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Bearded seal vocalisations across seasons and habitat types in Svalbard (Norway)

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Samuel Martínez Llobet

BIO-3950 Master's thesis in Biology, August 2019

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Front photo: Bearded seal hauling out in Svalbard

Preface

This thesis has been written as an article for submission to the journal "Polar Biology". The manuscript has thus been prepared according to the author guidelines for this journal. The figures and their captions were held together for a better visualisation of the data.

I want to thank Kit Kovacs for giving me the opportunity to discover the fascinating world of acoustics of marine mammals, as she first placed her trust on me and "let me in" in this fantastic institution and family which is the Norwegian Polar Institute. She was inspiring for me during the whole period. I want to thank Christian Lydersen as well for his fantastic attitude towards me and the motivation he inspired me in key moments. Thanks to Rolf Ims for projecting his calmed wisdom and experience in busy moments. Together they have provided me with valuable support and knowledge.

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Thanks very much to my family for cultivating my love to marine mammals and biology since I have memory. I would never have done this work without that passion. Thanks for all the sacrifice that my parents have done and have encouraged me to do. My friends are always a reason to smile and continue to walk in this mysterious and exciting path called life.

Contents

Abstract

Male bearded seals use vocal displays to attract females and compete with other males during the mating period, making it possible to monitor breeding populations using passive acoustic monitoring (PAM). This study analysed year-round acoustic data from underwater recorders at three sites with different environmental conditions in Svalbard (Norway). Male bearded seals vocalised for an extended period at the drift-ice site (Atwain; January-July), while the vocal season was shorter at the fast-ice site (Rijpfjorden; February-June) and shortest at a site where a dramatic reduction in sea ice cover has occurred (Kongsfjorden; April-June). Generalised Additive Models showed marked seasonal segregation in the use of different trill call types at Atwain where call rates reached 400 per h, with long trills dominating during the study period over step and sweep trills. Modest seasonal segregation was seen at Rijpfjorden, where call rates reached 300 per h and no seasonal segregation in trill types occurred in Kongsfjorden (peak call rate 80 per h). Sea ice cover was available throughout the vocal season at Atwain and Rijpfjorden, while at Kongsfjorden there was a mismatch between the peak in vocal activity (May-June) and the time when ice was present (until April). Some call types might be preferentially used if their properties make them more suitable for attracting females in certain environments. This study provided novel information about vocalising male bearded seals at sites with different environmental conditions in Svalbard and confirmed that PAM is a useful tool for studying this species in a warming Arctic.

Keywords Arctic · *Erignathus barbatus* · Mating period · Passive acoustic monitoring · Trill · Sea ice

Introduction

Bearded seals (*Erignathus barbatus*) are the largest phocid seal living in the Arctic. This species has a circumpolar distribution, preferentially occupying areas with drifting pack-ice over shallow shelf waters (Burns 1981; Kovacs 2018). They are primarily benthic foragers, though they have been reported to feed on a variety of pelagic organisms in some parts of their range (e.g. Hjelset et al. 1999). During the winter, bearded seals tend to choose areas with polynyas, or places where the occurrence of flaw leads is recurrent over years, and avoid areas with heavy concentrations of ice (Kovacs 2018). In some parts of their range, bearded seals maintain a close association with drifting sea ice year-round (Cameron et al. 2018). In other parts of their range, bearded seals use ice that has calved from glacier fronts during the summer when annually formed ice is not available (Lydersen et al. 2014), or even use land-based haul-out areas in regions that do not have ice cover in summer (Merkel et al. 2013; Kovacs 2018). During spring, female bearded seals give birth on ice floes or along fast-ice edges, with the timing somewhat variable across the range of this species (between mid-March and early-May; Burns 1981; Kovacs et al. 1996). Mothers nurse their pups for approximately 24 days (Kovacs et al. 1996; Lydersen and Kovacs 1999). During the lactation period, female bearded seals continue to forage, with their pups accompanying them after they are a few weeks old (Lydersen et al. 1994; Krafft et al. 2000). Mating in bearded seals takes place in the water; mating is assumed to take place towards the end of the lactation period (Van Parijs et al. 2001).

During the breeding season, adult male bearded seals produce elaborate underwater vocalisations (e.g. Cleator et al. 1989; Van Parijs et al. 2001; Davies et al. 2006). There is considerable geographical variation in vocal repertoire among populations in Alaska, the Western Canadian Arctic, the Canadian High Arctic and Svalbard (Risch et al. 2007). Differences in vocal phenology also exist. Bearded seals vocalise year-round in Beaufort Sea (MacIntyre et al. 2013), whereas they are more seasonally restricted in Svalbard, vocalising from February to July (Van Parijs et al. 2001; Parisi et al. 2017). Some call types like the moan, a short duration call of low to mid-frequency, seem to be widely used also outside the mating season, but proportional use of these shorter calls seems to decrease in some locations towards the peak of the mating period (Frouin-Mouy et al. 2016). Trills are the dominating call type during the months that mating takes place (Van Parijs et al. 2001; Risch et al. 2007; Frouin-

Mouy et al. 2016). Trill calls are longer in duration, occur across a wider frequency band compared to moans and are assumed to advertise the breeding condition of males (Burns 1981; Cleator et al. 1989). The use of vocalisations such as trills, with highly stereotyped, narrowband frequency calls, high minimum frequencies, long duration and redundancy in the display repertoire, reduces the masking of these calls from other competitors and the background noise, increasing the opportunities of attracting mates (Cleator et al. 1989; Terhune 1999; Rogers 2003; Stirling and Thomas 2003). These longer call types have been used as a proxy to estimate the duration of the mating season both in Svalbard and in northeastern Chukchi Sea (Van Parijs et al. 2001; Frouin-Mouy et al. 2016). Through the study of trill vocalisations, Van Parijs et al. (2001, 2003, 2004) demonstrated that male bearded seals used different breeding strategies and that mating tactics were strongly influenced by sea ice conditions. Some males maintained underwater territories with little overlap under variable ice conditions, returning to the same location year after year, while other males patrolled larger areas and were not present when ice was extensive (>60 %). These territorial males produced significantly longer trills than males that displayed a roaming strategy. Extensive cover of fast-ice prevented territorial males from maintaining their territories and they did not vocalise under this type of ice. The territorial tactic was dominant in Svalbard (Van Parijs et al. 2003). However, In Alaska, territorial males produced shorter trill vocalisations than roaming males and the later strategy was the dominant tactic in this area, where ice conditions were more unstable (Van Parijs and Clark 2006). Differences in ice conditions likely drive the different mating tactics chosen by vocalising males in the different Arctic regions.

Reduction in the geographic and seasonal extent of sea ice in the Arctic is a concern for all ice-breeding seals including bearded seals (Kovacs and Lydersen 2008; Moore and Huntington 2008; Kovacs et al. 2011). Less sea ice will likely result in higher energy expenditure, poorer body condition and reduced recruitment (Moore and Huntington 2008; Kovacs et al. 2011; MacIntyre et al. 2013), but the lack of base line data on bearded seal abundance and trends in population sizes will make it challenging to detect changes for this species (Laidre et al. 2015).

Acoustic monitoring has proven to be a useful tool to study vocal marine mammal populations. Acoustic studies have increased knowledge about the distribution, habitat use and phenologies of different species, as well as the relationship of different species with environmental variables and anthropogenic activities (e.g. Moore et al. 2012; Stafford et al. 2012; Reeves et al. 2014; Ahonen et al. 2019). Previous studies on acoustic behaviour of Svalbard's bearded seals have all been conducted in Kongsfjorden (Fig.1) (Van Parijs et al. 2001, 2003, 2004; Parisi et al. 2017; de Vincenzi et al. 2019). These research efforts have contributed to a better understanding of the vocal biology of this species and provide a base line for future monitoring efforts. However, Kongsfjorden represents only one location in Svalbard where bearded seals reproduce and this location has experienced large changes in hydrological conditions over the last decades, with markedly reduced sea ice cover being one consequence of these changes. Comparative studies involving other locations within the archipelago are likely to be insightful regarding how bearded seals might be responding to climate change on a regional scale. In this study, bearded seal acoustic data collected at three Passive Acoustic Monitoring (PAM) sites, representing a variety of markedly different ice conditions around the Svalbard Archipelago, were explored. The phenology of the vocal behaviour was studied with the aim of describing how bearded seals are responding to reduced sea ice availability in western Svalbard compared to the northeastern parts of the archipelago, which are less impacted to date by warming. Additionally, bearded seal acoustic data from a third site provides information regarding the presence of bearded seals and the phenology of trill production in a drift-ice environment north of Svalbard.

