

1 **Distributional shifts among seabird communities of the Northern Bering and**  
2 **Chukchi seas in response to ocean warming during 2017-2019**

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13

14 **ABSTRACT**

15

16 In the northern Bering Sea and eastern Chukchi Sea, 2017-2019 were record-breaking years for  
17 warm ocean temperatures and lack of sea ice. The region supports millions of seabirds that could  
18 be affected by shifts in prey distribution and availability caused by changing environmental  
19 drivers. However, seabirds are highly mobile and often flexible in diet, and might alter their  
20 foraging distributions accordingly. To determine if there was evidence of long-term changes in  
21 abundance of seabirds, or if seabirds used the offshore habitat differently during recent warm  
22 years, we compared species richness, community composition, and distribution and abundance of  
23 selected species and Total seabirds (all species combined) between two periods, 2007-2016 and  
24 2017-2019. We also evaluated annual changes in abundance during 2007-2019. We used 79,426  
25 km of transects from vessel-based surveys conducted July through September. Total seabird  
26 density for the entire study area increased by ~20% during 2017-2019, but changes were not  
27 consistent across the study area, nor among species, and species richness declined except for a  
28 slight increase in the northern Chukchi Sea. Total seabird density declined most in the northern  
29 Bering Sea (-27%), although it increased in the Chirikov Basin by 73%. During 2017-2019,  
30 abundance of piscivorous murrets (*Uria* spp.) decreased everywhere, whereas planktivorous  
31 *Aethia* auklet density increased by 70% in Chirikov Basin; auklets apparently abandoned their

32 post-breeding migration to the Chukchi Sea. Short-tailed shearwaters (*Ardenna tenuirostris*)  
33 expanded farther into the northern Chukchi Sea, with nearly twice the density of the previous  
34 decade. We identified five seabird community types, three of which (all dominated by an alcid  
35 species) contracted spatially in the later period, and shifted south or near colonies. In contrast, a  
36 short-tailed shearwater dominated community expanded northward, and a community defined by  
37 low seabird density expanded throughout the eastern portion of both the northern Bering and  
38 Chukchi seas, suggesting higher-density communities had shifted westward. The variable  
39 responses among species correspond to documented changes in the environment as well as their  
40 natural history.

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### 43 **1. Introduction**

44

45 The Bering and Chukchi seas have been undergoing warming events and subsequent  
46 alteration of biological ecosystem components over the last 20 years (Grebmeier et al., 2006;  
47 Stabeno and Bell, 2019). However, events during 2017-2019 appear to have been distinctively  
48 disruptive of long term physical and biological patterns. Sea ice plays a critical role in primary  
49 productivity of these marine ecosystems. The formation of ice algae feeds phytoplankton blooms  
50 as the ice retreats (Brown and Arrigo, 2013), supporting zooplankton production (Campbell et  
51 al., 2016; Stabeno et al., 2010), and ultimately upper trophic levels. Early ice retreat, or lack of  
52 sea-ice formation, impacts these mechanisms with repercussions throughout the food web (Hunt  
53 et al., 2011). In the northern Bering Sea, warm conditions lead to early ice retreat, resulting in  
54 early and high primary productivity, particularly near the ice edge (Brown et al., 2011; Brown  
55 and Arrigo, 2013).

56 During 2017, sea ice formed over the eastern Bering Sea shelf, but there was an unusual  
57 and early retraction of ice over the northwestern Bering Shelf, attributed to persistent southerly  
58 winds. As a result, the northern Bering Sea was characterized by ice conditions similar to those  
59 of a ‘warm’ year, despite ice coverage farther south (Siddon and Zador, 2018). In 2018 and again  
60 in 2019, ocean temperatures were above normal in winter, and ice extent in the Bering Sea was  
61 the lowest recorded in four decades. In both years, sea ice retreated north of Bering Strait before  
62 spring (Siddon and Zador, 2018, 2019; Cornwall, 2019). The extremely low ice cover during

63 2017-2019 in the northern Bering Sea and Chukchi Sea resulted in altered oceanographic and  
64 biological conditions; these were most evident in 2018, and included impacts to lower and upper  
65 trophic levels (Duffy-Anderson et al., 2019).

66 Seabirds are indicators of ocean conditions (Murphy, 1936; Piatt et al., 2007 and  
67 references therein; Velarde et al., 2019). By understanding responses of seabirds to broad-scale  
68 ecological shifts we may better predict impacts to upper trophic-level taxa in a rapidly changing  
69 environment. In the Bering Sea, recent responses of seabirds to ocean warming have included  
70 mass mortality (Jones et al., 2019), failed nesting attempts and low reproductive success (Dragoo  
71 et al., 2020; Romano et al., this issue). Since 2015, seabird mass mortality events have occurred  
72 almost annually in the Bering Strait region (Duffy-Anderson et al., 2019). Species-specific  
73 mortality events and seabird reproductive success at monitored colonies can be indicative of food  
74 web changes (Abraham and Sydeman, 2004; Jones et al. 2019; Piatt et al., 2020). However, these  
75 metrics do not necessarily provide insight into how the broader seabird community has  
76 responded to an altered ecosystem.

77 Seabirds are long-lived, with adaptations to buffer variability in their environment.  
78 Forgoing a breeding season or undergoing a few years of low breeding success may not  
79 necessarily lead to substantial population-level repercussions (Cairns, 1992; Velarde and  
80 Ezcurra, 2018). Seabirds are also highly mobile, and can search for prey over a large area,  
81 particularly when not attending a colony. Further, seabirds spend most of their lives at sea, and  
82 their temporal and spatial distribution across the seascape often reflects the productivity and  
83 foraging conditions of large marine areas (Ballance et al., 1997; Gall et al. 2013; Suryan et al.,  
84 2012; Yen et al., 2006). Here, we examine broad-scale responses of seabirds to a warm period  
85 (2017-2019) in the Northern Bering and Chukchi Sea Large Marine Ecosystem (LME) relative to  
86 the preceding decade (2007-2016). Specifically, we use vessel-based surveys to assess how  
87 seabirds differed in species-specific and community-level abundance and distribution between  
88 these two time periods.

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90

## 91 **2. Methods**

92

### 93 *2.1. Study area*

94

95           Our study area encompassed offshore waters of two regions, the northern Bering Sea  
96 (hereafter, Bering Sea) and eastern Chukchi Sea (hereafter, Chukchi Sea) (Fig. 1), and we  
97 considered southern and northern subregions within each region. We refer to the subregions (Fig.  
98 2) as the Northern Bering (59.5°N to St. Lawrence Island; distinct from the general northern  
99 Bering Sea), the Chirikov Basin (St. Lawrence Island to Bering Strait at ~65.8°N, including  
100 Little Diomede Island), the Southern Chukchi (Bering Strait to 70°N) and Northern Chukchi  
101 (70°N to 72.5°N). The western boundary of all regions followed the U.S. Exclusive Economic  
102 Zone to 175°W and the eastern boundary followed an offshore buffer bordering coastal Alaska,  
103 to include only waters where our surveys occurred in most years (Fig. 2).

104           The northern Bering Sea is hydrographically and biologically distinct from the southern  
105 Bering Sea, separated at approximately 60°N (Stabeno et al., 2010; Sigler et al., 2011, 2017).  
106 The shallow continental shelf of the northern Bering Sea includes the Inner Shelf domain (<50 m  
107 deep) and Middle Shelf domain (50-100 m deep), with some influence from the more dynamic  
108 Outer Shelf and slope domains, which are beyond our study area. The Inner Shelf is bordered by  
109 the Alaska Coastal Current on the east side and the more saline, colder and nutrient rich waters  
110 of the Anadyr Current in the west (Fig. 1). Both of these water masses pass through Bering Strait  
111 and, as Bering Sea Water, facilitate structure of the Chukchi Sea. The Chukchi Sea is also  
112 structured by the Siberian Current, which flows eastward along the northern coast of Russia. The  
113 Chukchi Sea, particularly in the north, is also heavily influenced by fresh, cold winter water,  
114 derived from sea-ice melt (Coachman et al., 1975; Weingartner et al., 2005, 2013). North of  
115 Bering Strait, the Bering Sea waters split and branch westward and eastward, encircling the  
116 bathymetrically complex, shallow, and nutrient rich Hanna Shoal in the northern Chukchi Sea  
117 (Coachman et al., 1975; Dunton et al., 2017; Fig. 1).

