band pass)
Standard Deviation of Frequency	kHz	sd	The weighted standard deviation of the frequency spectrum (i.e. weighted by the amplitude within the supplied band pass)
Median Frequency	kHz	freq.median	The frequency at which the frequency spectrum is divided in two frequency intervals of equal energy
First Quartile Frequency	kHz	freq.Q25	The frequency at which the frequency spectrum is divided in two frequency intervals of 25% and 75% energy respectively
Third Quartile Frequency	kHz	freq.Q75	The frequency at which the frequency spectrum is divided in two frequency intervals of 75% and 25% energy respectively
Interquartile Frequency Range	kHz	freq.IQR	Frequency range between 'freq.Q25' and 'freq.Q75'
Skewness		skew	Asymmetry of the frequency spectrum
Kurtosis		kurt	Peakedness of the frequency spectrum
Mean Peak Frequency	kHz	meanpeakf	Frequency with highest energy from the mean frequency spectrum, typically more consistent than peakf in the presence of noise.
Energy			
Spectral Entropy*		sp.ent	Energy distribution of the frequency spectrum. Pure tone ~ 0; noisy ~ 1
Time Entropy*		time.ent	Energy distribution on the time envelope. ~0 means amplitude concentrated in a specific time point, 1 means amplitude equally distributed across time

Spectrographic Entropy*		entropy	Product of time and spectral entropy sp.ent * time.ent
Spectral Flatness*		sfm	Similar to sp.ent (Pure tone ~ 0; noisy ~ 1)

Table 0.2. Classification success of departure calls made by six razorbills during the early (chicks were 3 to 5 days old) and late (chicks were 15 to 19 days old) nestling stage. Classification success (%) was determined using discriminant function analyses with leave-one-out cross-validation for both stages.

	Early Stage							Late Stage							Age in Late Stage	Age at Fledge
	B	C	F	J	N	T	%	B	C	F	J	N	T	%		
B	4	3	2	1	1	0	36.3	8	3	0	1	0	6	44.4	17-18	19
C	3	7	0	1	0	0	63.6	0	18	0	0	0	0	100	18-19	20
F	2	0	8	0	1	0	72.7	0	1	10	3	4	0	55.6	17-18	19
J	0	3	0	7	0	1	63.6	1	0	3	13	1	0	72.2	15-16	16
N	1	0	2	0	8	0	72.7	0	0	2	2	14	0	77.8	16-17	17
T	0	0	0	1	0	10	90.9	5	0	0	0	1	12	66.7	15-16	18

Table 0.3. Potential of individual coding (PIC) values of acoustic parameters measured on departure calls made by razorbill chicks during the early nestling stage (chicks were 3 to 5 days old) and late nestling stage (chicks were 15 to 19 days old). See Table 3.1 for a full description of the acoustic parameters.

Acoustic Parameter	PIC	
	Early	Late
Temporal		
duration	1.367479	2.671876
time.median	1.210625	1.485952
time.Q25	1.027546	1.303754
time.Q75	1.351582	2.202725
time.IQR	1.379756	2.049046
Spectral		
meanfreq	1.015602	1.247141
sd	0.966582	1.174502
freq.median	1.027175	1.093084
freq.Q25	0.940391	1.262873
freq.Q75	0.980485	1.056286
freq.IQR	0.862352	0.984735
skew	0.909277	0.882833
kurt	0.960352	0.922769
meanpeakf	0.983838	0.809914
Energy		
sp.ent	1.146028	1.097811
time.ent	1.469557	3.065196
entropy	1.149101	1.112176
sfm	1.37379	1.205392

