1   **Year-round distribution of bearded seals, *Erignathus barbatus*, throughout the Alaskan**

2   **Chukchi and northern Bering Sea**

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9   **Abstract**

10   Bearded seals are pan-Arctic ice-obligate phocids; for the threatened Beringia population, the

11   majority of the population feeds in the summer in the Chukchi Sea, then migrates south to

12   overwinter in the northern Bering Sea. Contemporary information on the impact of rapidly

13   changing climatic conditions on bearded seal distribution is essential for effective management.

14   To monitor for marine mammals, passive acoustic recorders were deployed throughout the

15   eastern Chukchi and northern Bering seas (64° N to 72° N), sampling at a rate of 16 kHz on a

16   duty cycle of either 80 or 85 minutes every five hours. Data from year-long deployments at nine

17   sites over four years (2012-2016) were manually analyzed, totaling 13,275 days (~75,000 hours).

18   Bearded seal calling activity was present at every site in every year. Calling activity increased

19   from September through February and reached sustained and saturated levels from March

20   through June, at which point calling ceased abruptly regardless of ice cover. The timing of

21   calling and its abrupt cessation correspond with the known breeding season of bearded seals.

22   However, the timing of the cessation of calling occurred earlier each year, corresponding with an

23   earlier sea ice retreat. The sustained calling detected overwinter at all locations suggests that this

24   is more than just a few animals that are remaining in the Chukchi Sea. Preceding this main pulse

25   was a smaller peak in calling that progressed southward, corresponding with the fall migration of

26   bearded seals to the Bering Sea. These results increase our knowledge on the year-round spatio-

27   temporal distribution and migration patterns of this pagophilic species, and the relationship

28   between calling activity and sea ice concentration.

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1. Introduction

The U.S. Arctic has been undergoing rapid climatic change and has been a region of major summer ice retreat since 2007 (Baker et al., 2020a). This region has already seen an increase in temperatures of 0.75° C, exceeding the global average, in just the past decade (Post et al., 2019). It is expected that the first ice-free Arctic summer (defined as $<1 \times 10^6$ km^2; Wang and Overland, 2012) will occur before 2050, with some models showing projections as early as 2034 (Peng et al., 2020; Notz and SIMIP Community, 2020; Wang et al., 2021). Additionally, thick multiyear sea ice (2+ years) has dramatically reduced, being replaced by thin first year ice (Wood et al., 2015). This sea ice loss has resulted in a shift in the timing of the annual ice retreat, longer open water seasons, and increased ambient noise from both natural and anthropogenic sources.

Bearded seals are an ice-breeding phocid with a circumpolar distribution (Cameron et al., 2010). Two subspecies have been described: *E. b. barbatus* occurs from the Laptev Sea to Hudson Bay and the North Atlantic (Rice, 1998), while *E. b. nauticus* occurs in the western Arctic Ocean and Bering and Okhotsk seas (Heptner et al., 1976; Cameron et al., 2010). Under the U.S. Endangered Species Act, the *E. b. nauticus* subspecies has been further divided into the Okhotsk Distinct Population Segment (DPS) in the Sea of Okhotsk and a Beringia DPS that inhabits the Bering, Chukchi, Beaufort, and East Siberian seas (Cameron et al., 2010). Both populations are primarily benthic feeders, feeding on crabs, shrimps, and snails; infaunal bivalves; and demersal fishes (Lowry et al., 1980). As such, they typically prefer relatively shallow (<200 m) habitats near areas of high benthic productivity (Burns, 1981; Bengtson et al., 2005; Cameron et al., 2010).

Seasonal ice dynamics are a major driver of movement patterns for pagophilic species like the bearded seal, *Erignathus barbatus* (Burns, 1981; Cameron et al., 2010; Breed et al. 2018). For

58 critical life history functions in the annual cycle of pupping, nursing, mating, and molting,

59 bearded seals tend to prefer a dynamic ice habitat, with leads, fractures, and polynyas (Burns,

60 1981; Nelson et al., 1984). Many Beringia bearded seals move south with the advancing ice edge

61 through the Bering Strait into the Bering Sea where they spend the winter (Burns and Frost,

62 1979; Frost et al., 2005), but others remain north of Bering Strait (Olnes et al., 2020). While

63 much of the population appears to overwinter in the central and northern Bering Sea (Fay 1974;

64 Heptner et al. 1976; Burns and Frost, 1979), recent studies have shown that some portion of the

65 population remains in the Chukchi over winter (Hannay et al., 2013; MacIntyre et al., 2013;

66 Jones et al., 2014; MacIntyre et al., 2015; Frouin-Mouy et al., 2016; Jimbo et al., 2019).

67 Throughout winter and early spring bearded seals are distributed on pack ice from the Chukchi

68 Sea to the ice edge in the Bering Sea (Burns and Frost, 1979; Cameron et al., 2010; Breed et al.,

69 2018). Their southern migration into the Bering Sea in the fall is less noticeable and predictable

70 than the spring northward migration (Burns, 1981; Kelly, 1988). In spring (April through June),

71 the population moves north with the ice edge into the Chukchi Sea for the whelping, mating, and

72 molting season (Burns, 1981; Cameron et al., 2010; Melnikov, 2017). Females give birth on the

73 ice from April to May (Burns, 1970, 1981), and pups are weaned within approximately three

74 weeks (Burns, 1970; Kovacs et al., 1996). Mating is thought to occur right after weaning

75 (Cameron et al., 2010). From August through October, bearded seals are primarily pelagic,

76 occupying areas that are completely ice free (Boveng and Cameron, 2013). Given the rapid rate

77 of Arctic sea-ice decline, contemporary information on how this is impacting bearded seal

78 reproductive success is crucial for efficient management and conservation efforts.

79 Acoustic communication plays an important role in behavior of pinnipeds, from establishing or

80 defending territories (Hanggi and Schusterman, 1994), communicating with conspecifics (Rogers

81 et al., 1996), advertising breeding condition (Van Parijs et al., 2003), and mother-pup

82 communications (Van Opzeeland and Van Parijs, 2004). Passive acoustics is ideal for monitoring

83 Arctic species year-round, when ship-based methods are not feasible, and for examining their

84 behavior and adaptability to changing climatic conditions. While all ice-breeding seals are

85 known to produce underwater vocalizations (e.g., Stirling and Siniff, 1979; Watkins and Ray,

86 1985; Perry and Terhune, 1999; Jones et al., 2014; Cziko et al., 2020), bearded seals, given their

87 highly vocal nature, are good candidates for passive acoustic monitoring, particularly during the

88 breeding season. Only males are thought to call underwater during the breeding season (Ray et

89 al., 1969; Cleator et al., 1989; Davies et al., 2006), and have shown geographical variation in