118           Sea-ice is a primary driver of both Bering and Chukchi ecosystems. The extent of ice  
119 coverage and the timing of ice retreat in the spring drives annual primary productivity by  
120 affecting sea surface temperatures and light availability for photosynthesis, and by providing a  
121 platform for epontic algal growth (Arrigo, 2003). Ultimately, the effects of spring conditions  
122 cascade to lower and upper trophic levels (Stabeno et al., 2010; Hunt et al., 2011, 2018). Sea ice  
123 generally retreats north of Bering Strait throughout late spring and summer, with the ice

124 minimum occurring between September and October. However, ice extent and duration was  
125 minimal overall during 2017-2019 (Siddon and Zador, 2018, 2019).

126 The study area includes large seabird colonies (Stephensen et al., 2003) with an estimated  
127 12 million birds nesting in the Northern Bering and Southern Chukchi subregions (USFWS,  
128 2014). The largest colonies are on St. Matthew and St. Lawrence islands in the Northern Bering,  
129 the two Diomede islands in the Bering Strait, and Cape Thompson and Cape Lisburne in the  
130 Southern Chukchi (Fig. 1). In late summer and early fall this LME is also used by equal numbers  
131 of migratory birds (Kuletz et al., 2015, 2019), particularly short-tailed shearwaters (*Ardenna*  
132 *tenuirostris*), which nest in the southern hemisphere. Other seasonal visitors that nest south of the  
133 study area include members of the Alcidae and Laridae families, as well as waterfowl  
134 (Anatidae), phalaropes (Scolopacidae), and loons (Gaviidae), which pass through from Alaska's  
135 North Slope after breeding.

136

## 137 2.2. Data collection

138

139 At-sea distribution and abundance of seabirds were obtained from surveys conducted  
140 from research vessels using U.S. Fish and Wildlife Service protocols (Kuletz et al., 2008). A  
141 single observer recorded all birds on one side of the vessel, within 300 m and a 90° arc from the  
142 centerline of travel. The observer recorded species, number of individuals, and behavior (on  
143 water, on ice, foraging, in air) and perpendicular distance from the centerline (using distance  
144 bins). Birds were identified to the lowest taxonomic level possible, using 10x binoculars, and  
145 sometimes a digital camera, to assist with species identification. Birds on water or actively  
146 foraging were recorded continuously, whereas birds in the air (not actively foraging by touching  
147 the water surface) were recorded during quick scans within the transect window, at  
148 approximately 1·min<sup>-1</sup> (varying with respect to vessel speed), and avoiding double counting.  
149 Surveys were conducted with seas of Beaufort scale  $\leq 6$  and were discontinued when dense fog  
150 or precipitation impeded visibility. Observations were entered into a laptop computer connected  
151 to a Global Positioning System (GPS), using software DLog3 (R.G. Ford, Portland, OR). Every  
152 record entry was stamped with time, latitude and longitude, and environmental conditions, and  
153 automatically updated at 20 sec intervals to record effort. We divided survey transect lines into  
154 ~3 km segments, with the segment centroid serving as sample location, and calculated density of

155 birds (birds·km<sup>-2</sup>) for each transect segment. Transect widths were narrowed from 300 m to 200  
156 m or based on observation conditions.

157

### 158 2.3. Data treatment and analysis

159

160 Survey effort (Table 1, Fig. 2) within the study area during 2007-2019 totaled 79,426 km,  
161 using only surveys conducted 1 July to 30 September; these months reflect peak breeding season  
162 for seabirds in the study area, and omit June, when we had little survey effort. We compared  
163 species richness, community composition, and abundance of key species within the subregions  
164 between two time periods, 2007-2016 and 2017-2019. The latter years were characterized by  
165 anomalously low sea-ice coverage in the study region, with the warmest year (2018) exhibiting  
166 the highest record of seabird mortalities and reproductive failure (Duffy-Anderson et al., 2019;  
167 Romano et al., this issue). We also examined annual differences in abundance of key species and  
168 Total seabirds (all species combined, including phalaropes and seaducks but excluding other  
169 shorebirds, waterfowl, land birds, and birds of prey; Appendix A).

170

#### 171 2.3.1. Species richness

172 Because sampling effort was not consistent among the four subregions and two time  
173 periods, we used rarefaction curves to examine species richness during each time period and  
174 within each subregion. We randomly resampled 3-km segments (without replacement) and  
175 generated plots of number of species observed vs. number of segments sampled, with 95%  
176 confidence intervals calculated using quantiles from 2000 random draws for each sample size.  
177 During surveys, it was not always possible to identify sightings to the species level, for example  
178 due to a brief or inadequate view. In the rarefaction analysis, a higher-order taxon was counted as  
179 a unique species if and only if a corresponding lower-order taxon was not present in the sample.  
180 For example, an unidentified murre (*Uria* spp.) would be counted as a species if and only if no  
181 common murre (*U. aalge*) or thick-billed murre (*U. lomvia*) occurred in a sample.

182 For the remaining analyses, we applied a 30-km hexagonal cell grid to the study area, and  
183 derived density of each species by cell using the mean of 3-km segments within each cell. Birds  
184 that had not been identified to species were apportioned from higher-order taxa to species based  
185 on the ratio of identified birds within a cell and year. If there were no identified species within a

186 higher-order taxon in a given cell and year (ranging from 0-7% of cells, with an average of 1%,  
187 depending on taxon), unidentified birds were prorated to species based on spatial interpolation of  
188 species ratios derived from kriging surrounding cells; kriging applied a cutoff distance of 60 km  
189 (~ 2 grid cells).

190 The number of sampled cells within a subregion varied among years, ranging from 98 to  
191 371 cells for a given year. Because spatial differences in sampling among years could bias  
192 comparisons, we imputed species densities for grid cells missing years using methods described  
193 in Renner et al. (2013) and Kuletz et al. (2014). Species densities of grid cells not surveyed in a  
194 given year were interpolated through time (not space). Within each grid cell, densities in any  
195 missing years were imputed using linear interpolation. Any missing values at the beginning or  
196 end of the time-series were imputed by replacing missing values with the closest neighbor in  
197 time (rather than projecting trends).

198

### 199 2.3.2. Abundance and distribution

200 During preliminary analyses, we examined the distribution and abundance of four  
201 foraging guilds (surface planktivore, diving planktivore, surface piscivore, diving piscivore)  
202 along with individual species. Because the foraging guild patterns were largely driven by the  
203 most abundant species within each guild, here we present results for Total seabirds and seven  
204 focal species: thick-billed murre, common murre, crested auklet (*Aethia cristatella*), least auklet  
205 (*A. pusilla*), northern fulmar (*Fulmarus glacialis*), black-legged kittiwake (*Rissa tridactyla*), and  
206 short-tailed shearwater. We selected these focal species because they were widespread in the  
207 study area (Appendix B) and relatively abundant during all years (Appendix A). Five of them  
208 were the predominate species for seabird communities identified in this LME during 2007-2015  
209 (Kuletz et al., 2019).

210 We used two methods to evaluate distribution and abundance of these species and groups.  
211 First, we calculated annual density estimates for species or species groups from the cell means  
212 within a subregion and year. The grid cell means for each species were used to plot standardized  
213 mean anomalies for each subregion and time period (2007-2016 and 2017-2019). Near the  
214 coastline, some cells were truncated, thus we used weighted averages based on the area of each  
215 hexagon cell; this avoided over-representation in the overall average due to the presence of large  
216 flocks in small cells. Second, we examined the spatial distribution of increases or decreases in

217 seabird densities (by species) by subtracting mean densities (by cell) for 2007-2016 from mean  
218 densities for 2017-2019, and mapping these differences.

219

### 220 2.3.3. Community composition

221 To identify seabird communities in the study area and compare their distribution between  
222 the two time periods, we used K-Means Cluster analysis (Hartigan and Wong, 1979). In the first  
223 step, we grouped the 30-km hexagon grid cells based on similarity in densities of birds, using  
224 log-transformed densities. Clustering was based on species densities, not geographic coordinates,  
225 and performed on all years combined, 2007-2019. Five communities were identified in the study  
226 area, based on the inflection point of within-group sum of squares vs. the number of clusters  
227 (Hartigan and Wong, 1979). In the second step, the clusters were then redistributed to their  
228 respective time-period maps (2007-2016 or 2017-2019).

229 We used R functions and scripts for analyses (R Core Team, 2015), with kriging for  
230 species' ratios applying function *krige* in package *gstat* (Pebesma, 2004). Cluster analysis used  
231 the R function *kmeans* (Hartigan and Wong, 1979).