Figures

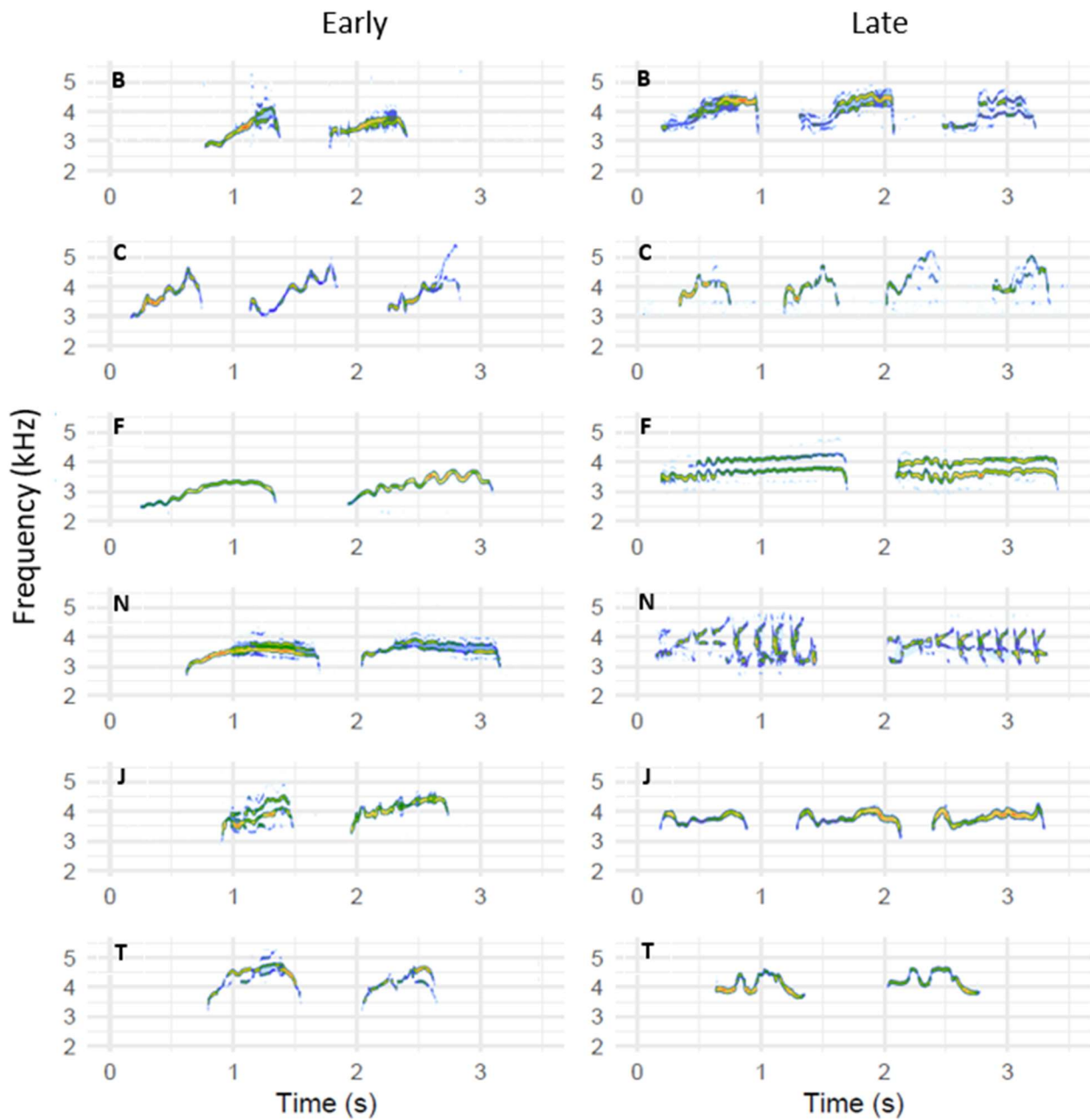


Figure 0.1. Spectrograms of razorbill departure calls when chicks were 3 to 5 days old (early nestling stage) and 15 to 19 days old (late nestling stage). Letters indicate the same chick recorded in both stages. Spectrograms were made using seewave (*Sueur et al. 2008*).