90 repertoires that may be indicative of discrete breeding stocks (Cleator et al., 1989; Risch et al.,

91 2007; Charrier et al., 2013). In the U.S. Arctic, male bearded seals produce primarily three call

92 types, trills, ascents, and moans, which appear to be stable over long temporal scales (Risch et

93 al., 2007; Jones et al., 2014; Frouin-Mouy et al., 2016). In addition to geographic variation, male

94 bearded seals have also demonstrated individual variation in their trills (Van Parijs et al., 2003;

95 Van Parijs and Clark 2006).

96 Male bearded seals are in breeding condition from April to July (Burns, 1981; Cleator, 1996;

97 Van Parijs et al., 2001), and will vocalize to either defend territories or advertise breeding status

98 to females (Ray et al., 1969; Burns, 1981; Cleator et al., 1989; Van Parijs et al., 2001). To that

99 end, males will employ either "roaming" or "territorial" mating strategies (Van Parijs et al.,

100 2003, 2004; Van Parijs and Clark, 2006). Territorial males will show strong site fidelity and

101 defend small territories, while roaming males travel over large areas (Van Parijs et al., 2003,

102 2004; Van Parijs and Clark, 2006); the efficacy of these alternating strategies is thought to relate

103 to differences in ice regimes (Van Parijs et al., 2004). In the Chukchi Sea, the less stable ice is

104   thought to favor the "roaming" strategy, and although males can switch mating tactics, studies

105   show they rarely do (Van Parijs et al., 2003, 2004; Van Parijs and Clark, 2006).

106   In this study, we investigated the spatio-temporal distribution of the species at a multitude of

107   sites and years throughout the U.S. Arctic using stereotyped calls of male bearded seals as an

108   indicator of species presence. The results presented here describe the cessation of calling relative

109   to ice concentration, and provide new information on the year-round presence of bearded seals

110   throughout the eastern Chukchi Sea.

111   **2. Methods**

112   *2.1 Data collection*

113   Data included in the current study were collected from year-round passive acoustic recorders

114   deployed from 2012-2016 at nine sites per year throughout the northern Bering, Chukchi, and

115   western Beaufort seas (Fig. 1a, Table 1). These bottom-mounted, sub-surface, moorings were

116   composed of an anchor, chain, acoustic release, passive acoustic recorder, and steel float (Fig.

117   1b; total length of mooring ~8 m; hydrophone ~6 m off the seafloor). Autonomous Underwater

118   Recorders for Acoustic Listening (AURAL-M2, Multi-Électronique, Rimouski, QC, Canada)

119   recorded for an entire year at a sampling rate of 16 kHz, with 16-bit resolution and 16 dB gain,

120   on a duty cycle of either 80 or 85 min of recording every 5 hours. With these settings the

121   AURALs had a sensitivity of -164 +/- 1dB re 1V/μPa (2 Hz – 30 kHz), a spectral noise floor of

122   52 dB re 1 μPa^2 /Hz (Kinda et al., 2013), and a maximum input pressure (a signal saturation

123   level) of 154 dB re 1 μPa, and a dynamic range of 90 dB over the effective bandwidth of the

124   system.

125

126 *2.2 Data analysis*

127 Image files (pngs) of spectrograms were pre-generated (FFT 1024 pts, 85% overlap, Hamming

128 window). We looked for the presence of bearded seal calls in consecutive 90 second samples

129 throughout each 80 to 85 minute recording interval; 90 s was an ideal length for spectrographic

130 analysis of calls. The five hour staggered duty cycle advanced by an hour each day, which

131 resulted in variable daily recording effort. To account for the difference in number of hours of

132 recording effort each day, data were normalized by daily recording effort (i.e., number of 10-

133 minute intervals with calls / number of total 10-minute intervals for that day). This will be

134 referred to as the percent of intervals with calls, or PIC, following Wright et al. (2018). The term

135 "100% PIC" will refer to the daily calling activity equaling 100%; i.e., 100% of 10-minute

136 intervals for that day had bearded seal calls present. Note that PIC does not refer to the number

137 of calls or number of calling animals.

138 All acoustic data (100%) were manually analyzed using an in-house MATLAB-based program

139 SoundChecker (see Wright et al., 2019 for full details). Each 90-s spectrogram was marked

140 yes/no/maybe for the presence/absence of bearded seal calls. "Yes" was selected when the

141 analyst was confident in species attribution; only "yes" detections are presented and analyzed

142 here, resulting in a binary format (1 = yes, 0 = no). Bearded seals were identified by their

143 stereotyped, species-specific trills, moans, and ascents as classified by Risch et al. (2007), based

144 on Cleator et al. (1989) (Fig. 2). A total of 13,275 days (over 75,000 hours) of data from nine

145 mooring locations over four years (2012-2016) were analyzed.

146 Calling activity was compared with satellite-derived sea ice concentration, obtained from 25-km

147 resolution data from the National Snow and Ice Center (https://nsidc.org/data/NSIDC-

148   0079/versions/3). Sea ice data used in this project were version-3 Bootstrap algorithm files

149   described by Comiso (2007). Mean daily sea ice concentrations were calculated with a 3-day

150   moving average for each location and year and plotted against calling activity.

151   Linear regression was used to quantify the trend in the date of calling cessation over time using

152   the *lm* function in R (ver. 1.4.11; R Core Development Team). Generalized additive models

153   (GAMs) were used to determine the effects of sea ice concentration, Julian date, latitude,

154   distance from shore, and year on calling activity (including zero calling days) using the *gam*

155   function in the *mgcv* package (Wood, 2006) in R. Given the binary nature of the data

156   (presence/absence of calls), we evaluated candidate models built using a binomial distribution

157   with a logit link. To accommodate mooring-specific effects, we also created hierarchical GAMs

158   (HGAMs) that allowed for interactions between factors and smoothed variables. Specifically, we

159   used the "GS" model from Pedersen et al. (2019), which creates a global smooth, plus group-

160   level smoothers (with the same wiggliness or smoothing penalty) corresponding to mooring. The

161   default basis dimensions were used to initially parameterize the smoothing splines for all models.

162   The *mgcv* function gam.check() was used to evaluate whether the basis dimensions were large

163   enough; because the effective degrees of freedom were all much lower than the associated

164   maximum basis complexity (i.e., the k-indices returned from gam.check()), there was no

165   evidence that the basis dimensions were insufficient. Model selection was based on percent

166   explained deviance, adjusted R-squared value, Akaike's Information Criterion, and expert

167   knowledge of the ecosystem.

168   To compare maximum detection range with other studies, and to determine independence of each

169   mooring location from the nearest location (i.e., to ensure calls were not detected on multiple

170   recorders simultaneously) propagation modeling was conducted using the Monterey-Miami

171   Parabolic Equation (Smith et al., 2007). Parameters used include a water column sound speed

172   profile obtained from conductivity, temperature, depth (CTD) data at the IC1 mooring (P.