Material and Methods

Study area and acoustic data collection

The study area was located between 78°- 81° north and 11°-32° east. At each of three locations (Fig. 1), an Autonomous Underwater Recorder for Acoustic Listening (AURAL; M2Multi-Électronique Inc.; system sensitivity of -155dB re 1 V/µPa) was deployed on an oceanographic mooring in order to collect year-round underwater acoustic data. These locations represent a gradient of environmental conditions (Cottier et al. 2007; Wassman et al. 2015; Renner et al. 2018). The first mooring was located in the middle of Kongsfjorden, a fjord situated in the northwest of the Svalbard Archipelago (Fig. 1). This fjord has undergone large changes in ice conditions in recent years, with an increase in both the volume and temperature of warm Atlantic

Water carried along the coast in the West Spitsbergen Current, which comes up onto the shelf following strong northeastly winds (Cottier et al. 2007; Blanchet et al. 2015; Tverberg et al. 2019). The second mooring was placed in the outer part of Rijpfjorden, a fjord situated on the north shore of Nordaustlandet (Fig. 1). The water masses in this fjord are less influenced by Atlantic Water compared to Kongsfjorden, resulting in this fjord being a more typical Arctic fjord (Wallace et al. 2010). The third mooring was situated at edge of the continental shelf north of the Svalbard Archipelago (Fig. 1). This mooring is part of an instrumentation platform that provides data for the A-TWAIN project (https://www.npolar.no/en/projects/a-twain/), whose aim is studying the Atlantic Water inflow to the Arctic Ocean north of Svalbard; henceforth this site will be referred to as Atwain in this study.

The data collection period in this study extended from September 2014 to August 2016 encompassing one year of data from each location. In Kongsfjorden, data were recorded from 25 September 2014 to 15 August 2015 with 25% duty cycle (the 15 first minutes of every hour). In Rijpfjorden, data were recorded from 20 September 2015 until 26 August of 2016, with 20% duty cycle (the 12 first minutes of every hour). For Atwain, the recording period started 20 September 2015 and extended until 31 August 2016. This recorder had a 20% duty cycle, similar to Rijpfjorden, recording the first 12 minutes of every hour. Sample rate for all instruments was 32768 Hz. Full deployment details for each location are presented in Table 1.

Acoustic data and bearded seal call detections

Spectrograms of each acoustic file were generated using the bioacoustics software Ishmael (version 3.0) in order to screen for bearded seal vocalisations (10-6000 Hz, FFT 20148/4096, 75% overlap, Hanning window). This study follows the most recent classification of the underwater vocal repertoire of bearded seals in Svalbard (Parisi et al. 2017), which recognizes nine call types. Vocal activity was noted in two ways. First, any bearded seal vocalisation within the nine different call types was explored to document vocal presence. Every one hour time bin was scored in a binary manner; positive detections were assigned a (1) and an absence of calling was assigned a (0). Secondly, three selected call types - long trill, step trill and sweep trill (Fig. 2) were scored to be used in the study of breeding phenology. These calls were chosen because they have a long duration (a feature characterising important call types during mating; Van Parijs et al. 2001; Frouin-Mouy et al. 2016) and they were used frequently by bearded seals in

Kongsfjorden, especially during late spring (Parisi et al. 2017), presumably for mating purposes. Long and sweep trill calls were used previously in other studies of the vocal behaviour of bearded seals (Van Parijs et al. 2001, Risch et al. 2007) although the sweep is referred to in this study as a sweep trill, following Parisi et al. (2017). In order to examine the phenology of these three call types during the breeding period, a subset of the data was selected for analysis, extending from 1 February to 31 July. The variables "long trill", "step trill", "sweep trill" and "trill" (the later as the sum of the three calls, hereafter referred to as overall trill activity) were counted to obtain information of seasonal trends in vocal patterns.

Data Analysis

<u>Seasonality of the different call types and vocal activity per location</u>

In order to test whether there were differences in vocal activity rates throughout the mating season of bearded seals, a Generalised Additive Model (GAM) with the response variable "trills" and a predictor variable "week" was run for each location. "Week" was included as a smooth term (thin plate spline) to allow the response variable to fluctuate over the selected period. To test whether there was differential use of the three call types through the mating season, a GAM model with the response variable "calls" (number of calls per day) and the predictor variables "week" and "type" (the later corresponding to call type) was run for each location. The variable "week" was once again included as a smooth term (thin plate spline) with "type" included as a "by" variable within the smooth term, so that a separate smooth term was made for each call type. The distribution family used for these models was Tweedie (Tweedie 1984). Tweedie is a flexible distribution that can be used for many different types of count data. It is also used as an alternative to the zero-inflated distribution for count data (Wood et al. 2016). Tweedie behaves like a Poisson distribution if the P parameter equals one, or it can adopt a Gamma distribution when P equals two. When using Tweedie in GAMs, the parameter P is automatically estimated by the model. After running the models, the function "predict.gam" (R package "mgcv 1.8-28."; Wood et al. 2016) was used to predict the overall trill vocalisation rate and to predict and compare the vocalisation rates of the three different trill calls. For model validation purposes, the residuals were plotted versus the fitted values and compared to those of other possible models (e.g. Poisson distribution, negative binomial distribution). The selected distribution dealt best with the zero-inflated and over-dispersed data, as demonstrated by the distribution of the residuals when using the Tweedie distribution.

Seasonality of the vocal activity per call type - comparison across locations

In order to compare vocal activity across locations with different recording times, as well as to test whether some call types were more or less abundant in the different locations, a GAM was run for each call type. In this case, four different models were run, three for the different call types and one for the overall vocal activity (containing the variables “long trill”, “step trill”, “sweep trill” and “trill”). These were the input response variables for the different models, which had the predictor variable “week” included as a thin-plate spline smooth term and “location” included as a “by” factor variable in each smooth term. Because the sampling rate was 12 minutes per h for Rijpfjorden and Atwain, and 15 minutes per h for Kongsfjorden, an offset term with the variable “time” was introduced in the model, which accounted for the difference in sampling rates when predicting vocal rates. The recording period (variable “period”, February-July 2015 for Kongsfjorden and February-July 2016 for Rijpfjorden and Atwain) was not included as a random effect because having only one year of data for each location could cause the model to confound the variables “location” and “period”. The distribution family selected for this model was again Tweedie. After running the models, the function “predict.gam” (Wood et al. 2016) was used to predict and compare the vocalisation rates of the three different trill calls and the overall trill vocalisation by location. Model validation was conducted similarly to the model described above.

Ice cover data

Sea ice data was obtained from the Norwegian Meteorological Institute (https://www. http://polarview.met.no) and used to calculate daily ice cover for each study site (spatial resolution of ~50 m). Most of bearded seal vocalisations are detected within a radius of 5 km from the recorder, though in very calm, quiet conditions up to 15 % of calls can be detected from as far away as 20 km (Cleator et al. 1989; MacIntyre et al. 2013). To study the ice cover in the area where bearded seal vocalisations occurred, 1,000 points were randomly generated (Gaussian distribution) within a radius of 20 km from the recorder at each location. Land points (Kongsfjorden, Rijpfjorden) were eliminated, as well as points falling in adjacent fjords or those outside a straight line with the recorder. The rest of the points were used to extract the ice cover information from a shapefile for each date over the data collection period (function "over" from R package "sp 1.3-1"; Bivand et al. 2013). If ice cover information was not available for a given date, the closest day was selected as being representative. Plots by location were generated in order to visualise and compare the ice cover with the vocal activity through the season (encompassing the February-July period). The ice cover was expressed as the proportion of the area covered by different ice concentration percentages (>10%, >40%, >70%, >90%, Fast-Ice). Plots of ice cover and trill vocalisations per day were generated to visualise and compare the ice cover and the vocal activity during the study period.

Results

Annual vocal presence

A total of 5260 h were screened for bearded seal vocalisations at the three study sites. In Kongsfjorden, vocal presence was detected for the first time towards the end of April 2015 (Fig. 3a). A pronounced increase in the hours of vocal presence per day occurred in the following weeks thereafter. A constant vocal presence, with calls occurring 24 h per day was documented from about mid-May until mid-June, after which the hours with calling dropped suddenly around 20 June 2015. No bearded seal signals were detected after the end of June. In Rijpfjorden, vocal presence was first detected at the start of February 2016 (Fig. 3b). By the end of March, bearded seal vocal presence was constant and remained so until the end of June, when it suddenly decreased to zero. At the northernmost recorder (Atwain), vocal presence was detected from the beginning of January 2016 (Fig. 3c). The number of hours per day with vocal presence of bearded seals increased towards the end of February 2016, with constant vocalisation (24 h per day) starting around the end of March. This constant vocal presence lasted until mid-July 2016, when the number of hours per day with vocal presence suddenly decreased to zero. Overall, Kongsfjorden had the shortest period with bearded seal vocalisations, and had the steepest increase in hours with vocal presence. The period of high vocal activity lasted around four months in Rijpfjorden, where the transition from days with a few hours of presence to constant vocal presence (24 h per day) was more protracted. The high vocal activity period was the longest at Atwain, where bearded seals vocalised almost hourly for approximately five months.

The transition from a few hours per day to 24 h per day of vocal presence was the longest among the three sites.

Seasonal variation in trill vocalisations

Kongsfjorden had the lowest call rates, in terms of trill vocalisations per h (Fig. 4a). Trills were performed from week 12 to week 21, with peak calling occurring in week 18 (first week of June). Rijpfjorden had much higher call rates than Kongsfjorden and a much longer season during which trills were produced (Fig. 4b). Here, trill vocalisations were performed from week 7 to 21 (mid-March to late-June). A sharp increase in the vocal rate occurred during April, followed by a progressive decline during May and June. A peak in calling rates in excess of 300 trills per h occurred in weeks 13 and 14 (end of April until early-May). Atwain had the longest season, with trills being produced from week 8 to week 24 (Fig. 4c). This site also had the highest trill call rates with more than 300 calls per h for an extended period from late-April through until June. Trill calls continued to be detected regularly until July, after which they declined sharply.