232

233

## 234 3. Results

235

### 236 3.1. Species richness

237

238 Estimated species richness was higher in the Bering Sea (~40 species) than in the  
239 Chukchi Sea (~30 species) during both time periods. Within the two Bering subregions, species  
240 richness was slightly lower during 2017-2019, whereas it remained similar overall in the two  
241 Chukchi subregions (Fig. 3). However, in both the Bering and Chukchi regions, there was a  
242 reversal in richness between subregions; i.e. during the later period the Chirikov Basin had  
243 slightly higher species richness than the Northern Bering, and the Northern Chukchi had higher  
244 richness than the Southern Chukchi (Fig. 3).

245

### 246 3.2. Spatial changes in density

247



248           Compared to 2007-2016, Total seabird density was higher in 2017-2019 (Table 2), but  
249 the direction of changes in density were not equal across the study area, nor among species.  
250 Mean densities indicated both murre species declined in the later period, whereas both auklet  
251 species and black-legged kittiwakes increased slightly, and short-tailed shearwaters nearly  
252 doubled in density (Table 2). During the later time period, Total seabird density increased along  
253 the Anadyr Current, and in the northern Hope Basin, the western portion of the Northern  
254 Chukchi, and over Barrow Canyon (Fig. 4a). Decreases occurred in most of the Northern Bering,  
255 but also in the eastern Chirikov Basin to southern Hope Basin and the eastern coastal waters of  
256 the Northern Chukchi. This pattern largely reflects that of short-tailed shearwaters, a numerically  
257 dominate species, although shearwaters also showed large increases in 2017-2019 northwest of  
258 Cape Lisburne and over the Hanna Shoal and Barrow Canyon areas (Fig. 4b). Northern fulmars  
259 did not have a clear pattern of spatial change, with both increases and decreases scattered  
260 throughout the study area and large areas with no change (Fig. 4c). Black-legged kittiwakes also  
261 showed little evidence of a clear pattern, although there were more increases in Hope Basin and  
262 northwest of Cape Lisburne (Fig. 4d).

263           Common murres showed few increases in abundance, with those mainly in the Northern  
264 Bering, and they otherwise decreased, particularly in the Southern Chukchi (Fig. 4e). Thick-  
265 billed murres increased in later years northwest of Cape Lisburne, but primarily decreased  
266 throughout the study area, including near the St. Matthew colony (Fig. 4f). Least auklets had  
267 large increases in the Chirikov Basin, but mainly decreased throughout the Chukchi Sea (Fig.  
268 4g). Crested auklets increased near the Anadyr Current in the Chirikov Basin and in the northern  
269 edge of the Northern Chukchi, but declined in other areas of the Northern and Southern Chukchi  
270 (Fig. 4h).

271

### 272 *3.3. Annual trends in abundance*

273

274           For Total seabirds, the annual trends in abundance indicated a general northward shift in  
275 distribution. This shift began around 2014 in the Bering Sea, 2015 in the Southern Chukchi, and  
276 2016 in the Northern Chukchi, although relative abundance was below the long-term mean in  
277 2019 for all but the Northern Chukchi (Fig. 5a). In contrast, abundance in the Northern Bering  
278 was below the long-term mean for most years after 2013. This general pattern reflected the

279 influence of the most abundant avian species in the study area, the short-tailed shearwater, the  
280 least auklet, and the crested auklet (Table 2). Short-tailed shearwaters differed from Total  
281 seabirds in having extremely high abundance in the Chirikov Basin and the Southern Chukchi in  
282 2015 (Fig. 5b). Trends of northern fulmars were mixed, with fluctuations between subregions of  
283 the Bering and in the Southern Chukchi, but generally lower use of the Northern Chukchi after  
284 2010 (Fig. 5c). Abundance of black-legged kittiwakes shifted from the Northern Bering during  
285 2007-2011 to the Chirikov Basin during 2012-2015, and to the Chukchi subregions from 2014-  
286 2019 (Fig. 5d).

287 In general, the diving alcids declined in recent years in the Chukchi, with the *Aethia*  
288 auklets increasing in the Chirikov Basin and Northern Bering, and the murre mostly decreasing  
289 throughout the study area after 2013. Starting in 2014 both common murre (Fig. 5e) and thick-  
290 billed murre (Fig. 5f) showed steadily declining trends in the Northern Bering and below  
291 average abundance (common murre) or very low abundance (thick-billed murre) in the Chirikov  
292 Basin. Abundances of both murre species were below the long term mean in the Chukchi  
293 subregions for most years after 2013. In contrast, least auklets, which were highly abundant in  
294 the Chukchi during 2010 to 2012, increased abruptly in the Chirikov Basin and Northern Bering  
295 during 2017-2019 (Fig. 5g). Crested auklets showed a similar pattern, although they were  
296 sporadically abundant in the Northern Chukchi and did not substantially increase in the Chirikov  
297 Basin until 2018 (Fig. 5h).

298

### 299 3.4. Seabird communities

300

301 Within our study area we identified five clusters of grid cells that differed from each  
302 other in seabird community composition and densities (Appendix C). Four of the clusters had the  
303 same primary species as the community types identified by Kuletz et al. (2019); these clusters  
304 were dominated by thick-billed murre, least auklets, crested auklets, and short-tailed  
305 shearwaters, plus a 'Low Density' cluster type defined by low total densities and no definitive  
306 predominant species (no species had a mean density of  $>0.54$  birds·km<sup>-2</sup>). A sixth community  
307 type identified by Kuletz et al. (2019), dominated by northern fulmars, was not distinguished in  
308 this new analysis, reflecting the omission of more southerly waters of the outer Bering Sea shelf  
309 that were part of the previous study.

310           The distribution maps for the five community clusters in each time period depicted a  
311 spatial contraction of the thick-billed murre, crested auklet, and least auklet-dominated clusters  
312 during 2017-2019 (Fig. 6). During the late period the thick-billed murre cluster was less  
313 extensive throughout the study area and was located primarily near St Matthew Island in the  
314 Northern Bering and the Cape Thompson and Cape Lisburne colonies in the Southern Chukchi.  
315 The crested auklet cluster covered a much smaller area and was concentrated in the northeastern  
316 portion of its previous range in the Chukchi Sea, although there were also isolated, scattered cells  
317 between Chirikov Basin and Hope Basin (Fig. 6). The least auklet cluster also covered less area  
318 in 2017-2019, and was found primarily south of Bering Strait, abandoning its earlier occupation  
319 of Hope Basin.

320           In contrast to the three alcid-dominated clusters, the short-tailed shearwater-dominated  
321 cluster expanded during 2017-2019, and was located primarily in the Chukchi Sea. Its increase  
322 was greatest in Hope Basin and contiguously along the western edge of the study area and in a  
323 band from Hanna Shoal to Wainwright and Point Barrow – the Barrow Canyon area (Fig. 6). The  
324 Low-Density cluster also expanded in the later period. During 2017-2019, this cluster covered  
325 more area (compared to 2007-2016) throughout the Bering Sea shelf, particularly in the Northern  
326 Bering subregion. Its distribution in the Southern Chukchi did not change much between time-  
327 periods, but in the eastern half of the Northern Chukchi, it greatly expanded during 2017-2019  
328 (Fig. 6).

329

330

#### 331 **4. Discussion**

332

333           During the exceptionally warm, low-ice years of 2017-2019, we found evidence of broad-  
334 scale shifts in distribution of individual species and of identified seabird communities compared  
335 to the previous decade. Sea-ice extent in the northern portion of the Bering Sea was the lowest on  
336 record during the late period of our study. In 2017, sea ice failed to form over the northwestern  
337 Bering Shelf due to atypical southerly wind patterns. Unprecedented open water predominated  
338 throughout the Northern Bering and Southern Chukchi subregions in 2018 and 2019 as well  
339 (Siddon and Zador, 2018, 2019). Nonetheless, density of Total seabirds increased approximately

340 20% during this period, with the increase largely due to short-tailed shearwaters in the Chukchi  
341 Sea, and least and crested auklets in the Chirikov Basin.