173   Stabeno, Pacific Marine Environmental Laboratory, NOAA), ambient noise levels of 70 dB re 1

174   µPa (Roth et al., 2012; Southall et al., 2020), sediment velocity of ~1520 m s^{-1} (Hamilton, 1980),

175   water depth of approximately 45 m, a source level of 158 dB re 1 µPa (Charrier et al., 2013), and

176   a detection threshold of 0 dB (Au et al., 2001).

3. Results

178   Bearded seal calling activity was ubiquitous at all mooring sites and years (Fig. 3; Table 3). At

179   all locations except the northern Bering Sea (NM1), calling increased from September through

180   March and reached 100% PIC (i.e., 100% of 10-minute intervals had calls) from April through

181   June before ceasing abruptly in late June/early July (Fig. 3; Table 4). Calling was detected year-

182   round at the higher latitudes (BF2, WT1), but was absent in summer months at lower latitudes

183   (NM1, KZ1, PH1) (Fig. 3). Among all mooring sites, the northern sites (BF2, WT1) had the

184   greatest proportion of days with calls, while the lowest latitude sites (NM1, KZ1) had the lowest

185   proportion of days with calls (Table 3).

186   There were low levels of calling activity at the northern and offshore sites (e.g., BF2, WT1, IC3,

187   IC2) in September and October, before the main pulse of calling began. Larger, more distinct

188   peaks occurred in October and November before the main calling pulse began at the southern

189   Chukchi sites (CL1, PH1, KZ1). This initial peak was absent at the northern Bering Sea site

190   (NM1), except one instance lasting only ten days in November 2014 (Fig. 3). The latitudinal

191   trend in the prominence of an autumn peak was less evident in 2016; the prominent initial peaks

192   in the southern Chukchi were either greatly reduced (PH1) or missing entirely (KZ1).

193   The date at which calling activity hit 100% PIC varied among years and locations; generally,

194   lower latitudes reached saturation earlier than higher latitudes. In all years, site PH1 reached

195   100% PIC before any other site (Fig. 3). The elapsed time between the onset of calling and the

196   first day of reaching 100% PIC also varied annually and spatially. Sites NM1 and PH1 had the

197   fewest number of days on average between the onset of calling and 100% PIC (57 ± 16 and $60 \pm$

198   38, respectively (average $\pm$ SD); Table 3), while the northernmost site, BF2, had the greatest

199   number (187 ± 41). Interestingly, despite its location between PH1 and NM1, KZ1 had over

200   twice the number of days between the onset of calling and 100% PIC, but had the lowest

201   standard deviation of all sites (125 ± 14; Table 3). Calling occurred on every day when ice

202   concentration was 100% at all sites and all years. At all sites with an evident initial peak, that

203   peak occurred before the ice arrived (most notably at CL1, PH1, and KZ1).

204   Calling ceased abruptly between mid to late June and early July at all locations, regardless of ice

205   concentration (Figs. 3, 4; Table 4). This cessation occurred earlier at lower latitude locations, and

206   a few weeks later at higher latitude locations (Fig. 4). At lower latitudes (NM1, KZ1), ice was

207   gone for weeks prior to cessation, whereas at northern sites (BF1, WT1) calling ceased several

208   weeks prior to the ice receding (Fig. 3). All locations showed a significant ($p<0.0001$) trend of

209   cessation occurring earlier in successive years of the study; this was most noticeable at the lower

210   latitude sites (Fig. 4; Table 4). Cessation of calling at the farthest south NM1 location occurred

211   on average four days earlier each year of the study (Fig. 4; Table 4). Cessation at the southern

212   Chukchi locations (KZ1, PH1, CL1) occurred an average of 3 days earlier each year. The

213   northern locations (IC1, IC2, IC3, WT1, BF2) showed more interannual variability, but calling

214   stopped an average of two days earlier each year (Table 4). The difference in cessation date

215   between the southernmost (NM1) and northernmost (BF2) sites increased by a week over the

216   course of the four-year study (Table 4). These trends were consistent with changes in sea ice

217   concentration over the course of the study. The lower latitude sites saw the greatest reduction in

218   sea ice over the four years, with ice formation occurring later, and sea ice breakup occurring

219   earlier each year (Fig. 3).

220   The top four candidate GAM models are defined in Table 2. GAM analyses showed that the

221   variable Julian date explained 73% of the deviance in calling activity in a univariate model,

222   while latitude and sea ice concentration explained 71% and 30%, respectively, in univariate

223   models. Univariate models comprising each of the remaining candidate predictor variables

224   explained less than 7% of the deviance in calling activity. The interaction between Julian date

225   and sea ice concentration explained 74% of the deviance. The HGAMs with mooring-specific

226   effects explained a higher percent of the deviance than the model comprising interactions among

227   Julian date, sea ice concentration, and latitude. The model with the highest performance metrics

228   indicated that the HGAM model that allowed for mooring-specific differences in the interaction

229   between Julian date and sea ice concentration explained 85% of the deviance in calling activity

230    $(p<0.001)$.

231   Results from the propagation modeling showed a maximum detection range of 40 km (assuming

232   a signal to noise ratio of 0 dB). The two closest moorings, IC1 and IC2 (Fig. 1a), were 60 km

233   apart. While a calling individual placed directly between these two recorders could potentially

234   have been detected on both recorders, all other moorings were situated at least 89 km apart. This

235   indicated that calling records from all other moorings were considered independent of each other.

236

4. Discussion

4.1 Spatio-temporal distribution

Bearded seal calling activity was detected at all sites in all years and corresponds with the phenology of this species. Calling increased over the course of the breeding season; this may be the result of an increase in the number of calling individuals within the detection range of the recorder, rather than only an increase in individual call rate (Van Parijs et al., 2001). This is also supported by the increase in number of co-occurring calls from simultaneously calling individuals (e.g., Fig. 2a; Frouin-Mouy et al., 2016). No calling activity was detected during the months of July, August, and September at lower latitudes (PH1, KZ1, NM1), which is consistent with the results presented in Jimbo et al. (2019) from the southern Chukchi. However, because a small number of subadults are thought to remain in the northern Bering Sea after the ice is gone (Burns, 1981; Cameron et al., 2010), this suggests that a lack of detections in summer is not necessarily indicative of a lack of animals.

Low levels of calling activity were detected during the summer at northern and offshore sites, which is in accordance with the results of MacIntyre et al. (2013), and with current knowledge on bearded seals preference for open water habitat in areas of high benthic productivity during the summer (Boveng and Cameron, 2013). Calling activity detected outside the known breeding season has been observed in other aquatic-mating pinniped species as well (e.g., Van Opzeeland et al., 2010; Jones et al., 2014; Frouin-Mouy et al., 2019). Given the inherent difficulties in studying social behaviors of aquatic pinnipeds in remote locations, few studies have investigated the functions of calls outside the breeding season.