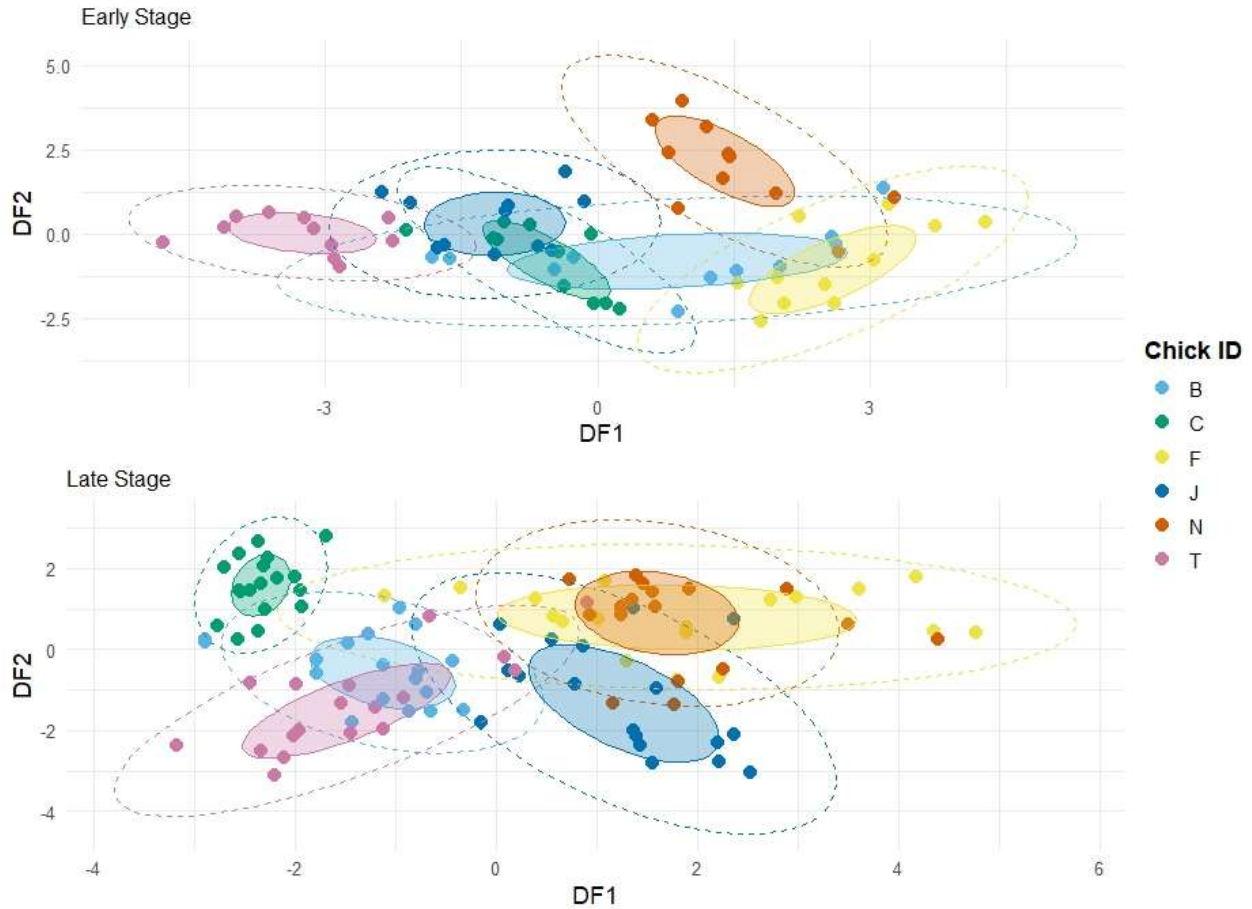


Figure 0.2. Discriminant function analysis conducted on combined acoustic parameters (PCs 1-4) of a random subset of departure calls made during the early (chicks were 3 to 5 days old) and late (chicks were 15 to 19 days old) nestling stages, with 95% (dashed) and 50% (solid) confidence ellipses. The number of calls randomly selected for the DFA was 11 in the early stage and 18 in the late stage.

Supplementary materials

Table S0.1. Mean (SE) of acoustic parameters of razorbill departure calls when chicks were 3 to 5 days old (early nestling stage) and 15 to 19 days old (late nestling stage). Acoustic parameters were calculated using the warbleR package (*Araya-Salas and Smith-Vidaurre 2017*). Letters represent chick ID, and the sample sizes (n) refer to the number of departure calls from each chick used in the Principal Components Analysis for both the early and late nestling stage. See Table 3.1 for a full description of the acoustic parameters.