342 Short-tailed shearwaters breed on islands off Australia's southern coast during the austral  
343 summer. After breeding they migrate to Alaska for the boreal summer, and reach the  
344 northernmost extent of their migrations in the Chukchi Sea. Untethered from nesting colonies  
345 during their non-breeding season, shearwaters can readily respond to shifts in prey distribution.  
346 In contrast, the two species of auklet nest during summer in dense colonies on islands in the  
347 Chirikov Basin and Northern Bering, although some auklets in the offshore waters could have  
348 originated from colonies in the Aleutian Archipelago (Will et al., 2017) or the Siberian coast  
349 (USFWS, 2014). What all three species have in common is a diet primarily composed of  
350 zooplankton. The short-tailed shearwater is considered an omnivore, with a varied diet that  
351 includes euphausiids, copepods, cephalopods, amphipods, and larval and juvenile fish (Hunt et  
352 al., 2002; Ogi et al., 1980), but recent studies suggest it primarily feeds on euphausiids while in  
353 Alaska (Nishizawa et al., 2017, this issue). Both auklet species are planktivorous, with the  
354 smaller-bodied least auklet feeding mainly on *Neocalanus* copepods, and the larger crested  
355 auklet feeding on a variety of large copepod taxa, euphausiids, and occasionally, larval fish  
356 (Sheffield-Guy et al., 2009; Gall et al., 2006).

357 The Chukchi Sea has a late seasonal plankton bloom tied to the timing of ice retreat, long  
358 daylight hours, and stratification, which makes copepods available into late summer  
359 (Weingartner et al., 2013, 2017; Danielson et al., 2017). In comparison to historic patterns  
360 (1940s to 1990s), seasonally early ice retreat in the 2000s was associated with higher primary  
361 productivity and larger biomasses of lipid-rich copepods (such as *Calanus glacialis*), euphausiids  
362 (*Thysanoessa* spp.) and amphipods (*Themisto* spp.) (Ershova et al., 2015; Matsuno et al., 2011).  
363 This may be why Gall et al. (2017) found higher predicted abundance of short-tailed shearwaters  
364 and crested auklets with earlier ice retreat, based on survey data from the Chukchi Sea during  
365 1975-2012. Our shearwater observations during 2017-2019 are consistent with that model.  
366 However, planktivorous seabirds, primarily short-tailed shearwaters and crested auklets, did not  
367 predominate in the offshore waters of the Chukchi Sea until sometime between the 1980s and  
368 2007 (Gall et al., 2017). The late summer and fall presence of crested and least auklets far from  
369 breeding colonies were presumed to be post-breeding birds replenishing body reserves before  
370 migrating back to the Bering Sea for winter (Kuletz et al., 2019; Will et al., 2017).

371 During the current decade, sea ice has further diminished. Zooplankton communities in  
372 the Chukchi Sea have shown highly localized influences of shifting water masses, resulting in  
373 high interannual variability (Pinchuk and Eisner, 2017; Spear et al., 2019). The irregular pattern  
374 of abundance exhibited by crested auklets in the Northern Chukchi may reflect these localized  
375 fluctuations (Fig. 5h). Preliminary examination of zooplankton samples from the Northern  
376 Chukchi found that large copepods were more abundant in 2017 than in 2019, albeit both years  
377 had lower copepod abundance than during cooler years of 2012-2015 (D. Kimmel, unpubl. data).  
378 Our observations suggest that crested auklets and short-tailed shearwaters took advantage of  
379 aggregations of large copepods and euphausiids in the Northern Chukchi, particularly in 2017  
380 (Fig. 5 b, h).

381 The abundance of crested auklets in the Northern Chukchi suggests that a portion of the  
382 Alaska-wide metapopulation rely on the prey in these cooler waters. However, the dynamics of  
383 sea ice, water temperature, primary productivity, and zooplankton are complex. Longer periods  
384 of open water and thinner sea ice have been linked to increased open water primary productivity  
385 in the Arctic (Arrigo et al., 2008; Brown et al., 2011) and an increase in advected Pacific-Bering  
386 zooplankton (Ershova et al., 2015). At the same time, warm, low-ice conditions have been  
387 associated with a decrease in production by ice algae, which are rich in long-chain omega-3 fatty  
388 acids (Søreide et al., 2010), and also with potentially lower local production of Arctic  
389 zooplankton fauna, including *C. glacialis* (Spear et al., 2019). In studies during the relatively  
390 cool years of 2010-2012, Spear et al. (2019) found highest concentrations of *C. glacialis* along  
391 the eastern waters of the Northern Chukchi, from Icy Cape to Barrow Canyon. Indeed, during  
392 those years the crested auklet community cluster extended well into these waters (Kuletz et al.,  
393 2019), whereas during the warmer period of 2017-2019 (this study), the Low Density seabird  
394 community predominated in this area (Fig. 6).

395 Although least auklets also appear to move into the Chukchi Sea in summer and fall, they  
396 primarily occur in the Southern Chukchi (Kuletz et al., 2015, 2019). Small copepods, which least  
397 auklets consume, are often abundant in Hope Basin and remained available there in 2017 and  
398 2019 (no data are available for 2018; Kimmel, unpubl. data). Small copepod taxa (*Acartia* spp.,  
399 *Pseudocalanus* spp., and *Oithona* spp.), were also abundant in the Northern Bering and Chirikov  
400 Basin in 2018 (Kimmel et al., 2018), when least auklets shifted to those subregions (Fig. 5g).

401 Concurrent with decreases in sea ice, northward flow from the Bering Sea has been  
402 increasing (Woodgate et al., 2012), which could increase advection of zooplankton and larval  
403 fish from the Bering shelf to Hope Basin and Hanna Shoal in the Chukchi Sea (Grebmeier et al.,  
404 2006; Dunton et al., 2017). Since the 2000s, zooplankton biomass has also increased along the  
405 Chukchi shelf break (Lane et al., 2008). Despite unusually high densities of least and crested  
406 auklets in the Chirikov Basin during 2017-2019, the Chukchi Sea will likely remain important  
407 post-breeding foraging habitat for these species, as evident in their overall distributions  
408 (Appendix B) and observed increases in some locations of the Northern Chukchi (Fig. 4 g, h).

409 An important feature of the Northern Chukchi is Barrow Canyon, which is a recognized  
410 hotspot of seabird activity (Kuletz et al., 2015), and where we found increased densities of  
411 several species in 2017-2019. Abundance of short-tailed shearwaters, and to lesser extent black-  
412 legged kittiwakes and northern fulmars, increased in the Barrow Canyon area during the late  
413 period. These surface feeders may forage over the canyon and adjacent waters because of the  
414 associated upwelling and concentration of euphausiids (Okkonen et al., 2011), as well as a  
415 variety of forage fishes attracted to large biomasses of copepods there (Logerwell et al., 2018).

416 The northward distributional shift observed for seabirds during this study was most  
417 evident for short-tailed shearwaters; higher densities began in the Chirikov Basin in 2014, the  
418 Southern Chukchi in 2015, and the Northern Chukchi in 2016, although shearwater abundance  
419 was near the long-term mean in 2018 and 2019 (Fig. 5b). This pattern coincides with seabird  
420 mortality events that included shearwaters in the Bering Strait region in summers of 2017-2019.  
421 The short-tailed shearwater was the main species impacted by the largest die off in the Bering  
422 Sea in recent years, in the southeast Bering Sea in 2019 (Siddon and Zador, 2019; USFWS,  
423 unpubl. data). Necropsies revealed birds were emaciated and starved, thus the large increases in  
424 shearwaters observed in the Chukchi Sea suggest foraging conditions were forcing ever-farther  
425 migration north to obtain energy stores for the migration back to breeding grounds. The extra  
426 distance may have contributed to the late arrival of shearwaters to breeding sites in Australia  
427 recorded in October-November of 2019 (Liao 2019).

428 Piscivorous seabirds could also have been impacted by changes in their prey. A variety of  
429 forage fish are available in the study area, with the lipid-rich Arctic cod (*Boreogadus saida*) the  
430 most abundant (De Robertis et al., 2017; Logerwell et al., 2018). Age-0 Arctic cod were  
431 particularly abundant in the Northern Chukchi during 2012 and 2013, suggesting it is an

432 important nursery ground for the species (De Robertis et al., 2017). In the northern Bering Sea,  
433 forage fish biomass in summer 2019 was low compared to previous years, indicating poor  
434 conditions for fish growth and survival, or alternatively, that the fish migrated north for better  
435 foraging (Yasumiishi et al., 2019). Arctic cod prefer cold, high salinity water masses, where  
436 there tends to be high biomass of large copepods (De Robertis et al., 2017; Logerwell et al.,  
437 2020). While the effects of warm conditions during 2017-2019 are not yet fully understood,  
438 evidence suggests that key seabird prey species, at least in the Bering Sea, were either low in  
439 abundance or shifted distribution (Duffy-Anderson et al., 2019; Siddon and Zador, 2018, 2019).  
440 These changes in prey availability could have differentially affected breeding seabirds, or birds  
441 that have restricted foraging ranges. Murres, which have high wing loading, tend to forage where  
442 prey patches are persistent and highly aggregated, or forage closer to their colony (Decker and  
443 Hunt, 1996; Sigler et al., 2012).