Calling ceased abruptly irrespective of ice concentration at all locations, corresponding to the end of the breeding season. Within a week, on average, each site went from 100% PIC to 0%

260 PIC (Fig. 3; Table 4); this abrupt cessation occurred over even fewer days at the southern

261 locations. There was also an overall significant (p<0.0001) trend toward earlier cessation in later

262 years (Fig. 4; Table 4), most notably in the lower latitudes. The timing of cessation of calling at

263 the southern latitude locations stopped an average of three days earlier during each year of the

264 study; NM1, the farthest south location and the site that showed the greatest reduction in sea ice

265 over the study, showed cessation occurring an average of four days earlier each year. Even the

266 northern locations, while showing increased interannual variability, saw a similar trend of

267 cessation occurring an average of two days earlier each year. While across all locations there was

268 a dramatic cessation of calling within a few weeks of each other regardless of ice cover, multiple

269 studies have shown the importance of ice concentration to bearded seal calling and reproduction

270 (Burns, 1970, 1981; Van Parijs et al., 2003, 2004; Jones et al., 2014; Frouin-Mouy et al., 2016).

271 GAM results in the current study suggest that sea ice concentration, when combined with Julian

272 date, are the most significant predictors of bearded seal calling activity, with mooring-specific

273 differences in the relationship between these covariates. As such, an earlier shift of the ice retreat

274 could have noticeable effects on both the timing of cessation of calling and bearded seal

275 reproductive success. It remains unknown whether this cessation in calling is due to an earlier

276 end to the breeding season, a distribution shift in the seals as the ice moves farther away, or some

277 other unknown reason. Additionally, the decrease in sea ice concentration may result in a shift

278 of reproductive strategies of males in the Alaskan Arctic from a "roaming" strategy toward a

279 "territorial" strategy (Van Parijs et al., 2003, 2004; Van Parijs and Clark, 2006). In Alaskan

280 bearded seals, the calls of "roaming" males were longer in duration than the "territorial" males

281 (Van Parijs and Clark, 2006); analyzing changes in the duration of calls could help determine

282 whether decreasing sea ice concentration is resulting in a shift in mating strategies.

283   A preliminary peak in calling activity in October-November was evident at many locations,

284   particularly the southern Chukchi Sea sites (CL1, PH1, KZ1; Fig. 3). The lower levels of calling

285   in the fall at the northern sites, followed later by these larger peaks at the southern sites, may be

286   evidence of many bearded seals' migration south to the Bering Sea (Boveng and Cameron,

287   2013). This initial peak was not documented by Jones et al. (2014) north of Barrow or Frouin-

288   Mouy et al. (2016) in the northeastern Chukchi Sea, though it was evident in the results

289   presented in MacIntyre et al. (2013), MacIntyre et al. (2015), and Jimbo et al. (2019) from the

290   western Beaufort and Chukchi seas. Interestingly, there is some evidence for a similar initial fall

291   peak in bearded seal observations occurring in October and November in Chukotka waters

292   (Melnikov, 2017), although there were no overlapping years between that study and this one.

293   Melnikov (2017) noted that the majority (81%) of bearded seals observed in October were

294   headed southeast toward the Bering Strait. Bearded seals are known to make their way south in

295   the fall with the advancing ice edge (Boveng and Cameron, 2013; Breed et al., 2018; Cameron et

296   al., 2018; Quakenbush et al., 2019). Shortly after being tagged in Kotzebue in October, juvenile

297   bearded seals began moving south toward the Bering Sea (Breed et al., 2018; Cameron et al.,

298   2018). In another study, tagged juvenile bearded seals gradually moved south toward the Bering

299   Sea during September and October after spending the summer in the Chukchi Sea (Olnes et al.,

300   2020), although the extent of latitudinal movement may be dependent upon tagging location

301   (Quakenbush et al., 2019). There have been few studies involving satellite tagged adult bearded

302   seals, but those few studies show a similar trend of moving south as the sea ice advances; by

303   December all tagged animals were in the Bering Sea (Boveng and Cameron, 2013; Quakenbush

304   et al., 2019). The timing of the calling peaks in the current study, beginning in the north in

305   September and October, and moving south, combined with the increase in levels at the lower

306   latitudes, suggests that these calls are associated with a southbound migration.

307   There are a few caveats to this study that must be considered. Multiple studies have shown that

308   for many aquatic-breeding phocids, it is primarily adult males that vocalize (e.g., Burns, 1981;

309   Hanggi and Schusterman, 1994; Van Parijs et al., 1999, 2001, 2003; Stirling and Thomas, 2003;

310   Davies et al., 2006; Miksis-Olds and Parks, 2011), particularly during the breeding season. While

311   juvenile bearded seals will vocalize, elaborate vocal displays in bearded seals typically develop

312   as the individual reaches sexual maturity (Davies et al., 2006). Although captive studies do show

313   that female bearded seals vocalize, it is only for a short period (March), and only after nuzzling a

314   vocalizing male (Mizuguchi, 2016). Furthermore, the females produced primarily snorts and

315   bells; no females were recorded producing trills. The results presented here, therefore, do not

316   account for females, young juveniles, or other non-vocalizing animals. As such, these results are

317   a conservative estimate of bearded seal presence throughout the northern Bering and eastern

318   Chukchi seas. Studies show that seal species with aquatic mating preferences tend to call louder

319   to be heard by isolated individuals at greater distances than species that haul out on land in large

320   aggregations (Rogers, 2003; Stirling and Thomas, 2003). Cleator et al. (1989) found that bearded

321   seal calls were detected as far as 30 km away, with an average of 15 km; propagation modeling

322   in the current study suggested a maximum detection range of 40 km. The closest pair of

323   recorders, at IC1 and IC2, were 60 km apart; it is possible that calls emitted in a small region

324   directly between those recorders could have been recorded at both sites, and their records should

325   be interpreted accordingly. However, all the other pairwise distances between recorders were

326   more than 89 km (i.e., more than double the modeled maximum detection range) and we are

327   confident that the records of calling from those moorings are independent.