Acoustic parameter	B		C		F		J		N		T	
	Early n = 48	Late n = 18	Early n = 16	Late n = 26	Early n = 11	Late n = 90	Early n = 39	Late n = 24	Early n = 16	Late n = 62	Early n = 16	Late n = 25
duration	0.80 (0.02)	0.71 (0.02)	0.68 (0.02)	0.51 (0.01)	0.96 (0.06)	1.12 (0.03)	0.91 (0.02)	0.96 (0.02)	1.16 (0.04)	1.12 (0.02)	0.72 (0.03)	0.79 (0.02)
time.median	0.44 (0.01)	0.41 (0.02)	0.32 (0.01)	0.22 (0.01)	0.51 (0.04)	0.50 (0.02)	0.46 (0.02)	0.57 (0.02)	0.56 (0.02)	0.55 (0.01)	0.38 (0.01)	0.43 (0.02)
time.Q25	0.24 (0.01)	0.26 (0.02)	0.15 (0.01)	0.11 (0.00)	0.31 (0.03)	0.25 (0.01)	0.24 (0.01)	0.33 (0.02)	0.28 (0.01)	0.30 (0.01)	0.20 (0.01)	0.24 (0.01)
time.Q75	0.59 (0.01)	0.55 (0.02)	0.50 (0.02)	0.36 (0.01)	0.69 (0.05)	0.78 (0.02)	0.67 (0.02)	0.73 (0.02)	0.84 (0.03)	0.80 (0.02)	0.54 (0.02)	0.62 (0.02)
time.IQR	0.35 (0.01)	0.29 (0.01)	0.34 (0.02)	0.25 (0.01)	0.38 (0.02)	0.53 (0.02)	0.43 (0.02)	0.41 (0.02)	0.56 (0.02)	0.51 (0.01)	0.34 (0.01)	0.38 (0.01)
meanfreq	3.58 (0.04)	3.92 (0.04)	3.80 (0.03)	3.74 (0.02)	3.45 (0.02)	3.73 (0.01)	3.97 (0.03)	3.80 (0.02)	3.73 (0.03)	3.70 (0.02)	4.20 (0.05)	4.14 (0.05)
sd	0.78 (0.02)	0.57 (0.03)	0.70 (0.03)	0.78 (0.01)	0.62 (0.05)	0.60 (0.01)	0.67 (0.01)	0.45 (0.03)	0.86 (0.02)	0.66 (0.01)	0.74 (0.02)	0.51 (0.03)
freq.median	3.53 (0.05)	3.96 (0.06)	3.73 (0.04)	3.86 (0.03)	3.36 (0.03)	3.68 (0.02)	3.98 (0.04)	3.81 (0.03)	3.62 (0.05)	3.68 (0.03)	4.32 (0.06)	4.16 (0.06)
freq.Q25	3.19 (0.06)	3.69 (0.05)	3.45 (0.03)	3.48 (0.04)	3.20 (0.03)	3.53 (0.01)	3.76 (0.04)	3.65 (0.03)	3.33 (0.03)	3.39 (0.03)	4.03 (0.06)	3.94 (0.06)
freq.Q75	3.70 (0.06)	4.15 (0.06)	4.08 (0.04)	4.08 (0.02)	3.48 (0.03)	3.86 (0.02)	4.25 (0.03)	3.93 (0.03)	4.00 (0.07)	3.94 (0.03)	4.58 (0.06)	4.41 (0.05)
freq.IQR	0.51 (0.03)	0.46 (0.05)	0.63 (0.03)	0.60 (0.05)	0.28 (0.02)	0.33 (0.01)	0.49 (0.03)	0.28 (0.03)	0.66 (0.05)	0.56 (0.02)	0.55 (0.05)	0.47 (0.03)
skew	4.76 (0.20)	4.37 (0.30)	4.00 (0.17)	4.55 (0.22)	4.42 (0.29)	4.82 (0.11)	4.29 (0.15)	5.17 (0.23)	4.96 (0.31)	3.78 (0.13)	4.05 (0.21)	4.43 (0.23)
kurt	33.06 (2.65)	28.46 (3.67)	24.53 (2.05)	31.40 (3.10)	27.64 (3.43)	32.75 (1.43)	26.82 (1.98)	37.46 (3.32)	36.81 (3.96)	22.39 (1.42)	24.39 (2.15)	29.48 (3.12)
meanpeakf	3.52 (0.06)	3.91 (0.10)	3.69 (0.06)	3.87 (0.04)	3.37 (0.03)	3.65 (0.02)	3.97 (0.06)	3.81 (0.04)	3.47 (0.06)	3.59 (0.05)	4.39 (0.09)	4.07 (0.08)
sp.ent	0.88 (0.00)	0.85 (0.01)	0.90 (0.01)	0.89 (0.00)	0.84 (0.01)	0.85 (0.00)	0.88 (0.00)	0.80 (0.01)	0.92 (0.01)	0.89 (0.00)	0.89 (0.01)	0.83 (0.01)