The relative use of the three different types of trills varied seasonally during the study period (Fig. 5). Kongsfjorden showed no differences in call rates among the trill types (Fig. 5a). Rijpfjorden showed minor differences among call types by month; the sweep trill was used more in April, and somewhat less in May and June compared to step trills or long trills (Fig. 5b). Atwain showed clear differences in use of the different trill types, with more long trills per h, and less sweep trills through the study period (Fig. 5c). All three trill types occurred in most weeks at all three sites, though only one or two trill types occasionally dominated whole weeks early or late in the season at all sites (Fig. 6).

Seasonality of the different call types and vocal activity

All three trill types showed a similar temporal peak in Kongsfjorden, and none of them had significantly higher rates over the study period (Fig. 7; SF 1a). In Rijpfjorden, the three trill types had somewhat different temporal patterns (Fig. 7; SF 1b) During April, sweep trill was the most common, although it did not have a significantly higher call rate than the long trill. Both sweep and long trills were significantly higher than the step trill in April. Long trill was the most common call type during May, while the number of sweep trills sharply declined during this month. Long and step trills had higher median values than sweep trill for the rest of the season. The overall trill activity increased sharply in April, but the high rates of long and step trills caused the period of decline to be delayed until late-June, being more gradual than in Kongsfjorden (Fig. 7d). Atwain showed a strong segregation in trill type phenology (Fig. 7; SF 1c). All trill types increased rapidly through April, with no significant difference among the three types found in this month. Sweep trill declined steadily thereafter and was always the least numerous trill type at Atwain. Long and step trills increased steadily through April and May with a sharp peak in early-June. Thereafter a sharp decline was observed until the end of the vocal period in mid-July. The difference in vocal rates per day among call types was high at Atwain, with long trill being the most abundant vocalisation. A bimodal distribution of the vocal phenology was seen at Atwain, with the first peak in late-April and a second peak in early-June. Therefore, different temporal distributions of maximum vocal activity were observed between Kongsfjorden (June), Rijpfjorden (April) and Atwain (April and June) (Fig. 7d). Overall, the month with the highest median number of vocalisations per day was May when data from all three sites were combined.

Vocalisations and sea ice cover

Kongsfjorden had the least ice cover among the three study sites, with most of the study area having only 10 to 40 % ice cover through the months when bearded seals were vocalising (Fig. 8a). Although there was some ice in the area until the beginning of April, vocalisations in Kongsfjorden started when the ice cover had almost completely disappeared. Rijpfjorden had 10 to 40 % ice cover prior to April, but in this area vocalisations took place when ice cover was 70 to 90 % (Fig. 8b). The decrease in vocal rates followed the break-up of the fast-ice and the reduction of the ice cover overall; sporadic increases in calling after the April peak matched temporary increases in ice cover (May and June). Vocalisations stopped soon after the ice concentration was below 10% for most of the area. Ice was present in Atwain for the complete vocalising period (Fig. 8c). The variations observed in the ice cover reflect the drifting nature of the sea ice in this area. The vocal increase matched the increase of sea ice cover in the area in the beginning of April. However, high concentrations of ice were detected before this time and seals vocalised at low rates during March when there was no sea ice at Atwain. The first peak in vocal activity coincided with ice cover over 70% and some reductions in vocal counts were found when there was a very high ice concentration (>90%). After the period of vocalisations stopped, ice cover of 40 to 70% remained in this area.

Discussion

PAM is an important tool for gaining information about marine mammals in logistically challenging environments (e.g. Stafford et al. 2012; Ahonen et al. 2019). This study provided year-round acoustic information on bearded seal vocalisations from three locations in Svalbard that represent a gradient of environmental conditions, including a fjord that has experienced strong Atlantification over the past decade (Kongsfjorden), a more typical Arctic fjord (Rijpfjorden) and a drift-ice environment (Atwain). The latter two locations have never been studied acoustically, while earlier studies of bearded seals have taken place in Kongsfjorden (Van Parijs et al. 2001, 2003, 2004; Parisi et al. 2017; de Vincenzi et al. 2019). Furthermore, Atwain is the northernmost location where bearded seal vocalisations have been obtained.

The vocal repertoire of bearded seals is characterised by narrowband and stereotyped calls. Vocalisations emitted by male bearded seals during the mating period are mainly long duration trills that shift downward in frequency, which males repeat in displays during the mating period (e.g. Cleator et al. 1989, Van Parijs et al. 2001). The duration of the calls, and perhaps their main frequencies might provide information to females and to other males regarding the size, social rank, fitness level or other traits of the vocalising male (Owings and Morton 1998; Van Parijs et al. 2003; Taylor and Reby 2010; Charlton and Reby 2016). Bearded seals were vocally present at all three sites, producing species-typical sounds across the region. There were marked differences in the length of calling periods, the timing of peak calling rates, the average number of calls during the peak periods and the type of trill calls produced in the different environments. However, a period with a constant presence (24 h per day) of trill vocalisations, which are assumed to be mate attraction/territorial advertisement calls, did occur at all three locations suggesting that bearded seals bred at all of the study sites.

The Atwain drift-ice site had the longest seasonal presence of bearded seals vocalisations, with detections from January until mid-July and a 24 h presence from the end of March until the end of the vocal period. These results are similar to those reported from drift-ice environments of the Chukchi and Beaufort seas in Alaska, although at these Pacific Arctic sites, vocal activity continued throughout the year (MacIntyre et al. 2015). In Rijpfjorden, bearded seals had a vocal presence from February until June, and a 24 h presence from March until the end of June. Kongsfjorden had the shortest period of bearded seal vocal presence among the three locations; at this site bearded seals were detected from late-April until late-June, with a constant vocal presence lasting approximately half of that period, from mid-May until mid-June. A recent study of bearded seal vocal behaviour in Kongsfjorden reported vocalisations from February until June during the same year as the present study (de Vincenzi et al. 2019). The de Vincenzi et al. (2019) study used two recording locations within the fjord. One recorder, which reported vocalisations in only May and June, was placed in the outer part of the fjord. The second recorder, which detected vocalisations from February until early-June, was placed close to the Kronebreen glacier front in the inner part of Kongsfjorden. The current study, which used a site intermediate between the de Vincenzi et al. (2019) recording locations, was not able to detect a portion of the vocal activity occurring close to the glacier fronts. This could be due to the presence of islands between the glacier fronts and the recorder's location in the current study, which may have served as a barrier to sound propagation. A study carried out in Kongsfjorden before the strong Atlantification of this fjord took place, reported bearded seal vocalisations occurring from April until July (Van Parijs et al. 2001). However, this study only commenced regular recordings in April, so the differences in seasonal pattern among the available studies for this area cannot be interpreted as a temporal shift in vocal behaviour. The variable seasonal detections by site within the same fjord system highlights the importance of local site knowledge and PAM recorder placement. The results from the current study show that there are pronounced differences in the length of the vocal activity period of male bearded seals in different locations in Svalbard. It is possible that longer periods of vocal activity reflects the number of available females and that the breeding period is longer in Atwain and Rijpfjorden than in Kongsfjorden. Furthermore, the overall length of the period with vocalisations (weeks to months at the three study sites) suggests that pupping is modestly asynchronous; most phocid females become receptive in the final days of lactation, in the case of bearded seals approximately 24 days after birth (Lydersen and Kovacs 1999).

Although vocal presence can provide information on the likely timing of the mating period and allow for comparisons among areas, finer scale information such as vocal rates are required to study the relation between vocal activity, mating tactics and environmental factors in detail and to assess relative abundance of bearded seal between locations. Trill calls have been used as crude indicators of the mating activity of bearded seals in previous studies (Cleator et al. 1989; Van Parijs et al. 2001). Additionally, rates of calling have been used to detect the peak of the mating period (Van Parijs et al. 2001). Calling activity (trills per day) was greatest at Atwain in this study, with a sustained period from late-April until late-June, in which hundreds of calls were recorded daily. These results resemble those reported for the drift-ice environment of the northeastern Chukchi Sea (Frouin-Mouy et al. 2016). Frouin-Mouy et al. (2016) also reported a large interannual variability in call rate. Given that pack ice environments are extremely variable from year to year, high interannual variability is likely present at Atwain; multiyear analyses will be required to confirm this suggestion. Call rates showed a single, distinct peak at Rijpfjorden. This peak occurred early in the season, in late-April. Given the extensive sea ice cover and protracted season in which sea ice is available in this fjord (Wallace et al. 2010), these findings were somewhat surprising. However, the pupping season has never been documented at this site, so it is impossible to confirm whether this early peak in vocalisation is concomitant with earlier breeding than in previous years at this site. The peak in trill vocal activity in Kongsfjorden occurred at the end of May-beginning of June, which was similar to what de Vincenzi et al. (2019) reported for their outer site in Kongsfjorden. Van Parijs et al. (2001) also reported a peak in trill vocal activity towards the end of May, suggesting that there is strong stability in the seasonal patterns of vocalising bearded seals over time in this area, despite major changes in the availability of annually formed sea ice in this fjord.