328   *4.2 Response to climate change*

329   The Alaskan Arctic has been undergoing rapid climate change in recent years, with record warm

330   ocean temperatures having cascading effects on the marine ecosystem (e.g., Walsh et al., 2018;

331   Duffy-Anderson et al., 2019; Piatt et al., 2020; Thoman et al., 2020). For ice-obligate species, the

332   loss of sea ice over their benthic habitat is expected to directly impact their reproductive and

333   foraging success (Moore and Huntington, 2008; Kovacs et al., 2011; Boveng et al., 2020). For

334   example, Boveng et al. (2020) related declines in body condition of other Alaskan Arctic phocid

335   seals to the loss of sea ice and the effects of the Northeast Pacific marine heatwave of 2014-

336   2016. In addition to the direct impacts of the loss of their sea ice habitat, other indirect impacts

337   will create additional challenges. Grebmeier (2012) suggested that the Alaskan Arctic ecosystem

338   will shift to a more pelagic system in the future; such a shift will support new communities of

339   secondary and tertiary consumers, potentially leading to a lack of suitable prey, increased

340   competition, or dietary shifts (Moore and Stabeno, 2015; Moore et al., 2018; Huntington et al.,

341   2020).

342   The results presented here were able to monitor for bearded seal vocal activity during a period of

343   rapid climatic change. The most powerful heat wave on record for the Gulf of Alaska and Bering

344   Sea region occurred from 2014 to 2016 (Walsh et al., 2018). During this period, changes in

345   calling behavior of bearded seals appear to be related to the rapid reduction in sea ice

346   concentration, most notably in the southern latitude locations. The date at which calling activity

347   stopped (i.e., reached 0%) happened earlier every year of the study, with the southernmost site

348   (NM1) having the cessation of calling occur almost two weeks earlier in 2016 than the start of

349   the project in 2012. This site also had a reduction in the number of days of 100% PIC over the

350   course of the four years. The difference in cessation date between the southernmost (NM1) and

351   northernmost (BF2) sites also increased by a week over the course of the four-year study, a result

352   of calling activity at the southern locations changing more rapidly than that at the northern

353   latitudes. These results could be an early indicator of changes in reproductive behavior as a result

354   of sea ice loss. If vocal activity during the breeding season is indicative of the overall length of

355   their breeding season, and if these warming conditions continue in the Arctic, this suggests a

356   possible shortening, or at least a shifting, of the breeding season as the conditions continue to

357   warm in the Arctic. This, in turn, could have detrimental effects on their reproductive success.

358   Vessel noise has been shown to alter the vocal behavior of aquatically breeding pinnipeds, with

359   the potential to alter the ability of harbor seal males to maintain their territories or attract females

360   (Matthews et al., 2020). Additionally, increased ambient noise from other anthropogenic sound

361   sources has been shown to impact calling rates and source levels of other U.S. Arctic marine

362   mammal species as well (Blackwell et al., 2015; Thode et al., 2020). With an increase in the

363   open water season, an increase in vessel traffic and anthropogenic activities is expected, which

364   will in turn increase ambient noise. Similar to what has been shown for bowhead whales

365   (Blackwell et al., 2015), bearded seals will vocally compensate for increased ambient noise, but

366   only up to an observable threshold, after which point their levels will plateau (Fournet et al.,

367   2021). This suggests a vulnerability to increased ambient noise and acoustic masking. If ambient

368   noise levels in the Arctic continue to rise as a result of lengthening open water seasons and the

369   resulting increase in vessel traffic, the resultant acoustic masking and/or the physical stress of

370   altering their calling behavior could have additional negative impacts on their reproductive

371   success.

372

5. Conclusions

Bearded seal calling activity was present on every mooring in every year, increasing from October through March before reaching 100% PIC from April through June. Calling ceased abruptly at all sites (100% to 0% PIC within 4-7 days), with cessation occurring earlier at lower latitude sites. These trends correspond well with the known breeding season. During the four years of the study, the timing of cessation of calling occurred earlier each year; this is thought to be in relation to changes in sea ice concentration as a result of the unprecedented Northeast Pacific marine heatwave, and may be indicative of changes in their reproductive behavior as they relate to sea ice loss. The high levels of calling activity at all locations throughout the Chukchi Sea overwinter indicates that some portion of the population remains in the Chukchi year-round instead of overwintering in the Bering. Finally, an initial peak in calling activity starts at higher latitudes in September and October and progresses southward through the Chukchi Sea, suggesting evidence of a southern migration of bearded seals toward the Bering Sea.

Understanding how marine mammals use acoustic cues is crucial to understanding how changes to their acoustic environment will affect their behavior and reproductive success. Future work will look at more recent years to see how these trends in calling behavior and migratory patterns persist or change in the face of unprecedented sea ice loss, and increases in open water seasons, vessel traffic, and background noise. Future analyses will also investigate call types within the initial migratory peaks in comparison with calls in the main pulse and during peak breeding season to determine if differences in call usage may elucidate either different age/sex classes as they migrate south, or a unique geographic breeding population structure. These results highlight the effectiveness of passive acoustics for monitoring marine mammal species in areas or times

395   when traditional visual surveys are not feasible, and in particular areas of rapid environmental

396   change.

397   **Acknowledgments**

410

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641

642   **Table 1**. List of all passive acoustic recorder locations and recording parameters used in analysis,
643   2012-2016.

Mooring Name Location Depth (m)	Mooring Year	Recording Start Date	Recording End Date	Duty cycle (min on/total)	Total # days with data
BF2 71.75°N, 154.46°W 109	2012-13	8/31/2012	8/31/2013	85/300	366
	2013-14	9/3/2013	9/29/2014	80/300	392
	2014-15	10/1/2014	9/14/2015	80/300	349
	2015-16	9/16/2015	9/8/2016	80/300	359
WT1 71.05°N, 160.51°W 42	2012-13	8/30/2012	8/27/2013	85/300	363
	2013-14	8/29/2013	10/10/2014	80/300	408
	2014-15	10/11/2014	9/13/2015	80/300	338
	2015-16	9/14/2015	9/7/2016	80/300	360
IC3 71.83°N, 166.08°W 43	2012-13	8/28/2012	8/26/2013	85/300	364
	2013-14	8/28/2013	9/26/2014	80/300	395
	2014-15	9/27/2014	9/17/2015	80/300	356
	2015-16	9/18/2015	9/14/2016	80/300	363
IC2 71.23°N, 164.21°W 41	2012-13	8/27/2012	7/31/2013	85/300	339
	2013-14	8/28/2013	9/26/2014	80/300	395
	2014-15	9/27/2014	9/13/2015	80/300	352
	2015-16	9/14/2015	9/14/2016	80/300	366
IC1 70.83°N, 163.11°W 43	2012-13	8/25/2012	8/27/2013	85/300	368
	2013-14	8/28/2013	9/25/2014	80/300	394
	2014-15	9/26/2014	9/18/2015	80/300	358
	2015-16	9/19/2015	9/15/2016	80/300	363
CL1 69.32°N, 167.61°W 49	2012-13	8/23/2012	8/25/2013	85/300	368
	2013-14	8/26/2013	9/24/2014	80/300	395
	2014-15	9/26/2014	9/19/2015	80/300	359
	2015-16	9/21/2015	4/2/2017	80/300	560
PH1 67.91°N, 168.20°W 58	2012-13	8/22/2012	8/22/2013	85/300	366
	2013-14	8/24/2013	9/29/2014	80/300	402
	2014-15	9/17/2014	9/20/2015	80/300	369
	2015-16	9/20/2015	2/10/2016	80/300	142
KZ1 67.12°N, 168.60°W 51	2012-13	8/21/2012	8/22/2013	85/300	367
	2013-14	8/24/2013	9/24/2014	80/300	397
	2014-15	9/25/2014	9/21/2015	80/300	362
	2015-16	9/22/2015	9/21/2016	80/300	365
NM1 64.85°N, 168.40°W 48	2012-13	8/20/2012	8/21/2013	85/300	367
	2013-14	8/22/2013	9/20/2014	80/300	395
	2014-15	9/22/2014	8/20/2015	80/300	333
	2015-16	9/10/2015	9/23/2016	80/300	380