444 Both species of murres also experienced mass mortality events in the Bering Sea during  
445 2017-2019, with evidence of starvation (Romano et al., this issue; Siddon and Zador, 2018,  
446 2019) and potentially avian disease (A. Will et al., this issue). The low numbers of murres at  
447 colonies in 2018 (Romano et al., this issue; Will et al., this issue), together with broad-scale  
448 reductions in offshore densities (this study) concurrent with the mortality events, suggest major  
449 reductions in murre populations have probably occurred. Notably, Piatt et al. (2020) speculated  
450 that based on satellite-tagged murres, the huge mass mortality of common murres in the Gulf of  
451 Alaska during the winter of 2015-2016 could have included birds from the Bering Sea. This  
452 would be consistent with the trend of lower abundance in offshore waters of our study area,  
453 although we show a decline in abundance of murres starting in 2014 (Fig. 5e, f). In addition,  
454 euphausiids make up a high proportion of the diets of adult thick-billed murres, but not common  
455 murres. The greater dietary diversity of thick-billed murres may be one reason their densities  
456 were more stable than that of common murres, particularly in the Chukchi Sea.

457 Despite broad-scale declines in abundance at sea, murre (and kittiwake) plot counts at the  
458 Cape Lisburne colony in the Southern Chukchi increased at a rate of 6-7% in 2019, with an  
459 average increase of ~ 4% per annum over the past decade (Dragoo et al., 2020). The unusually  
460 high rate of growth would likely require immigration (D. Dragoo, pers. comm.), perhaps an  
461 indication of better foraging conditions near Cape Lisburne. In contrast, the murre colony at  
462 Cape Thompson (~100 km over water to the south) has decreased since the 1960s (Dragoo et al.

463 2000), indicating that murre breeding population trends have not been consistent among Chukchi  
464 Sea colonies. Nonetheless, it is noteworthy that at least the northernmost large colony in the  
465 Chukchi Sea shows increases in murre and kittiwakes, while the four colonies monitored by the  
466 Alaska Maritime National Wildlife Refuge in the southern Bering Sea show evidence of declines  
467 in murre, particularly common murre, and three of these colonies show declines in kittiwakes  
468 (Dragoo et al. 2000). The decrease in abundance of murre that we detected in offshore waters  
469 may reflect population declines in murre throughout the Bering Sea. Black-legged kittiwakes  
470 show a similar but less conclusive pattern of convergence between colony and offshore trends.

471         During 2017-2019, seabird species richness of the Northern Chukchi increased, while  
472 richness of other subregions converged at a slightly lower level than during the prior decade.  
473 This suggests that less-abundant seabird species were occurring in the Northern Chukchi with  
474 increasing frequency during the later period. The convergence of species richness estimates  
475 between the Bering and Chukchi regions was mainly due to a decrease in species richness in the  
476 Bering Sea, and was concurrent with the expansion of the Low Density community cluster.  
477 Notably, the expansion of the Low Density community during the three warmest years (2017-  
478 2019) was nearly entirely along the eastern side of the study area. This expansion occurred in the  
479 Northern Bering and Chirikov Basin throughout the Inner Shelf, including areas east and south  
480 of St. Lawrence Island, which has large seabird colonies (Fig. 6). The Low Density community  
481 primarily displaced the short-tailed shearwater and thick-billed murre community clusters in the  
482 Bering Sea, and in the Northern Chukchi it displaced the short-tailed shearwater, thick-billed  
483 murre, and crested auklet communities. Thus, multiple foraging guilds appear to have been  
484 affected by conditions that concurrently led to the expansion of the Low Density community  
485 type.

486         The Inner Shelf waters of the Bering Sea, influenced by the fresher, warmer waters of the  
487 Alaska Coastal Current, have long been recognized as being nutrient-poor. These waters tend to  
488 have smaller zooplankton species, lower fish biomass (Eisner et al., 2013) and fewer seabirds  
489 compared to Anadyr waters to the west (Piatt and Springer, 2003; Sigler et al., 2017). The  
490 expansion of a Low Density seabird community in recent years suggests that large-scale  
491 ecosystem changes are altering the Inner Shelf, and to some degree the Middle Shelf and  
492 associated currents, thereby expanding the area of low productivity. In contrast, seabird density  
493 remained high near the Anadyr Current and western portions of the northern Bering and Chukchi



494 seas. However, we lack sufficient data on seabird distribution west of the International Dateline  
495 to determine how far west those conditions exist. A long-term examination of marine fish from  
496 the Bering and Chukchi seas found that taxa respond to climate-related changes at different  
497 spatial and temporal scales (Alabia et al., 2018); similarly, we show that seabird species  
498 demonstrate a diversity of distributional responses, which may provide some level of resilience  
499 to their long-term prospects in the Pacific Arctic.

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501

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503

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### 743 **Figures and Tables**

744

745 Fig. 1. The Bering Sea and Chukchi Sea study area, showing generalized trajectories of major  
746 water masses. Map by EAL, based on Dunton et al. (2017).

747

748 Fig. 2. Four subregions of the study area: Northern Bering (light green), Chirkov Basin (dark  
749 green), Southern Chukchi (light blue) and Northern Chukchi (dark blue), with seabird survey  
750 transects overlaid for each time period.

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752 Fig. 3. Species richness (rarefaction curves) in four subregions of the study area, for 2007-2016  
753 and 2017-2019. Mean (solid lines) and 95% confidence intervals (shading) were derived from  
754 random selection of 3-km transect segments from surveys conducted during each time period and  
755 subregion.

756

757 Fig.4. Distribution of increases (oranges) and decreases (blues) in densities of Total seabirds and  
758 seven focal species in 2017-2019, compared to 2007-2016. Mean densities were calculated per  
759 30-km grid cell within each time period for cells surveyed in both time periods.

760 Fig. 5. Standardized mean anomalies for Total seabirds and seven focal species, for each  
761 subregion across all years, 2007-2019.

762 Fig. 6. Distribution of five identified seabird community types (clusters) during two time  
763 periods, based on K-means Cluster Analysis. Colors represent community types referred to by  
764 the most abundant species (Clusters 1 – 4), or by low density and lack of a dominant species  
765 (Cluster 5).

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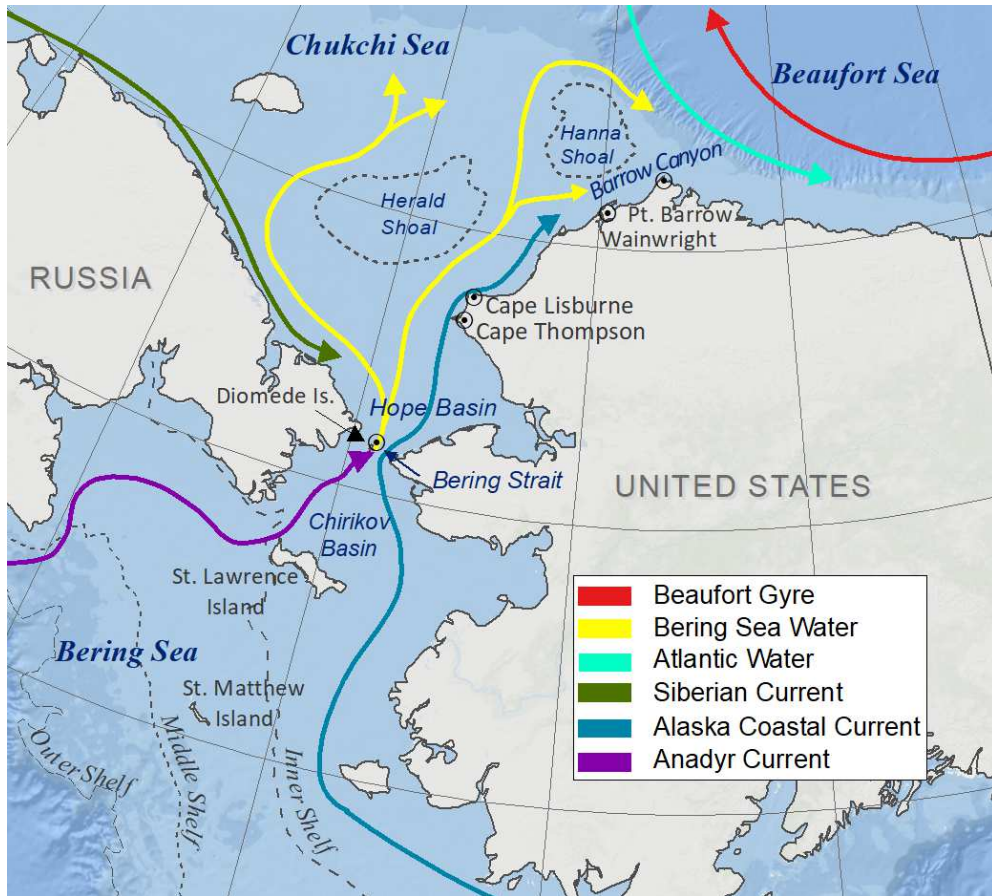


Figure 1. The Bering Sea and Chukchi Sea study area, showing generalized trajectories of major water masses. Map by EAL, based on Dunton et al. (2017).