Calling rates are thought to be a reasonably good reflection of the number of males vocalising in an area, as individuals have been shown to maintain constant calling rates throughout the breeding season (Van Parijs et al. 2001). Atwain had the highest rates of trill production, with close to 400 trills per h recorded during the peak weeks of the season. These rates are somewhat lower than those reported from the Chukchi Sea by Frouin-Mouy et al. (2016), but more call types were included in that study than the three call types in the current study. The trill rates in Rijpfjorden were above 300 calls per h during a two-week period in the peak of the season, suggesting that this site also had a high abundance of vocalising males in late-April. The trill rates found in Kongsfjorden during the peak of the season were similar to those documented at the outer fjord site in de Vincenzi et al. (2019). Once again, the results are not directly comparable, in that all nine call types were counted in that study, versus the three call types that were thought to reflect male mating displays, which were counted in this study. Although it is challenging to compare rates across different studies, it does seem that calling rates have declined in Kongsfjorden over the last few decades. Van Parijs et al. (2001) reported an average of 100 vocalisations per 10 minutes while the current study documents approximately 80 vocalisations per h, and de Vincenzi et al. (2019) reported approximately 100 vocalisations per h including all nine call types. Therefore, although no temporal shift was found in the calling period, a reduction in the number of males vocalising seems to have occurred.

Few studies attempt to address the functional traits of the vocal repertoire of bearded seals. In this study, the seasonal use of different types of trills was explored to gain insight into what call type or types might be most important in a mating context. It is clear that, by increasing the duration and redundancy in their calling behaviour, bearded seal males increase the probability of reaching their target audience (oestrus females) with their signals, despite their dispersed distribution in various types of sea ice environments, where signal to noise ratios tend to be low (Urick and Kuperman 1989; Geyer et al. 2016). The long trill has a longer duration than step and sweep trills, starts at higher frequencies, has more pronounced steps (frequency modulation) in the low frequency range and a sudden decrease in frequency early in the vocalisation. These properties have been suggested to contribute to good propagation and reduced masking of this call type in environments where sea ice cover is the norm (Cleator et al. 1989; Terhune 1999; Hildebrand 2009). The long trill has previously been reported to be the most commonly used call type during the mating season for bearded seals in Svalbard (Van Parijs et al. 2001; Risch et al. 2007).

Differential use of call types was exhibited on a seasonal basis at two of the three locations in this study. At Atwain, the long trill was by far the most commonly used call type followed by step trill. Atwain represents a drift-ice environment with a lot of open water and highly variable ice conditions over the season, largely driven by variable wind regimes (Renner et al. 2018). However, in this study, this site had much more extensive ice cover compared to the other two locations. The high use of the long trill likely reflects an attempt by males to signal to a dispersed audience of females whose distribution is unpredictable in a noisy environment. Nursing females would continuously be drifting by when hauled out on sea ice. If the ice they are hauled out on drifts over the edge of the continental shelf and into the deep waters of the Arctic Ocean Basin, females would have to swim back to the shallow shelf waters with their pup in order to continue foraging. In that situation, high vocal rates over long periods, and a roaming strategy by singing males would become advantageous. In similar drift-ice environments at the edge of the Chukchi Sea and Beaufort Sea, longer trill types were also observed to increase in proportion towards the peak of the mating season (Frouin-Mouy et al. 2016). Segregation in the call use was also found in Rijpfjorden, but to a lesser degree than in Atwain. Rijpfjorden is a true Arctic fjord in terms of ice cover and hydrographical conditions. The ice at this site is more stable than in Atwain, with fast-ice covering the fjord during much of the spring and early summer. Large quantities of drift-ice are also often advected to the outer part of the fjord (Wallace et al. 2010; Hop et al. 2019). The distribution of breeding females is likely more predictable in Rijpfjorden than in Atwain, where the drift-ice shifts large distances over short periods, but perhaps less predictable than in Kongsfjorden. The segregation in call rates was moderate in Rijpfjorden compared to Atwain, but long trills became the most abundant call type after the break-up of the fast-ice platform began, when the overall trill rates were highest. In contrast, there was no seasonal segregation of call use in Kongsfjorden. The three call types were used in similar proportions throughout the calling period, in agreement with the results reported by de Vincenzi et al. (2019) for this location. Van Parijs et al. (2001) found a constant higher proportion of long trills during the breeding period in Kongsfjorden than in the present study, when ice conditions were more extensive than in recent years. It is probable that these differences in ice conditions might have played a role in the changes observed in segregation of call types over the last decade. Clearly, more studies are needed on the mating behaviour of bearded seals in different environments to disentangle call function and what drives the selection of the different mating strategies displayed by males of this species.

Some studies have addressed the effect of environmental factors on the evolution of mating systems in pinnipeds, in which vocal behaviour plays an important role for many species (Rogers 2003; Stirling and Thomas 2003; Davis et al. 2008). Because bearded seals are an ice-breeding species, the relationship between the ice conditions and the vocal behaviour during the mating period is important. A positive relation between ice cover and vocal presence has been reported in other studies (MacIntyre et al. 2015; Frouin-Mouy et al. 2016). Atwain had the most extensive ice conditions of the three study sites, with ice concentrations >40% prevailing much of the time when bearded seal males vocalised. However, trill vocal activity at Atwain was not correlated directly with any particular sea ice concentration; high vocal activity occurred with ice concentrations from near zero to over 90%. Rijpfjorden is generally covered with fast-ice from six to eight months of the year (Wallace et al. 2010). However, in this study, extensive ice cover was present for only two months, with solid land fast-ice in the outer part of the fjord for approximately one-month. Trill vocalisations were more tightly coupled to the period with heavy ice cover in this location. However, in Kongsfjorden, trill vocalisations started in the beginning of May, shortly after the ice disappeared in this area. This suggests a mismatch between the period with the best environmental conditions for breeding and the actual timing of pupping and subsequent display and mating (Lydersen and Kovacs 1999). The lack of trill vocalisations detected in this study prior to May could be explained by males occupying the tidal glacier fronts earlier in the breeding period (de Vincenzi et al. 2019). These authors suggested that males moved from the glacier fronts to traditional display territories in the outer part of the fjord in May (Van Parijs et al. 2001). High site fidelity might limit male's flexibility in responding to changes in environmental conditions, although previous studies suggest that plastic responses in mating tactics by this species are possible (Van Parijs and Clark 2006; Frouin-Mouy et al. 2016).

The consequences of climate change and its impacts on bearded seals are difficult to predict. Bearded seals in Kongsfjorden seem to have adapted to exploiting ice calved from glaciers in areas where tidewater glaciers meet the sea, for birthing, nursing their young and resting (Lydersen et al. 2014), but the results of this study show reduced vocal activity compared to 20 years ago in this area (Van Parijs et al. 2001). Vocal rates are currently much higher in Rijpfjorden compared to Kongsfjorden. However, as temperatures increase in the coming decades, the hydrographic regime and community composition in Rijpfjorden are expected to undergo changes similar to what has taken place in Kongsfjorden over the past decade (Hop et al. 2019). Substantial reductions in the period of ice cover in Rijpfjorden are expected as the influence of the Atlantic Water that runs along the continental slope north of Svalbard increases, overrunning the Arctic Water influence that traditionally dominated the shelf in northeast Svalbard (Wallace et al. 2010; Onarheim et al. 2014). Heat advection from Atlantic Water is expected to increase in the future, which will continue to drive sea ice losses and the displacement of the pack ice towards the north, beyond the shelf and into the deep Arctic Ocean Basin (Polyakov et al. 2017). This would highly affect the breeding ecology of bearded seals in

Atwain. Female bearded seals feed during lactation, so ideal breeding environments have ice for birthing and nursing pups over shallow water where females can easily reach benthic food resources (Krafft et al. 2000; Kovacs 2018). Ice platforms over the deep Arctic Ocean Basin are not suitable habitat for bearded seals, particularly when they have dependent young (Hammill et al. 1994). As the ice recedes northward, increased primary production is expected over the Arctic shelves (Randelhoff and Sundfjord 2017). However, increased primary production will not benefit bearded seals if there is no sea ice over shallow areas during the pupping period (Kovacs et al. 2011, MacIntyre et al. 2015). Hauling out on land has been observed in Svalbard in recent years (Merkel et al. 2013). Nursing on land has not been observed, but it would represent a positive adaptation for the survival of the species in this region.

The results of this study show that bearded seals vocalise for a longer period than previously thought in Svalbard. The call rates found in the two new locations indicate that the abundance of vocalising bearded seals in these locations could be considerably higher than found in previous studies in Kongsfjorden. A reduction in the vocalisation rate of breeding bearded seals seems to have occurred in Kongsfjorden, which could indicate a reduction in the number of male bearded seals in this area. Furthermore, this study presents information about the functional traits of the different call types. Although the three call types seem to be important for breeding in all places, segregation in their use was found at two of the three locations. There was clearly a preferred use of long trills in the drift-ice location, where the challenging sound environment, unpredictable location of females and high competition between males could make this call type the most suitable for attracting a mate. Future studies should explore PAM data over longer periods (multiple years of data) preferably including all call types, and over even greater environmental gradients to better understand how bearded seals and their vocal behaviour will be affected by climate change. Ideally, surveys or other forms of direct observational study, together with tracking studies should accompany PAM.