644

645 **Table 2.** Formulations and summary statistics for the top four bearded seal calling activity
646 models. The models were formulated as generalized additive models (GAMs) and hierarchical
647 GAMs (HGAMs). For each model, the formula as specified in the R package *mgcv* is provided,
648 along with the English translation. Models are arranged in order of decreasing % explained
649 deviance. Yes/Pngs refers to the number of time intervals with "yes" calls per day divided by the
650 total number of time intervals per day.

mgcv Model Formula	Smoothing Spline	Adj. R²	% Explained Deviance	ΔAIC
gam(Yes/Pngs ~ te(CalJulian, Ice, bs=c("cc", "tp"), m=2, k=30) +t2(CalJulian, Ice, Mooring, bs=c("cc", "tp", "re"), m=2, full=TRUE)	HGAM with: 1) a shared global smoother comprising a tensor product interaction between Julian date (a cyclic cubic regression spline) and sea ice concentration (a thin plate regression spline); and 2) mooring-specific trends in the interaction between Julian date and sea ice concentration, with similar smoothness (shared penalty) across moorings.	0.866	85.7	-
gam(Yes/Pngs ~ s(CalJulian, bs="cc", m=2, k=30) +s(CalJulian, Mooring, bs="fs", m=2, k=30)	HGAM with: 1) a shared global smoother for Julian date (a cyclic cubic regression spline); and 2) mooring-specific trends in Julian date, with similar smoothness across moorings.	0.859	84.5	38818
gam(Yes/Pngs ~ te(CalJulian, Ice, Latitude, bs=c("cc", "tp","tp"), m=2, k=c(20, 20, 9))	GAM with a tensor product interaction among Julian date (a cyclic cubic regression spline), sea ice concentration (a thin plate regression spline), and latitude (a thin plate regression spline).	0.835	80.8	151685
gam(Yes/Pngs ~ te(CalJulian, Ice, bs=c("cc", "tp"), m=2, k=20)	GAM with a tensor product interaction between Julian date (a cyclic cubic regression spline) and sea ice concentration (a thin plate regression spline).	0.813	78.8	358171

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654   **Table 3.** Summary of calling presence for each mooring site and year.

Location	Total # days with data	Total # days with bearded seal calls	% days with bearded calls	Avg (± SD) # days b/t onset and 100% PIC
BF2	1466	1047	71.4%	187 (± 41)
WT1	1469	1021	69.5%	152 (± 22)
IC3	1478	955	64.6%	138 (± 26)
IC2	1452	1016	70.0%	181 (± 55)
IC1	1483	857	57.8%	159 (± 49)
CL1	1682	1032	61.4%	152 (± 27)
PH1*	1279	868	67.9%	60 (± 38)
KZ1	1491	847	56.8%	125 (± 14)
NM1	1475	718	48.7%	57 (± 16)

655   *Mooring stopped early in 2016 (see Figure 3).

656   **Table 4.** Date calling activity ceased after 100% PIC, the average number of days from the last
657   day of 100% PIC to the first day reaching 0%, and the total number of days for calling to stop at
658   all locations (i.e., number of days from first site reaching 0% to last site reaching 0%).
659

| Mooring	2012-13	2013-14	2014-15	2015-16	Avg # days from 100% to 0%
BF2	7/7/2013	7/4/2014	7/3/2015	7/2/2016	7
WT1	7/2/2013	7/5/2014	6/30/2015	6/28/2016	6
IC3	7/3/2013	7/2/2014	6/29/2015	6/30/2016	5.75
IC2	7/1/2013	7/6/2014	7/1/2015	6/25/2016	7.25
IC1	6/26/2013	6/27/2014	6/29/2015	6/18/2016	7.5
CL1	6/21/2013	6/19/2014	6/15/2015	6/14/2016	4.75
PH1	6/19/2013	6/16/2014	6/13/2015	n/a	2.67
KZ1	6/20/2013	6/14/2014	6/13/2015	6/14/2016	5.25
NM1	6/18/2013	6/14/2014	6/11/2015	6/6/2016	4.75
# days for cessation	20	23	23	27	

660

661 **FIGURE CAPTIONS**

662 **Figure 1.** Study area and mooring diagram. A) Map showing the location of all moorings (black
663 circles) used in analyses. B) Schematic of the subsurface passive acoustic moorings.