time.ent	0.86 (0.00)	0.86 (0.00)	0.86 (0.00)	0.86 (0.00)	0.86 (0.00)	0.86 (0.00)	0.86 (0.00)	0.86 (0.00)	0.86 (0.00)	0.86 (0.00)	0.86 (0.00)	0.86 (0.00)
entropy	0.75 (0.00)	0.73 (0.01)	0.77 (0.01)	0.77 (0.00)	0.72 (0.01)	0.73 (0.00)	0.76 (0.00)	0.69 (0.01)	0.79 (0.01)	0.76 (0.00)	0.77 (0.01)	0.71 (0.01)
sfm	0.41 (0.01)	0.33 (0.02)	0.48 (0.03)	0.46 (0.01)	0.28 (0.04)	0.34 (0.01)	0.41 (0.01)	0.21 (0.03)	0.58 (0.02)	0.39 (0.01)	0.45 (0.02)	0.24 (0.02)

Table S0.2. Principal component analysis (PCA) factor loadings by acoustic parameter for departure calls of razorbill chicks made at 3 to 5 days old (early nestling stage) and 15 to 19 days old (late nestling stage). Acoustic parameters were measured using warbleR (Araya-Salas and Smith-Vidaurre 2017), and descriptions of these measurements are found in Table 3.1. Sample sizes indicating the number of departure calls per chick can be found in Table S3.1.

	Early				Late			
	PC1 (31.22%)	PC2 (29.52%)	PC3 (18.81%)	PC4 (8.55%)	PC1 (33.30%)	PC2 (24.80%)	PC3 (21.09%)	PC4 (9.50%)
duration	0.24318544	0.26163648	-0.2580534	0.12151258	0.1481252	0.3727837	0.2151342	0.0170918
time.median	0.26694086	0.18805491	-0.299369	0.03713471	0.0394089	0.3529557	0.2956127	-0.0446342
time.Q25	0.26340532	0.05187877	-0.3150641	0.02997459	-0.0415421	0.3101091	0.2673128	-0.0805046
time.Q75	0.23213761	0.27192014	-0.276373	0.12314203	0.1122622	0.3697891	0.2827278	-0.0140158
time.IQR	0.13459414	0.33549065	-0.1592269	0.14744052	0.1890108	0.3043087	0.2111471	0.0374261
meanfreq	-0.3578121	0.13631872	-0.2068095	-0.1146449	-0.2361188	-0.1652441	0.3630695	-0.0131449
sd	0.1415745	0.27354625	0.26232258	-0.2390558	0.3090226	-0.2048103	0.0600044	0.3033838
freq.median	-0.3547853	0.11412828	-0.2265308	-0.1220183	-0.2182475	-0.2185523	0.3519266	0.0196534
freq.Q25	-0.3413844	0.04647498	-0.2936175	-0.0749991	-0.3195903	-0.0781345	0.2682194	0.0342349
freq.Q75	-0.3523384	0.17672125	-0.1528146	-0.0992874	-0.1179642	-0.2701122	0.377351	-0.0413609
freq.IQR	-0.0700493	0.28108106	0.25657535	-0.061538	0.2578073	-0.2440844	0.137941	-0.0963496
skew	0.2302716	-0.1036826	-0.1458379	-0.5915505	-0.2251401	0.1261104	-0.1090363	0.5677008
kurt	0.22191114	-0.0764552	-0.1383103	-0.6194123	-0.2005205	0.1100698	-0.0847306	0.5952748
meanpeakf	-0.3136679	0.07227599	-0.26344	-0.1442466	-0.2137751	-0.1758079	0.3063564	0.1721392
sp.ent	-0.0481715	0.37487773	0.23874852	-0.0637482	0.3522782	-0.1742426	0.1413911	0.0753448

time.ent	0.0599652	0.22490389	-0.1920178	0.17201046	0.2208852	0.0858446	0.1264952	0.3126083
entropy	-0.0455469	0.37944797	0.23001742	-0.0576367	0.3550233	-0.167071	0.1442657	0.0875982
sfm	-0.0056329	0.36228186	0.21889108	-0.2241006	0.3309486	-0.1752376	0.0894049	0.2598621