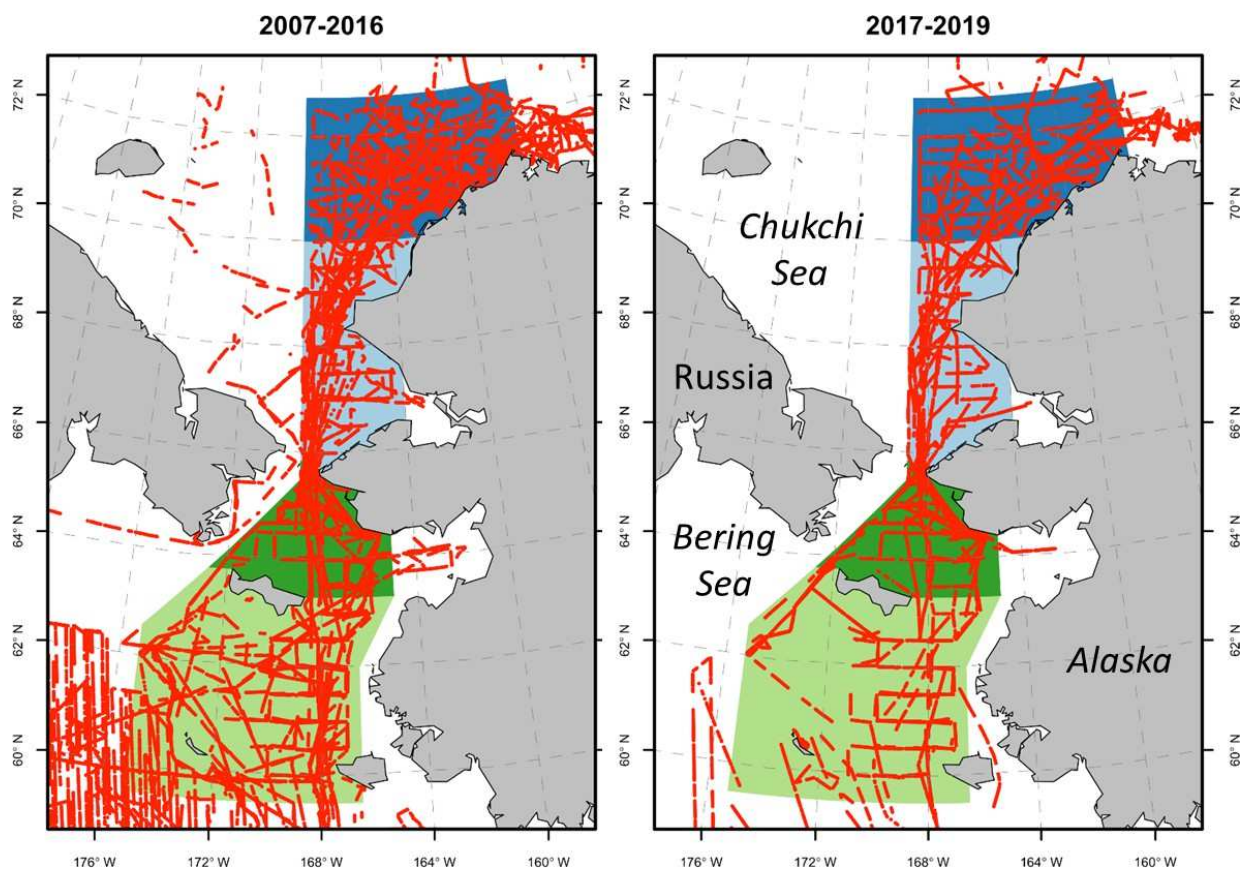


Figure 2. Four subregions of the study area: Northern Bering (light green), Chirkov Basin (dark green), Southern Chukchi (light blue) and Northern Chukchi (dark blue), with seabird survey transects overlaid for each time period.

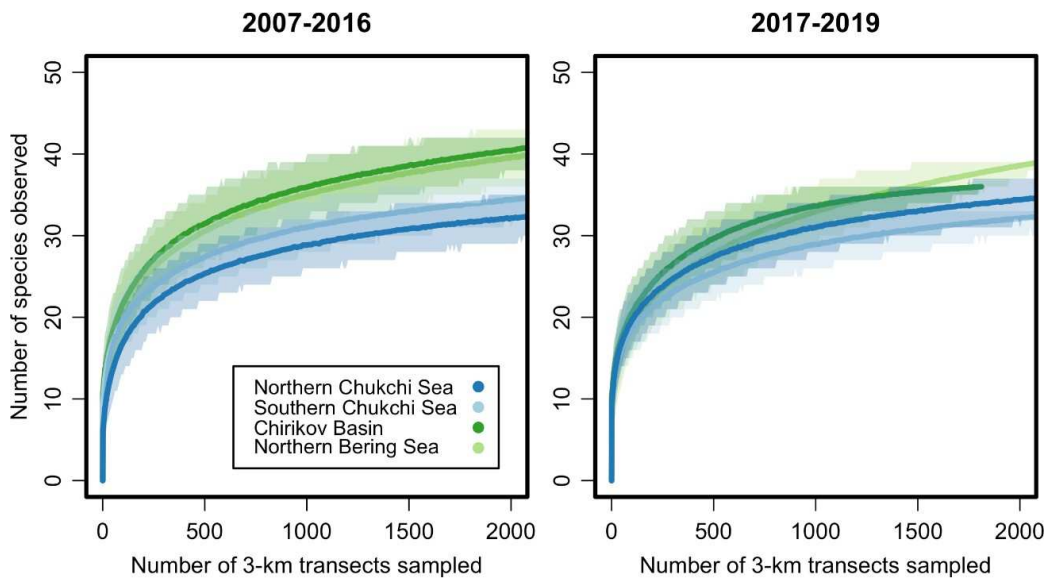


Figure 3. Species richness (rarefaction curves) in four subregions of the study area, for 2007-2016 and 2017-2019. Mean (solid lines) and 95% confidence intervals (shading) were derived from random selection of 3-km transect segments from surveys conducted during each time period and subregion.

Figure 4. Distribution of increases (oranges) and decreases (blues) in densities of Total Seabirds and seven focal species in 2017-2019, compared to 2007-2016. Mean densities were calculated per 30-km grid cell within each time period for cells surveyed in both time periods.