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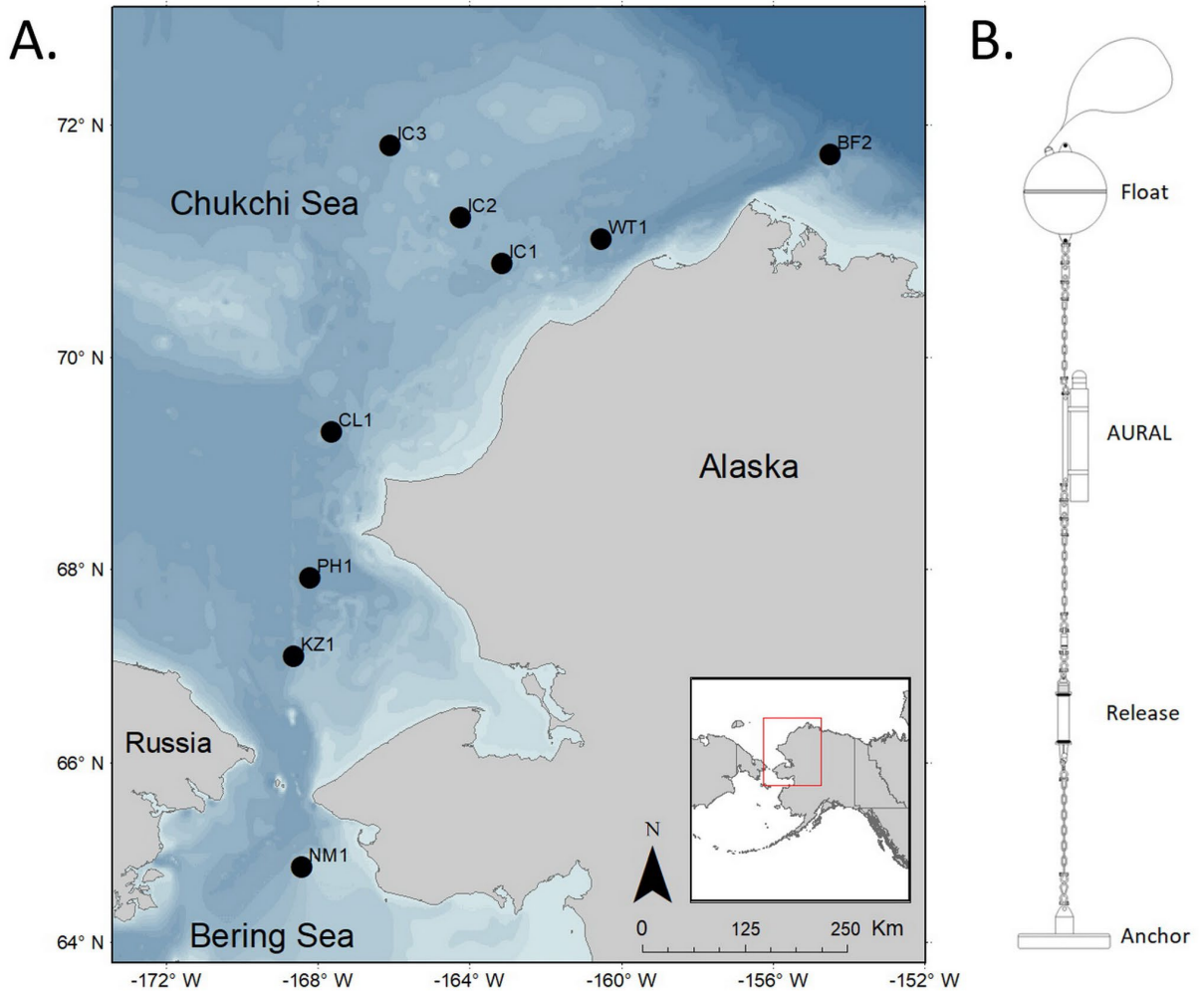
Figure 2. Examples of the three primary call types used to identify bearded seals. A) Trill. B) Ascent. C) Moan. All clips recorded at site IC3. All spectrograms Hanning window, 95% overlap. FFT size either 2048 (A and B) or 1024 (C).
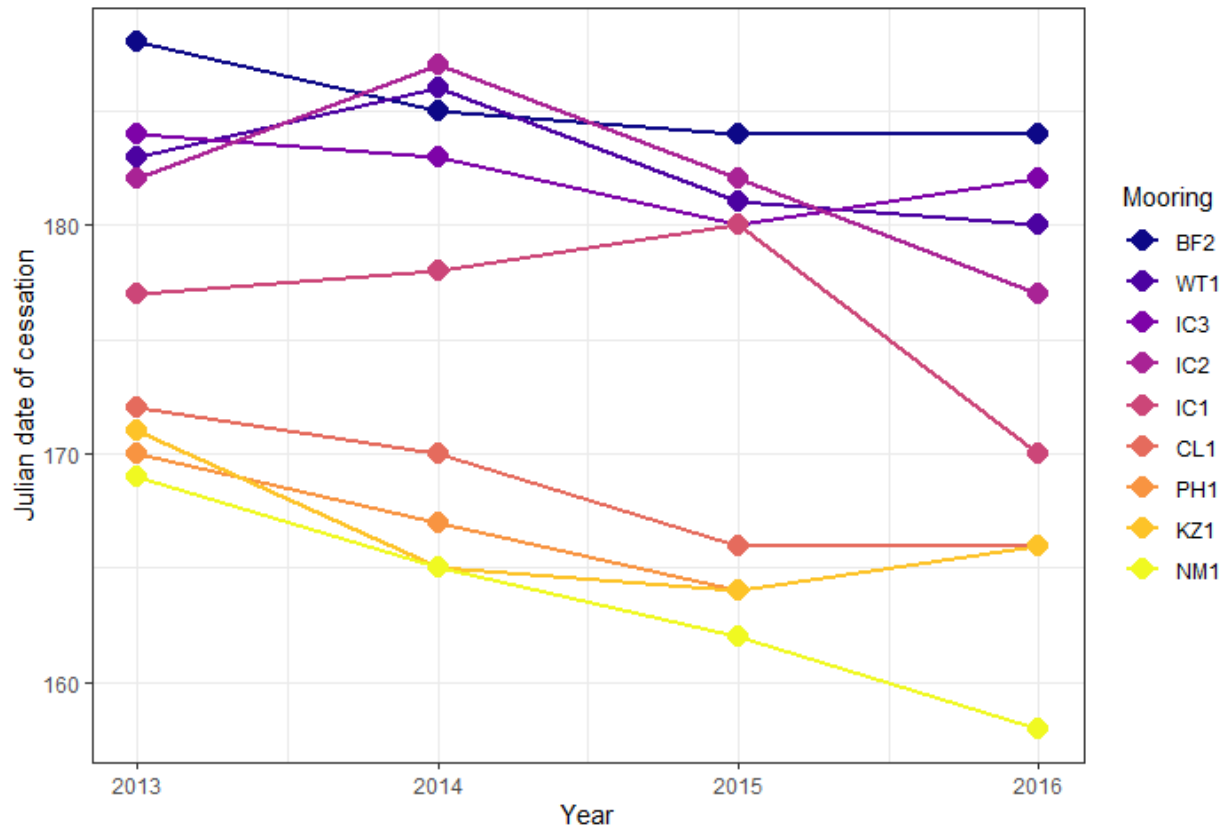