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Tables

Table1. Deployment details for each location in Svalbard, 2014-2016

Location	Coordinates	Recording dates	Water/Recorder depth (m)	Duty cycle (min)
Kongsfjorden	78.96N 11.80E	25/09/14-15/08/15	223/50	15
Rijpfjorden	80.29N 22.30E	20/09/15-26/08/16	236/55	12
Atwain	81.40N 31.23E	20/09/15-31/08/16	200 / 57	12

Figures

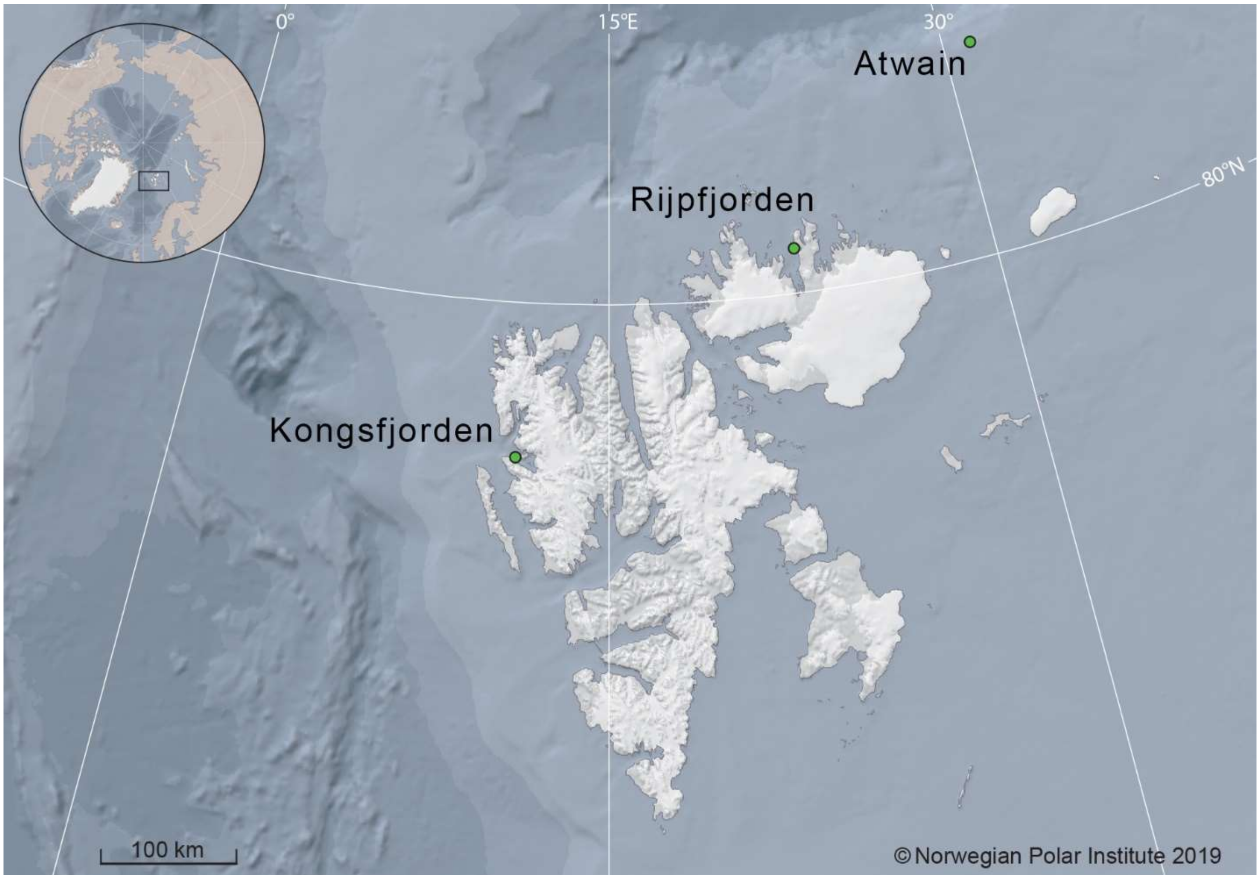


Fig. 1 Study area and location of the three AURAL recorders as indicated by green dots.

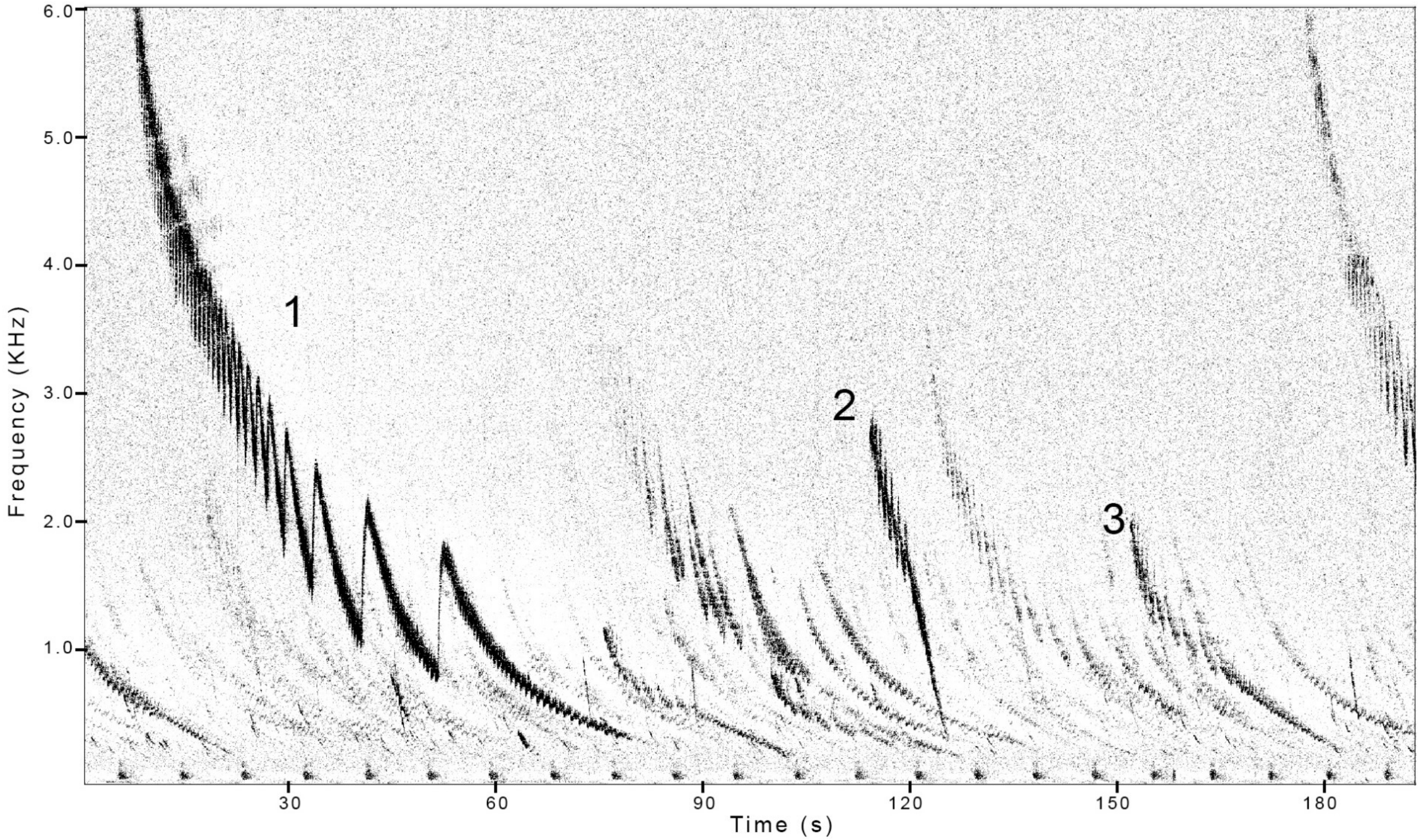


Fig. 2 Spectrogram (FFT size 8192 points; Hann Window) of bearded seal vocalisations in Atwain. The number one corresponds to long trill (1), the number two is sweep trill (2) and the number three is step trill (3). Frequency and time are indicated in y-axis and x-axis respectively