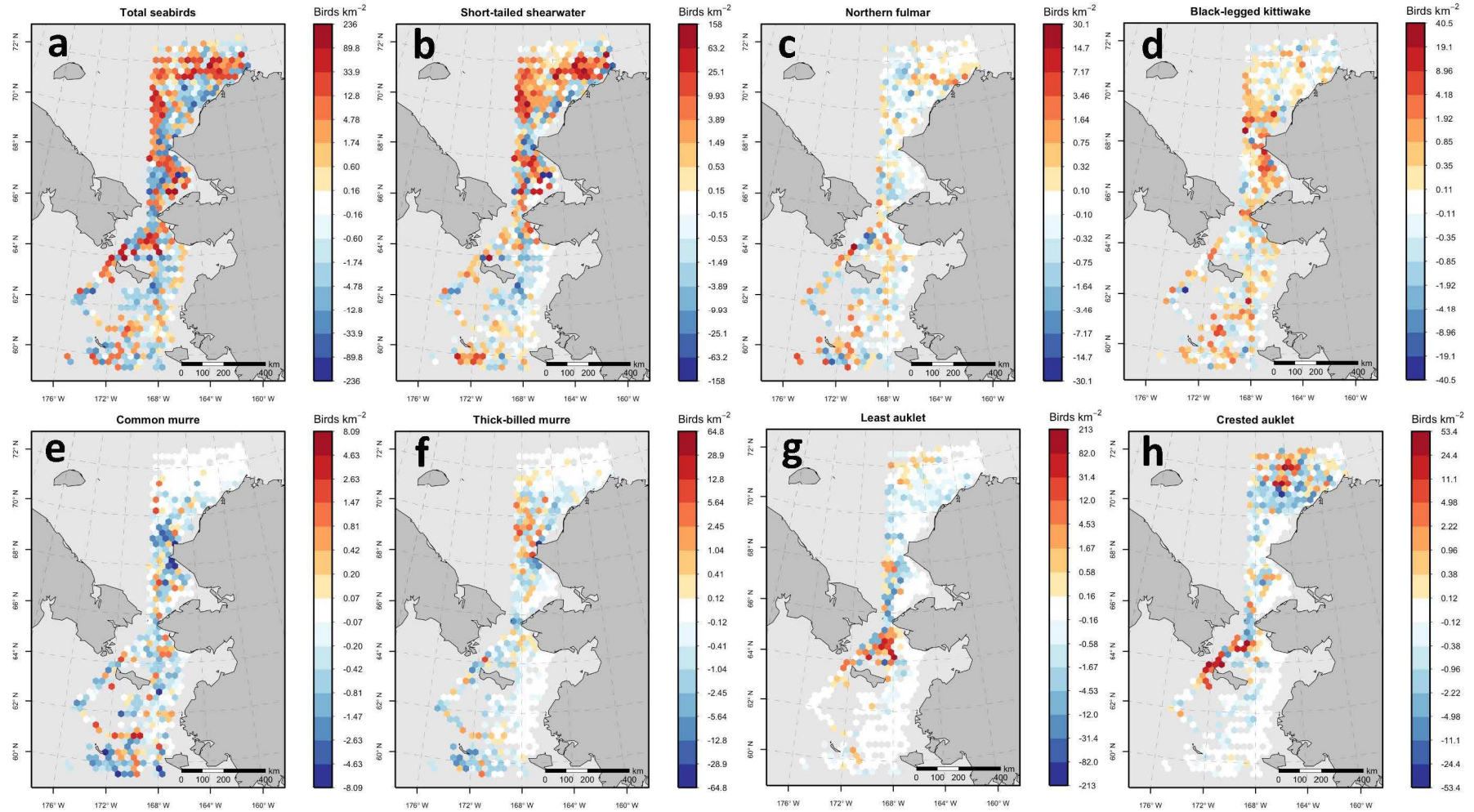




Figure 5. Standardized mean anomalies for Total Seabirds and seven focal species, for each subregion across all years, 2007-2019.

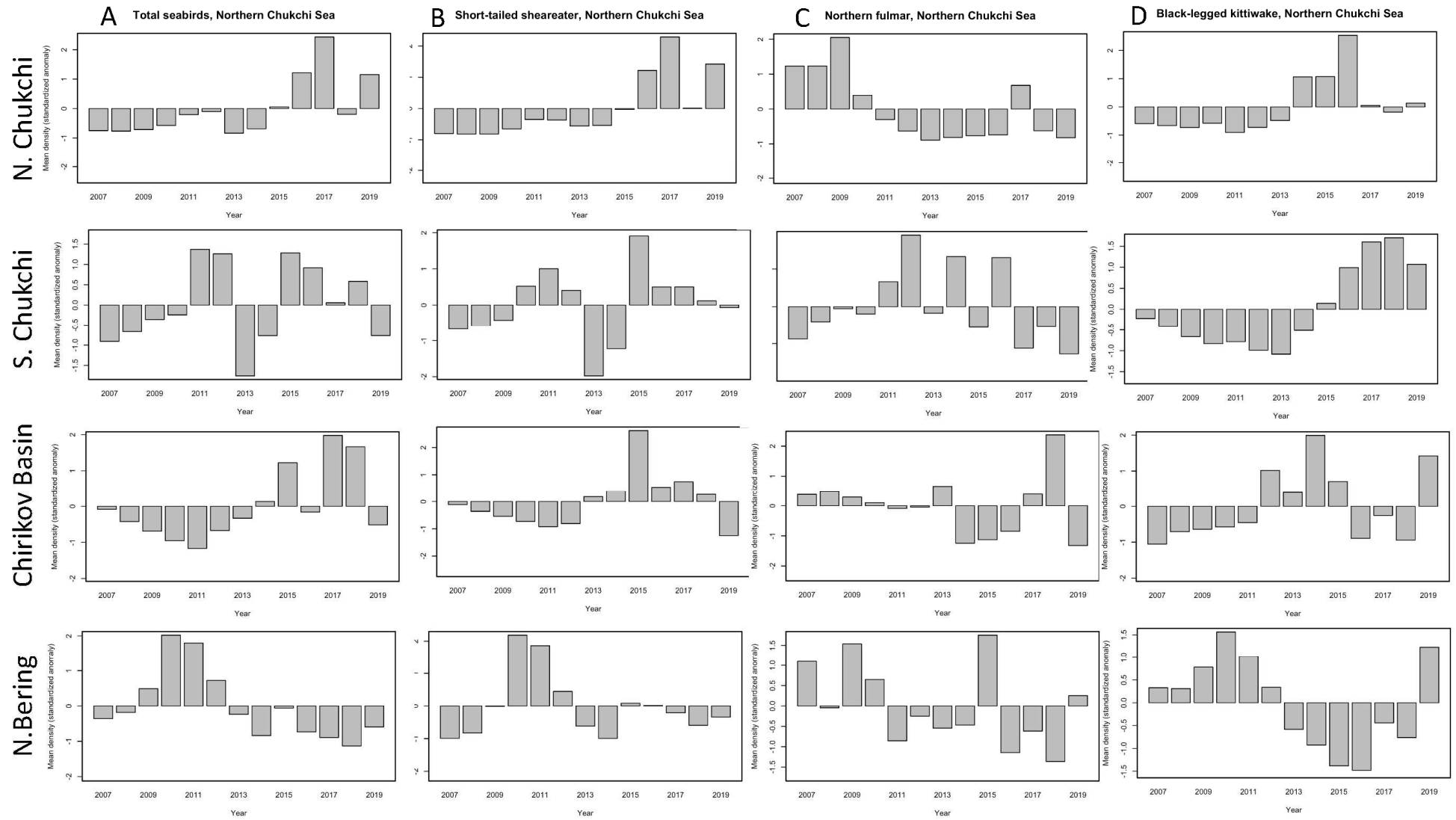
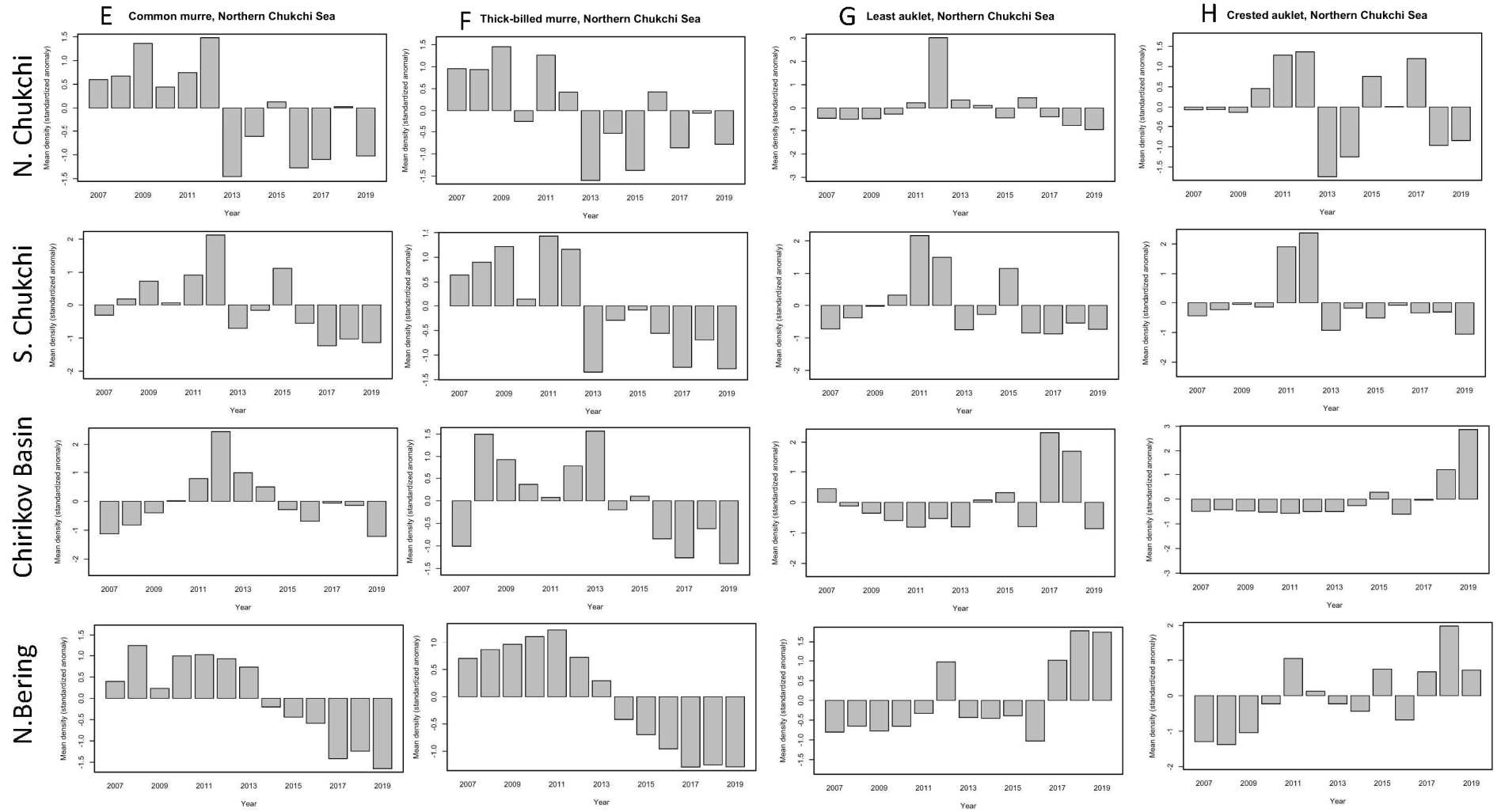