668
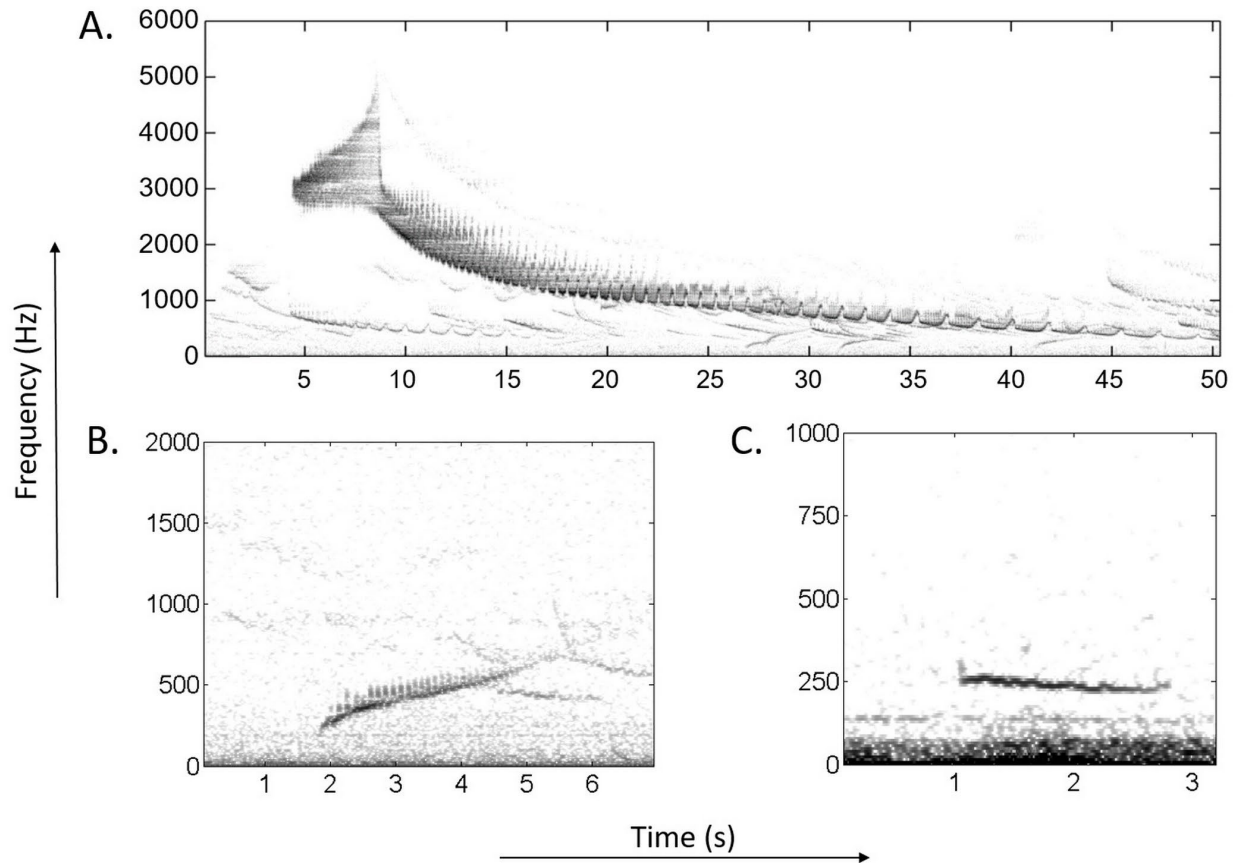
Figure 3. Bearded seal calling activity (black lines, presented as PIC, or the percentage of ten-
minute time intervals per day with calls, adjusted for recording effort) for all locations, 2012-
2016. Moorings are generally arranged latitudinally from north to south (see Figure 1 for map of
locations). Blue line indicates percent ice cover (zero-phase, three-day moving average). Gray
shading indicates no data.
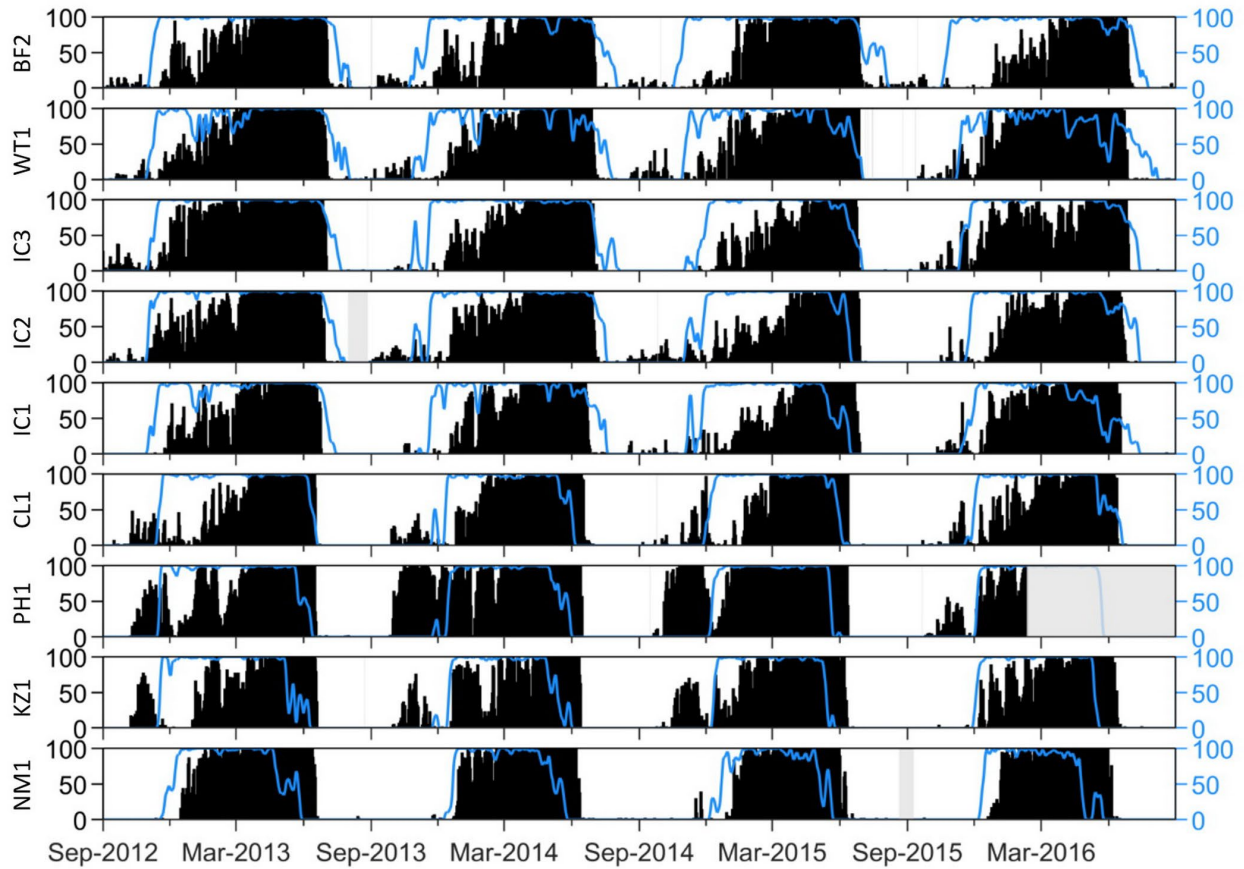
675 **Figure 4.** Julian date at which bearded seal calling activity dropped to 0% ("date of cessation")
676   at all sites for each year of the study, color coded by mooring location.

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