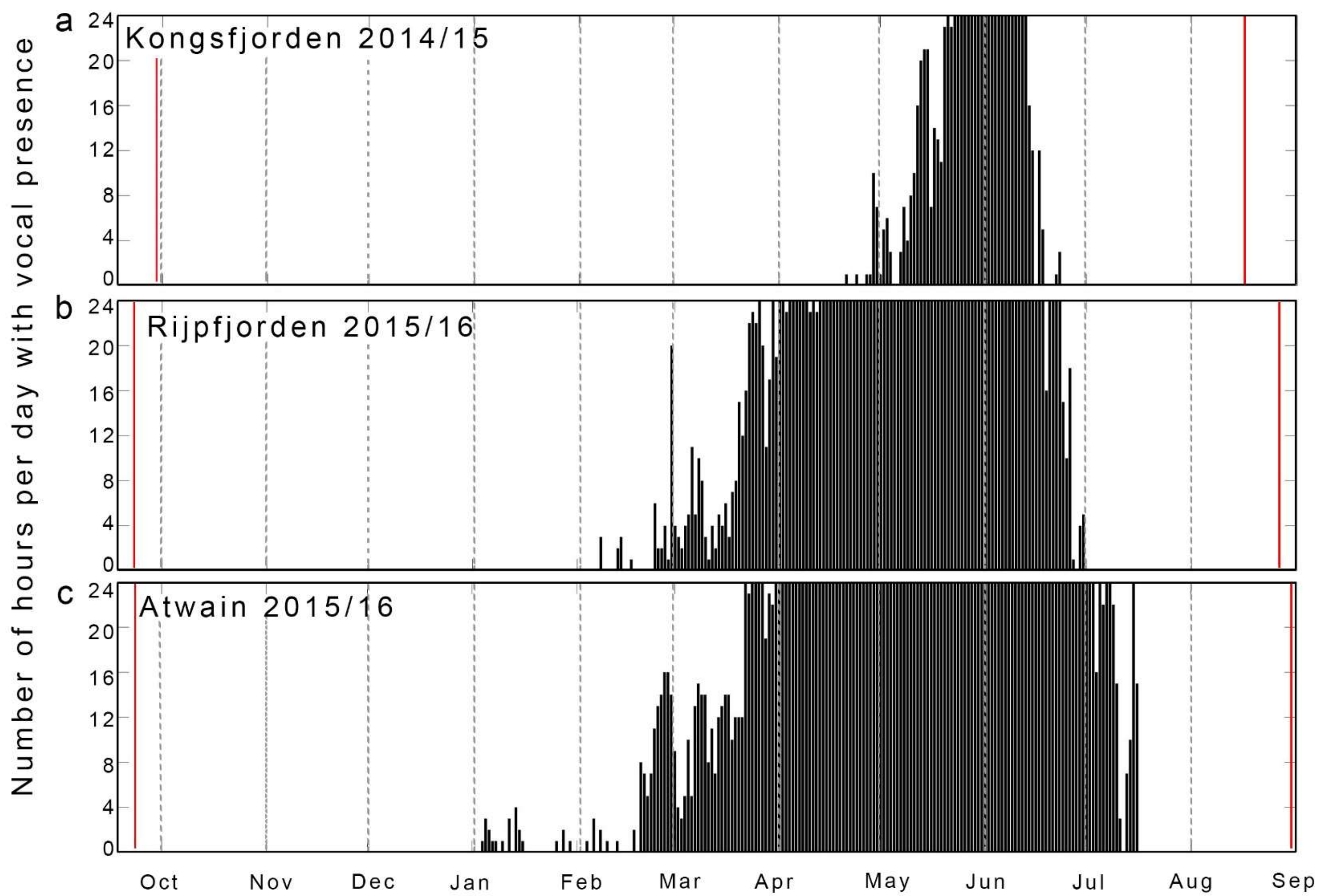


Fig. 3 Acoustic detections of bearded seal vocalisations in **a** Kongsfjorden 2014/15, **b** Rijpfjorden 2015/16 and **c** Atwain 2015/16. The black histogram shows the number of hours per day with acoustic detections as indicated by the y-axis. The vertical red lines show the start and end of the recording period in each location

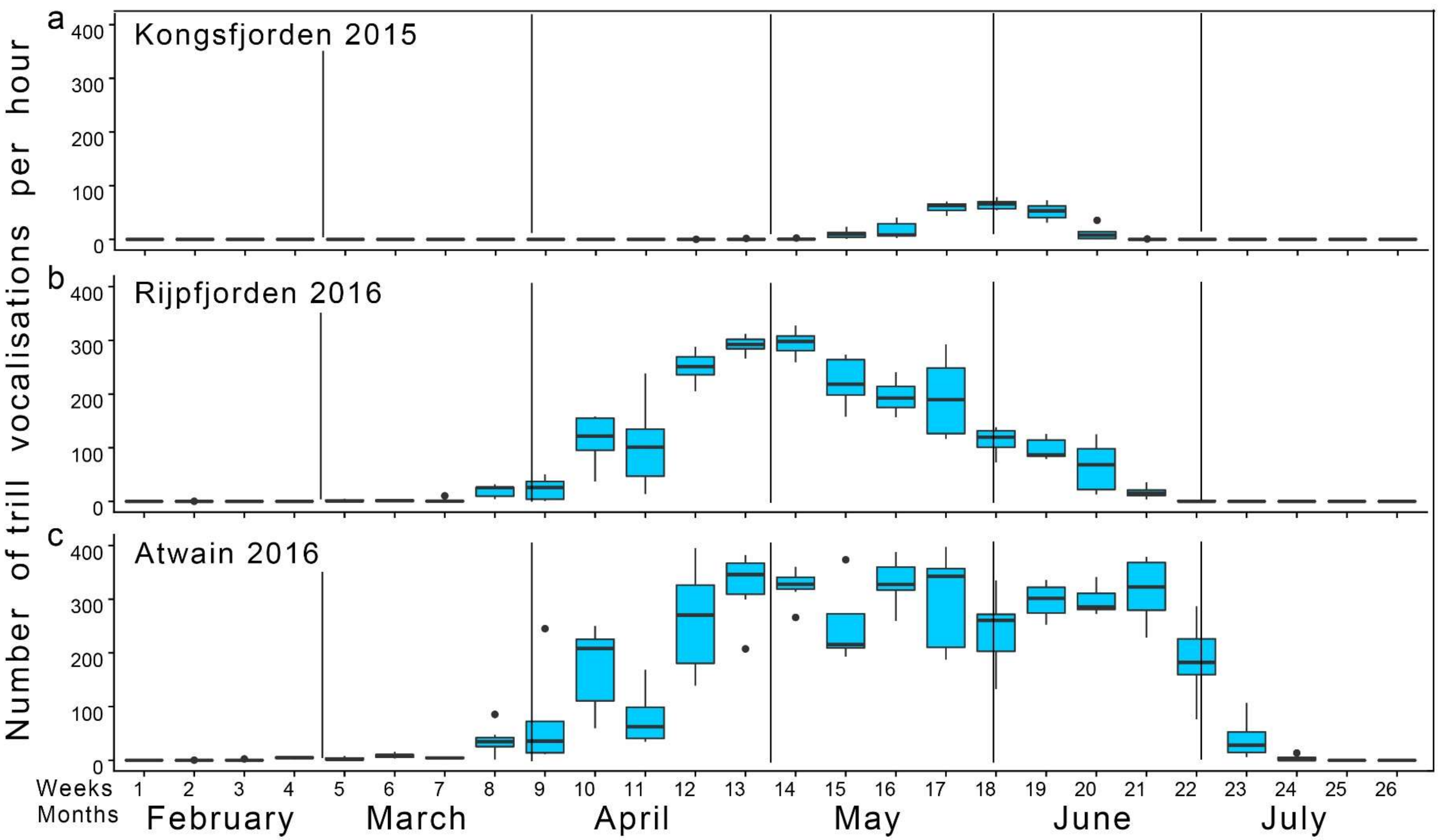


Fig. 4 Median hourly number of trill vocalisations in each sampled week from February to July in **a** Kongsfjorden 2015, **b** Rijpfjorden 2016 and **c** Atwain 2016. Weeks are numbered from 1 to 26 for the given period and indicated in the primary x-axis. The secondary x-axis divides the sampled period in months, indicated in the main plot by vertical bars. Boxes: 25-75th percentiles; whiskers: 1st-99th percentiles