Figure 5. continued





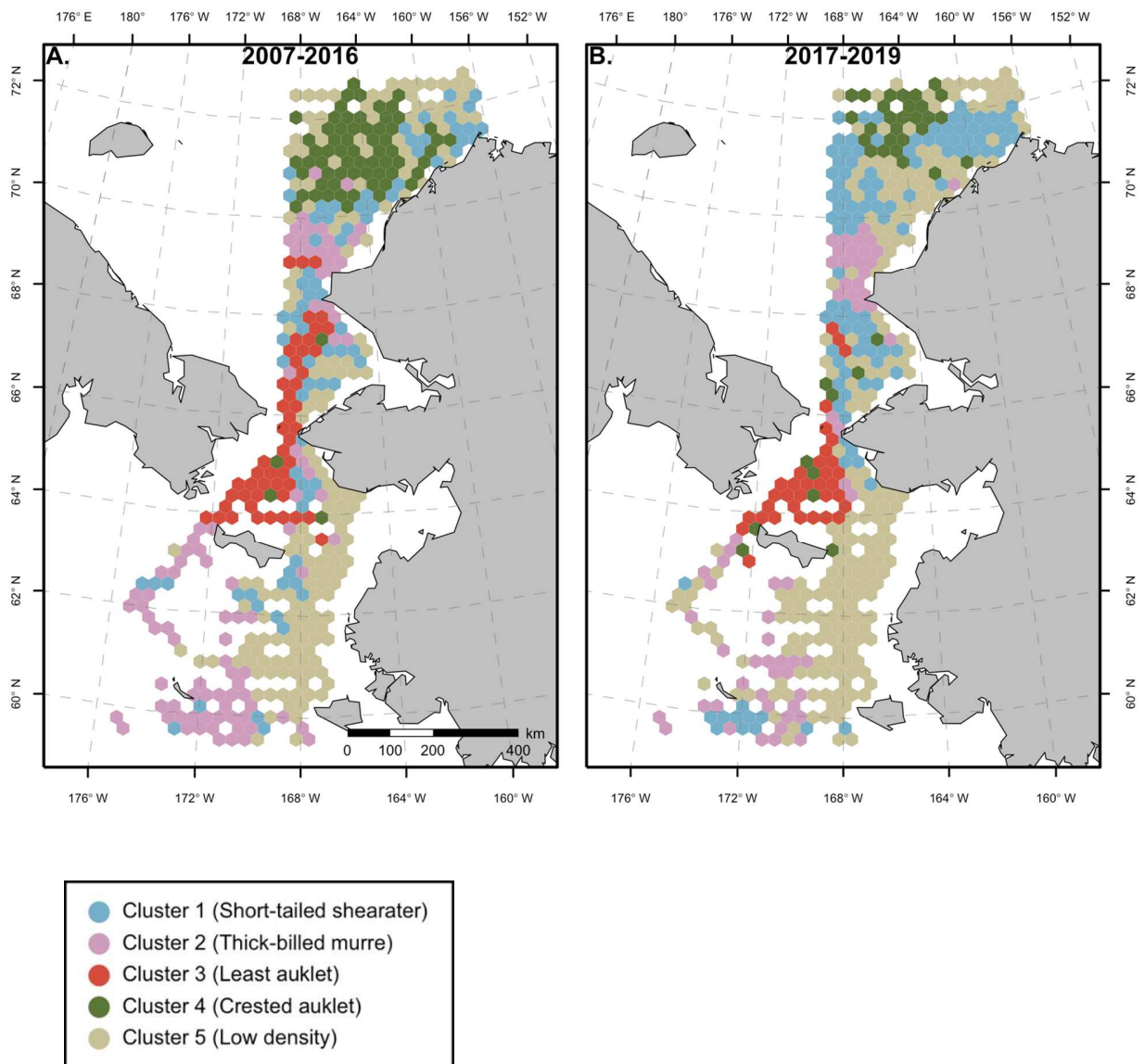


Figure 6. Distribution of five identified seabird community types (clusters) during two time periods, based on K-means Cluster Analysis. Colors represent community types referred to by the most abundant species (Clusters 1 – 4), or by low density and lack of a dominant species (Cluster 5).

Table 1. Survey effort during two time periods, 2007-2016 and 2017-2019.

	2007-2016	2017-2019	Total
Subregion	Number of km surveyed		
Northern Chukchi	16969	9096	26065
Southern Chukchi	11393	7335	18728
Chirikov Basin	7212	5110	12322
Northern Bering	16268	6043	22311
	Number of 30-km grid cells		
Northern Chukchi	608	299	907
Southern Chukchi	425	197	622
Chirikov Basin	306	164	470
Northern Bering	820	295	1115

Table 2. Mean density (birds·km<sup>-2</sup>), by subregion, of 7 focal species and for Total Birds (includes all species in Appendix A), during two time periods, 2007-2016 and 2017-2019.

Common Name	Latin name	2007-2016					2017-2019				
		Mean density					Mean density				
		Northern Bering	Chirikov Basin	Southern Chukchi	Northern Chukchi	all Regions	Northern Bering	Chirikov Basin	Southern Chukchi	Northern Chukchi	all Regions
Common Murre	<i>Uria aalge</i>	0.91	0.78	0.92	0.08	0.62	0.37	0.48	0.37	0.05	0.28
Thick-billed Murre	<i>Uria lomvia</i>	0.88	0.87	1.79	0.35	0.91	0.29	0.53	1.29	0.23	0.52
Least Auklet	<i>Aethia pusilla</i>	0.07	6.98	2.85	0.43	1.87	0.16	10.48	0.64	0.12	1.95
Crested Auklet	<i>Aethia cristatella</i>	0.15	1.97	0.57	2.27	1.21	0.24	4.70	0.34	1.74	1.50
Black-legged Kittiwake	<i>Rissa tridactyla</i>	0.61	0.71	0.82	0.38	0.60	0.75	0.68	1.66	0.31	0.78
Northern Fulmar	<i>Fulmarus glacialis</i>	0.95	0.59	0.42	0.23	0.54	0.73	0.99	0.22	0.22	0.49
Short-tailed Shearwater	<i>Ardenna tenuirostris</i>	1.79	3.71	5.74	4.22	3.76	1.27	3.06	6.46	11.48	6.05
<b>Total Birds*</b>		<b>6.24</b>	<b>18.70</b>	<b>15.76</b>	<b>8.58</b>	<b>11.02</b>	<b>4.53</b>	<b>23.29</b>	<b>14.68</b>	<b>14.83</b>	<b>13.16</b>
* Includes all species observed, see Appendix A											