Chapter Four: Conclusions

In this thesis, we aimed to investigate the at-sea behaviour of alcids. First, we described the vocal repertoire of common murrelets at a foraging hotspot and compared defined call types to previously described colony-based repertoires (Ch.2; Lefevre *et al.* 2001, Smith *et al.* 2023) to determine whether murrelets make distinct calls at sea. We found that common murrelets emitted four call types at sea, supported by multivariate analysis and observer agreement. Three of these four call types visually resembled those described at breeding colonies, suggesting that these ubiquitous call types convey important information across both contexts. We observed temporal gradation within and across call types, which may convey context-specific information at sea. We also quantitatively described a novel call type ('eur') emitted at sea that did not visually resemble those described at breeding colonies, and thus, may be unique to the at-sea environment. Second, we described razorbill chick vocalisations to investigate acoustic parameters that encode identity in one call type used in parent-communication at sea, along with the ontogeny of individual acoustic signatures (Ch. 3). We found that razorbill chick departure calls were assigned to individuals during both early and late nestling stages with 66.7% (early) and 69.4% (late) success, although the overall classification success varied among chicks. Temporal features appeared to have the highest potential of individual encoding ($PIC > 1$) in these calls, which may allow for long-distance communication (Morton 1975, Falls 1982), and the PIC of temporal features increased across the nestling period. Together, these findings provide insight into alcid ecology at sea by highlighting the diversity of acoustic signals used by seabirds in this understudied environment and increasing understanding of the acoustic adaptations to specific ecological pressures experienced away from breeding colonies.

This study is important as it is the first to quantitatively investigate the vocal behaviour of common murrelets at sea. The functions of these described at-sea call types, however, remain unclear. By pairing these defined call types with their behavioural and social contexts at sea, we postulated functions related to social cohesion, coordination of foraging activities, and managing competitive interactions among conspecifics. Vocal behaviour emitted from within foraging aggregations may also inadvertently allow for searching birds to cue to foraging opportunities, which may be especially useful when murrelets forage in foggy conditions or at night (Regular *et al.* 2011). We recommend that future research systematically quantifies the variation of acoustic parameters held within defined call types emitted at both colony and at sea, which would represent a key step in understanding the functions of vocalisations at sea. The call types defined here could also be used in audio playback experiments to directly test behavioural responses of murrelets to better infer functions of these vocalisations at sea. Novel miniature animal-borne acoustic recorders affixed to breeding murrelets may also be used to pair call types with more specific behaviours, further elucidating call functions, as done recently in gannets and penguins (Thiebault *et al.* 2016, 2019a, Choi *et al.* 2017, McInnes *et al.* 2020), and may additionally provide activity budget estimations (Thiebault *et al.* 2021).

Similar methods could be used to investigate whether murrelets vocalise underwater. Indeed, recent studies have shown a heightened focus on underwater vocalisations emitted by diving birds (Johansen *et al.* 2016, Hansen *et al.* 2017, Thiebault *et al.* 2019b, Sørensen *et al.* 2020, Larsen *et al.* 2020, McGrew *et al.* 2022, Anderson Hansen *et al.* 2023). The common murrelet is one of very few seabird species that have been shown to react to sound underwater, and auditory thresholds have been derived for both in-air and underwater (Mooney *et al.* 2019, Anderson Hansen *et al.* 2020, 2023, Smith *et al.* 2023). As murrelets face similar foraging

environments as penguins, who vocalise underwater while hunting prey and coordinating group foraging (Choi *et al.* 2017, Thiebault *et al.* 2019a, McInnes *et al.* 2020), they may have similarly evolved underwater communication. This presents a fascinating and important area of study, especially considering increasing anthropogenic noise at sea due to shipping traffic (Aulanier *et al.* 2017, Possenti *et al.* 2024), seismic surveys (Pichegru *et al.* 2017, Merchant *et al.* 2020), and the construction and operation of resource extraction infrastructure (Mooney *et al.* 2014, Duarte *et al.* 2021).