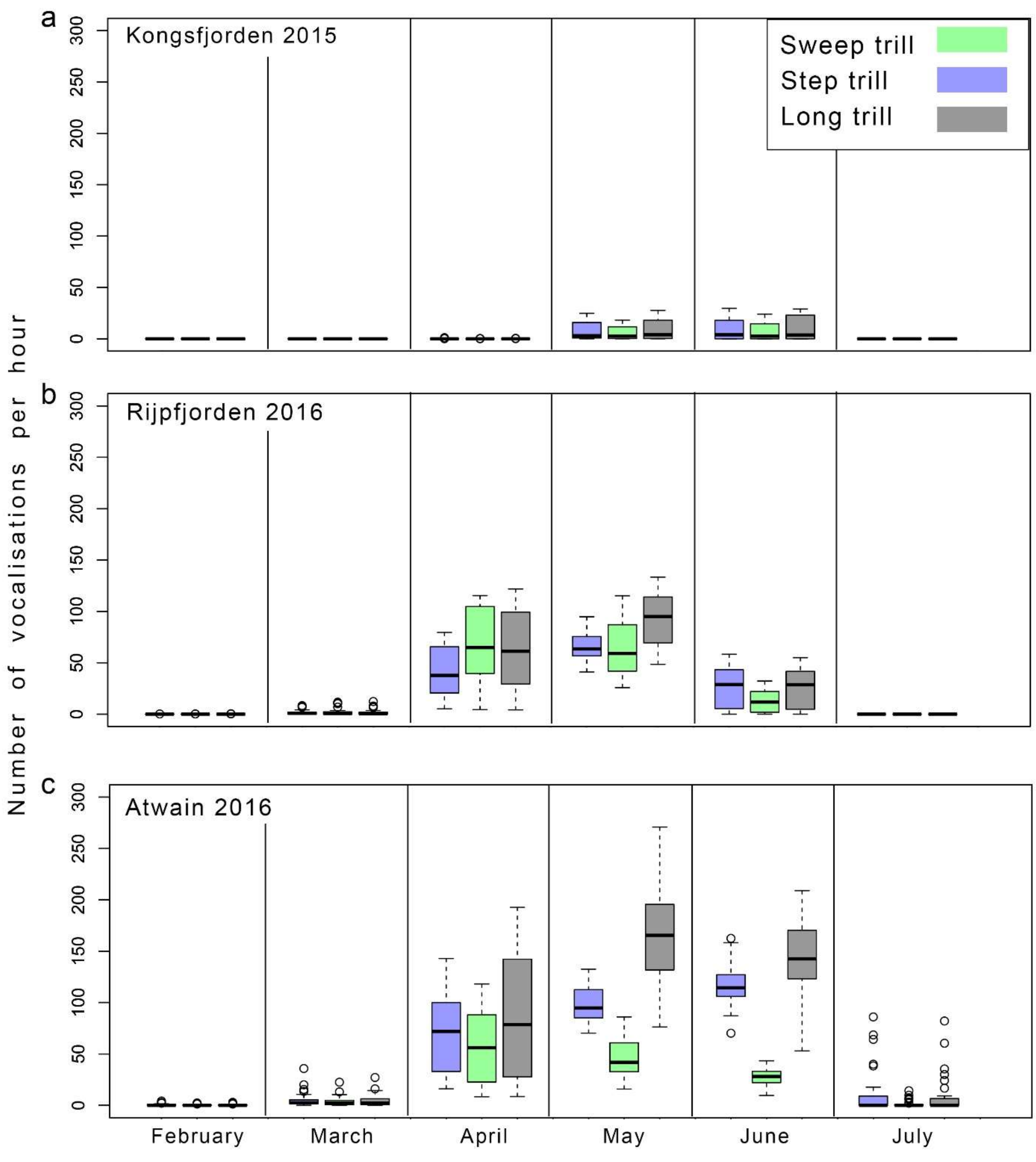


Fig. 5 Hourly number of vocalisations for each call type and sampled month in **a** Kongsfjorden 2015, **b** Rijpfjorden 2016 and **c** Atwain 2016. Boxes: 25-75th percentiles; whiskers: 1st-99th percentiles

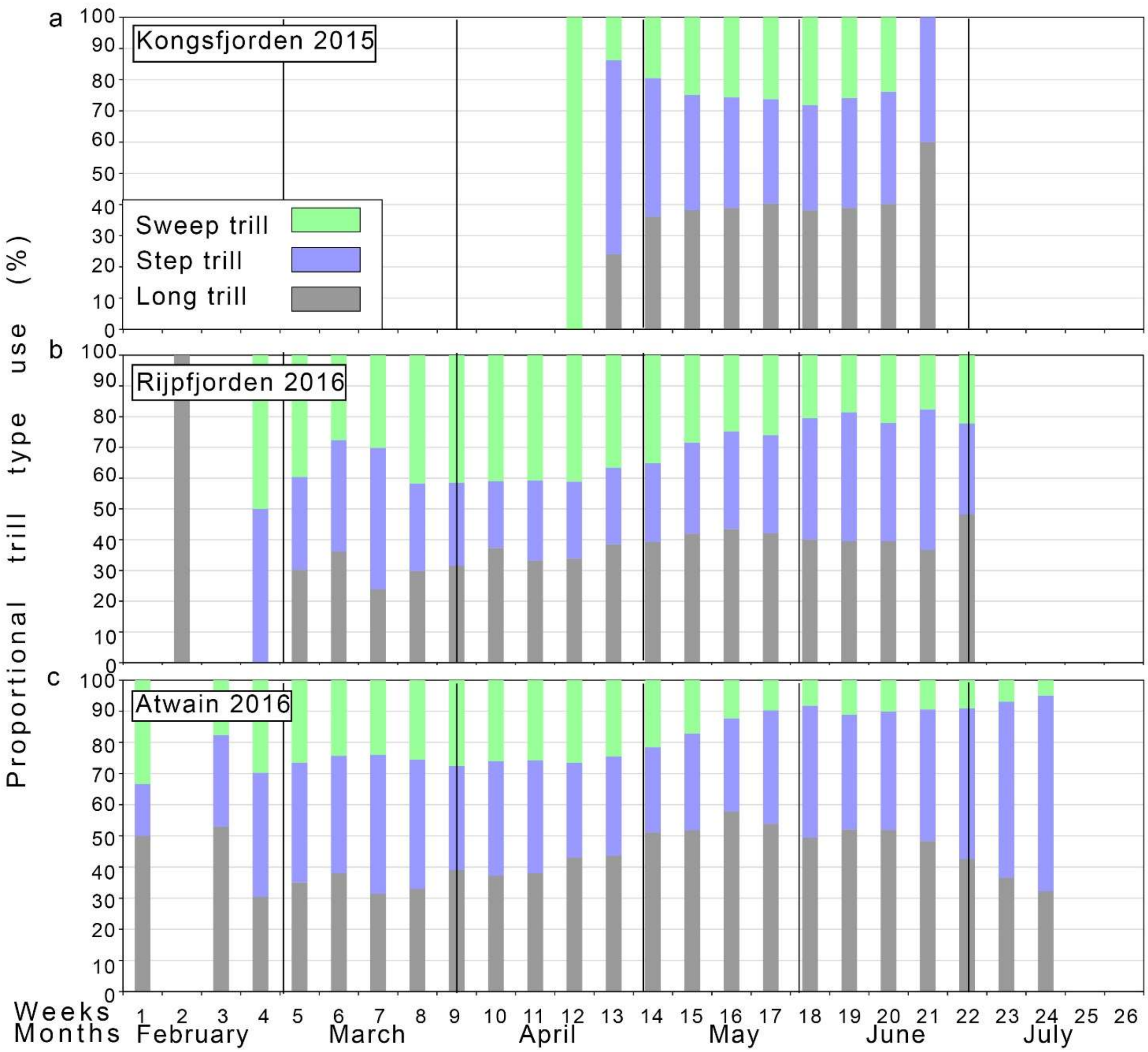


Fig. 6 Proportional call type use from February to July by week in **a** Kongsfjorden 2015, **b** Rijpfjorden 2016 and **c** Atwain 2016. Weeks are numbered from 1 to 26 for the given period and indicated in the primary x-axis. The secondary x-axis divides the sampled period in months, indicated in the main plot by vertical bars

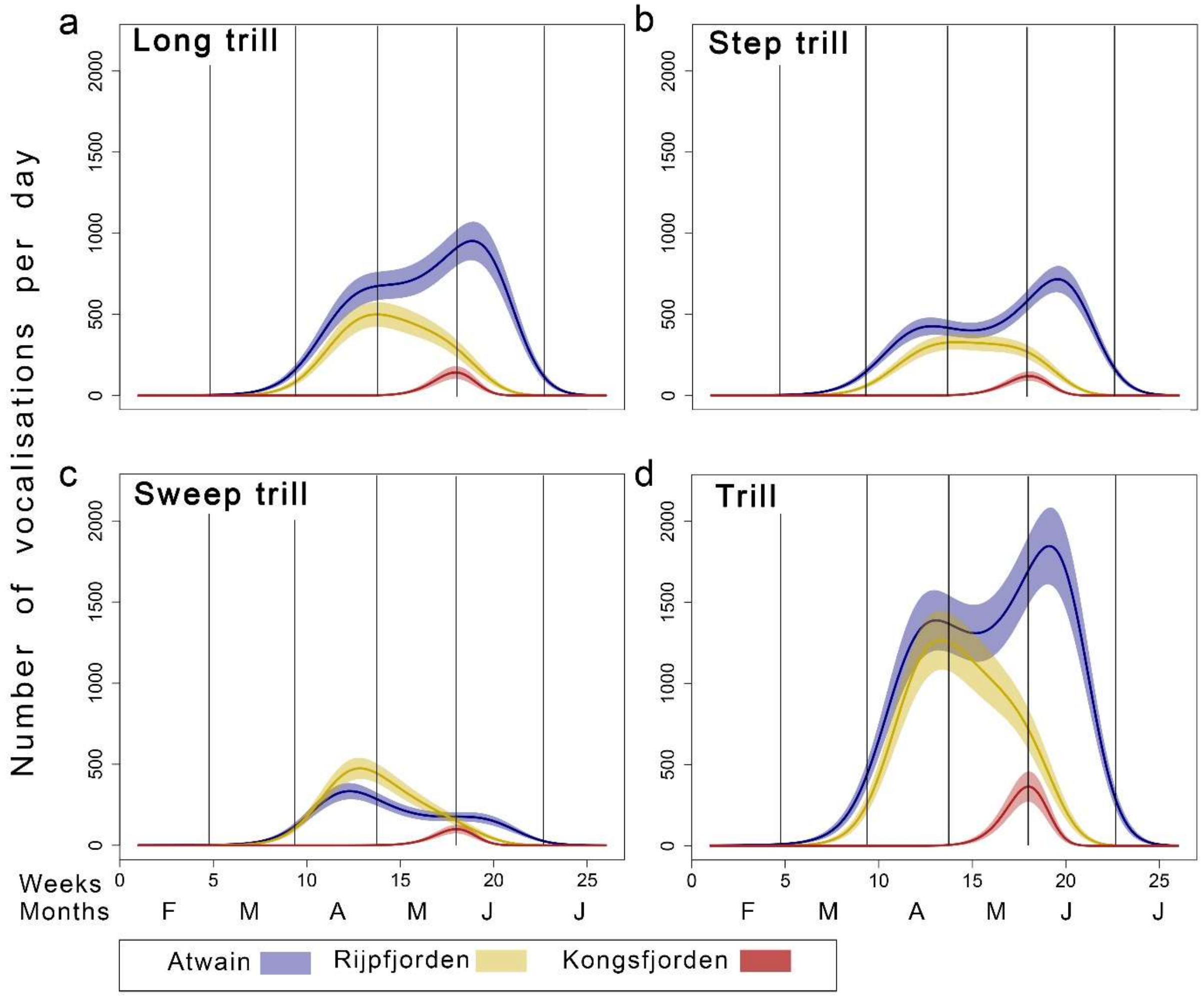


Fig. 7 Results of Generalised Additive Models predicting the daily rate of vocalisations for each location. The results of the models corresponding to different call types and the overall trill rates are shown in different plots (**a**= long trill, **b**= step trill, **c**= sweep trill and **d**= overall trill activity). The y-axis indicates the number of vocalisations per day. The x-axis shows date in weeks (data from week 1 to 26). The vertical bars in the plots correspond to monthly divisions, indicated by capital letters in the secondary x-axis (F-J). Values shown are mean ± 95 % CI

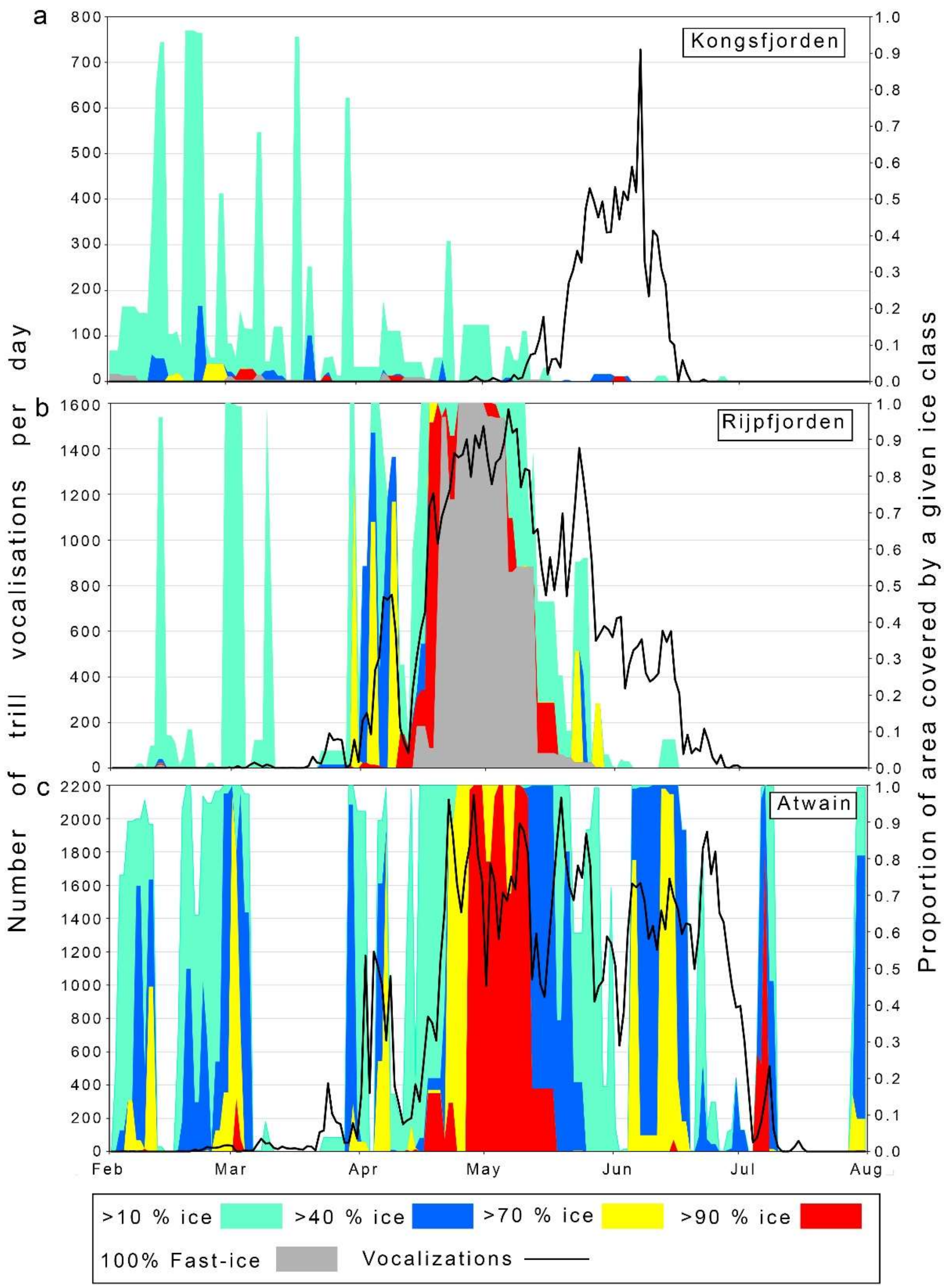
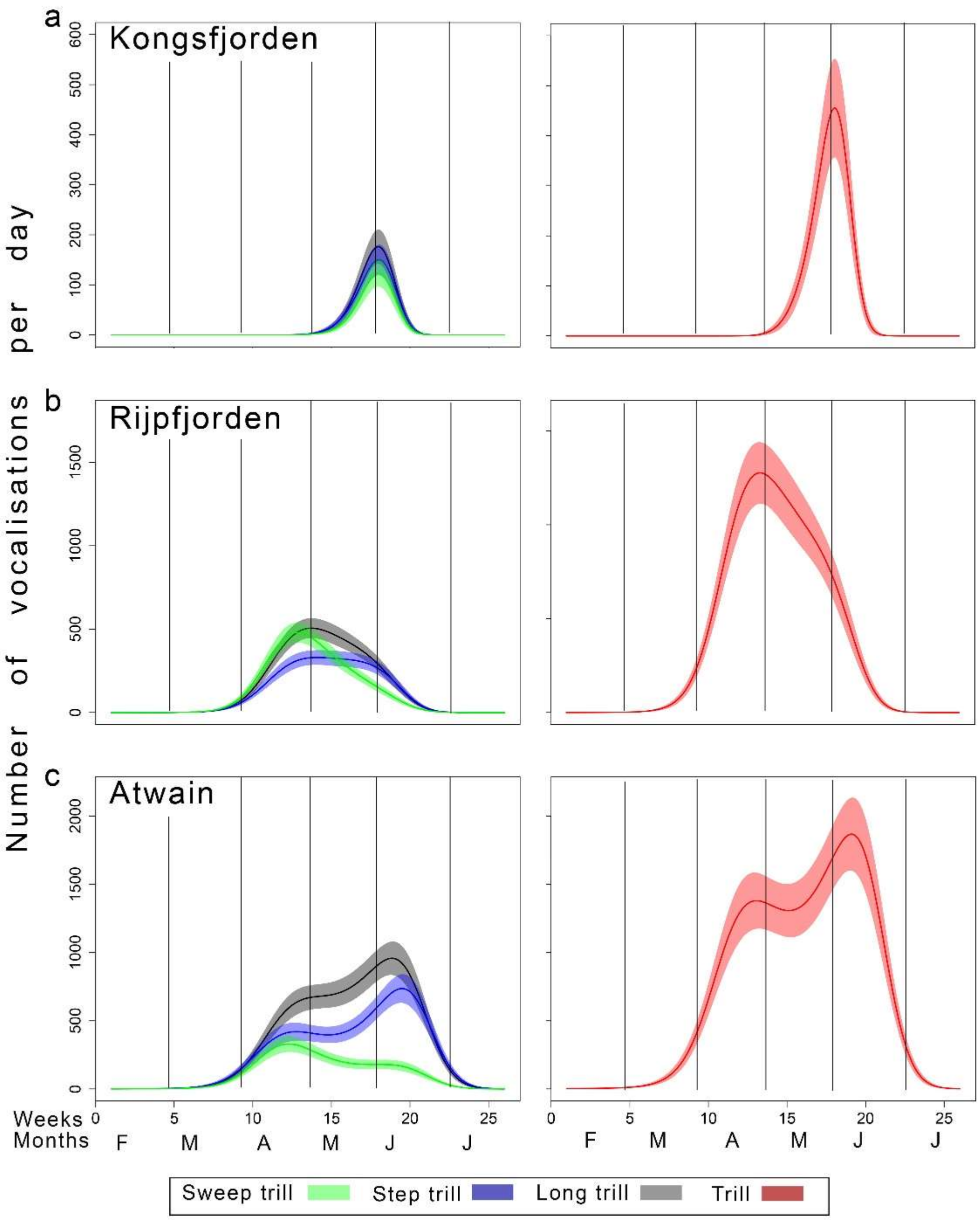


Fig. 8 Daily vocal rates of bearded seals in relation to the ice cover from February to July in **a** Kongsfjorden 2015, **b** Rijpfjorden 2016 and **c** Atwain 2016. Daily trill rates (overall trill rates) are shown in the main y-axis and indicated by the black line. The secondary y-axis shows the proportion of the area covered by the ice class indicated in colors

Supplementary figures



Supplementary figure 1 Results of Generalised Additive Models predicting the daily rate of vocalisations for each call type. The results of the models corresponding to **a** Kongsfjorden 2015, **b** Rijpfjorden 2016 and **c** Atwain 2016 are shown. The y-axis indicates the number of vocalisations per day. The main x-axis shows date in weeks (data from week 1 to 26). The vertical bars in the plots correspond to monthly divisions indicated by capital letters (F-J) in the secondary x-axis. Values shown are mean ± 95 % CI