In razorbills, parental discrimination of chick departure calls appears to develop approximately ten days after the chick hatches (Ingold 1973, Insley *et al.* 2003); however, we found individual-specific call signatures in razorbill chick vocalisations as young as three days old. This finding was not expected and may indicate a difference between a chick's ability to signal individually distinct information and the male parent's ability to recognize their chicks' call or that the male parent does not behaviourally respond to their chick's call earlier relative to later in nestling development (Beecher 1991). This study quantitatively described the presence and ontogeny of individual signatures present in razorbill chick vocalisations, adding to our limited understanding of seabird communication adapted for the ocean soundscape. However, due to the low number of chicks recorded, we were unable to quantify the number of chicks that may be discriminated by parents based on the observed variability in departure calls (e.g., Osiecka *et al.* 2024), and quantitatively compare among other alcid chick species (Linhart *et al.* 2019). We recommend that future studies increase the number of chicks recorded and number of calls per chick included in the analysis, the latter of which may be needed to increase understanding of the variation of identity signals between early and late nestling stages. After razorbill chicks fledge, the transition of their vocalisations to adult characteristics also is not well-understood, although

first-winter razorbills were described to “peep” (Carboneras 1988), and thus, may sound more like nestlings than adults during the first winter (Lavers *et al.* 2020). In semi-precocial alcids, the transition from chick to adult vocalisations appears to develop in a jump-like manner after the chick fledge date (Klenova and Kolesnikova 2013). Investigating the transition into adult vocalisations of precocial species and species with intermediate development strategies (murre and razorbills) may reflect unique transitions, as they maintain contact with one or two parents for a longer period at sea.

Throughout this thesis, we refer to past studies to identify and qualitatively compare call types, allowing for a better understanding of vocal behaviour in different contexts (in Ch. 2) and compare our findings with those of historical studies in other species (in Ch.2 and Ch. 3). However, our comparisons are limited due to a lack of information regarding the variation held within defined call types described at colonies and limited or absent recordings of the specific call types. To allow for quantitative comparisons among species’ repertoires and an increased understanding of context-specific variation, we recommend that future publications provide multiple spectrograms of each call type within manuscripts and provide access to multiple call clips (for both discrete and graded call types) that display their variability in supplementary material to allow for quantitative comparisons among studies.

Management Implications

The study of vocal behaviour in seabirds at sea addresses large ecological knowledge gaps, and findings presented in this thesis can be applied in the context of seabird monitoring for management. For example, the murre vocalisations described in this thesis could be monitored using aerial autonomous recording units (ARUs) deployed at sea in known over-wintering areas (e.g., Runnells *et al.* 2024) to quantify inter-annual variation in the presence and relative

abundance of murre. Additionally, ARUs could be deployed in other potential high-use areas to identify critical foraging and overwintering regions. Identifying and monitoring this critical habitat would provide a list of target areas to mitigate negative human-wildlife interactions without requiring costly ship-based observations and tracking devices, while reducing human disturbance (Laiolo *et al.* 2007, Shonfield and Bayne 2017). In particular, acoustic monitoring in coastal Newfoundland during the fall could indicate areas where hunting pressure of murre is high during the annual ‘turr hunt’ (Canadian Wildlife Service 2022). The proportion of specific call types emitted by murre and their acoustic parameters could also provide important information related to the behavioural states and contexts experienced by murre in these understudied areas (Teixeira *et al.* 2019, Lewis *et al.* 2021).

Finally, there is a heightened focus on the negative impacts of increasingly noisy ocean soundscapes due to transportation, resource exploration, and infrastructure development (Kunc *et al.* 2016), but quantitative studies on the impacts to seabirds are lacking (Duarte *et al.* 2021, Affatati and Camerlenghi 2023). Murre and other alcids are known to detect and avoid anthropogenic noise (Mooney *et al.* 2019, 2020, Anderson Hansen *et al.* 2020, 2023, Smith *et al.* 2023a), and consequently may be displaced from important foraging areas (Masden *et al.* 2010, Pichegru *et al.* 2017), incurring additional energetic costs. For example, although offshore wind energy production provides many environmental benefits, seabirds are generally expected to be displaced away from short-term construction activities of offshore wind turbines and possibly their long-term operation. Knowledge of seabird vocal behaviour at sea in conjunction with mooring ARUs at these development sites before and after development begins, would provide insight into whether, and how, seabirds are negatively impacted (Mooney *et al.* 2014). Due to the importance of razorbill and murre chick-male parent communication at sea during the

approximate one-month period of parental provisioning at sea after fledging (Lavers et al. 2020, Ainley et al. 2021), noise associated with construction and operation of offshore wind turbines could be minimized during this critical period to lessen impacts on parent-chick communication and energetic demands associated with avoidance of these structures (Masden et al. 2010, Peschko et al. 2020). The study of seabird acoustics at sea also provides insight into the long-term impacts of higher background noise associated with wind turbine operations, as these critical communication signals may be lost (Kunc et al. 2016, Duarte et al. 2021).

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