

*DSR2\_2018\_91\_Kuletz et al. Seabirds in the DBO array-Final draft 03.28.19*

1 **Representation of the Pacific Arctic seabird community within the Distributed Biological**  
2 **Observatory array, 2007-2015**

3

4 Kathy J. Kuletz<sup>a\*</sup>, Daniel Cushing<sup>b</sup>, Erik E. Osna<sup>a</sup>, Elizabeth A. Labunski<sup>a</sup>, Adrian Gall<sup>c</sup>,

5 <sup>a</sup>U.S. Fish and Wildlife Service, 1011 E. Tudor Rd., Anchorage, AK 99503, USA

6 <sup>b</sup>Pole Star Ecological Research, LLC, Anchorage, AK, USA

7 <sup>c</sup>ABR, Inc., Environmental Research & Services, P.O. Box 80410, Fairbanks, AK 99708, USA

8

9 **ABSTRACT**

10

11 An array of eight Distributed Biological Observatory (DBO) sites serve as long-term monitoring areas for  
12 three geographic regions: the northern Bering, eastern Chukchi, and Beaufort seas. The locations of the  
13 DBO sites were largely determined based on abundance and diversity of benthic invertebrates. It is not  
14 clear how well these fixed sampling sites can detect changes in processes and populations that operate  
15 over spatial scales that are 1–3 orders of magnitude greater than the areas sampled by the DBO sites. In  
16 this paper, we examine whether the DBO array provides a reasonable method by which to describe and  
17 monitor the distribution and community composition of seabirds in the eastern Pacific Arctic, and if it  
18 captures areas of high seabird abundance. We used vessel-based survey data totaling ~115,860 km of  
19 transects within the study area from July-October, 2007-2015. We compared species richness, diversity,  
20 abundance, and community composition of seabirds among DBO sites and to the broader geographic  
21 regions. In general, the avifauna of DBO sites were representative of their respective surrounding region,  
22 although sampling effort in the Beaufort was limited. Species richness (totaling 63 species) was highest in  
23 the Bering region and lowest in the Beaufort region. Species diversity indices were similar among DBO  
24 sites and regions, except for exceptionally low diversity in the two easternmost DBO sites of the Beaufort  
25 region. Total seabird abundance was highest in and near Bering Strait, and dropped abruptly northward  
26 and eastward of Point Barrow. We used K-means cluster analysis to identify six community types across

27 the entire study area, with five community types identified as having at least one numerically dominant  
28 species, and one community type defined by very low densities of a variety of species. Several  
29 community types were associated with major current systems (e.g. Anadyr Current, Alaska Coastal  
30 Current), and for two community types, breeding colony locations were also influential. Short-tailed  
31 shearwaters were the most abundant species in five of the eight DBO sites, and they were the numerically  
32 dominant species in a community that was represented from DBO 1 through DBO 6. Overall, variance in  
33 abundance was much greater by DBO site (or region) than by year for total birds and for seven of eleven  
34 taxa. Taxa with greater interannual variance than spatial variance were shearwaters and phalaropes  
35 (among regions), and murrelets (among DBO sites), all of which are late summer migrants to the study  
36 area, and glaucous gulls, a circumpolar species. The consistency in species' abundance by site indicates  
37 that DBO sites will be useful for monitoring seabirds in each region. As an array, the DBO sites captured  
38 major hotspots of seabird abundance as well as the seabird communities, except for the fulmar-dominated  
39 community in the outer Bering Shelf. However, all DBO sites will need to be surveyed to capture the full  
40 range of seabird communities in this study area. The Beaufort DBO sites require more survey coverage  
41 than currently achieved to fully evaluate their effectiveness to monitor changes in seabirds for that region.

42

43 **Keywords:** Distributed Biological Observatory, Pacific Arctic, Seabird communities, Seabird  
44 distribution, Seabird species richness, Bering Sea, Chukchi Sea, Beaufort Sea

45

46 \*Corresponding author,

47 *E-mail address:* kathy\_kuletz@fws.gov (K.J. Kuletz)

48

## 49 1. INTRODUCTION

50

51 A rapidly changing Arctic requires monitoring of ecological processes and biological components at  
52 large spatial and temporal scales, which can be difficult to maintain over time (Moore et al., 2018).

53 Starting in 2010, five Distributed Biological Observatory (DBO) regions were identified as sites for long-  
54 term monitoring to track biological responses to rapid biophysical changes occurring from the northern  
55 Bering Sea to the northeastern Chukchi Sea. In 2012, the five sites were expanded to eight, to include  
56 three sampling regions in the Beaufort Sea (Moore and Grebmeier, 2018). The five original sites were  
57 established primarily on the basis of benthic diversity and abundance. Seabirds are among the upper  
58 trophic level groups that can be used to detect change in the Pacific Arctic marine system (Moore et al.,  
59 2014). In contrast to the benthic organisms and even many fishes, seabirds are highly mobile in their  
60 distribution and abundance, which complicates sampling and interpretation of observed distribution  
61 patterns with respect to the DBO array (Moore and Kuletz, 2018). In addition, seabird communities  
62 change dramatically throughout the year in the Pacific Arctic, and include locally breeding birds as well  
63 as migrants that move into the area during summer to feed (Gall et al., 2017; Kuletz et al., 2015).

64 Seabirds are predators that have shown phenological, dietary, and distributional changes coincident  
65 with rapidly changing Arctic and Subarctic conditions (Divoky et al., 2016; Gall et al., 2017; Renner et  
66 al., 2016). Seabird population sizes and breeding success can be monitored at their breeding colonies, but  
67 they can also be counted at sea, where they spend the majority of their time when foraging and migrating.  
68 Seabirds of the Pacific Arctic include species that eat zooplankton, fish, benthic organisms, and  
69 combinations of these. Bottom-up biological and physical processes that operate at hierarchical scales  
70 influence seabird distribution, as seabirds respond to seasonal and annual changes in climate and lower  
71 trophic levels (Hunt and Schneider, 1987; Piatt et al., 2007).

72 At the broadest spatial scales (>1000 km), seabirds are associated with oceanographic habitats and to  
73 variable extent, by distribution of prey within those habitats (Hunt and Schneider, 1987). At small scales  
74 (<100 km), seabirds are patchily distributed, with the highest densities typically found in areas with high  
75 prey availability (Hunt and Schneider, 1987; Benoit-Bird et al., 2011, 2013). Hunt and Schneider (1987)  
76 proposed that meso scale processes (100–500 km), combined with prey patchiness, result in distinct  
77 seabird communities associated with particular physical habitats. In addition, breeding birds are  
78 constrained to foraging within range of their colonies (10–100 km) while they incubate eggs and raise

79 chicks (Coulson, 2002). Nonetheless, seabirds can range over huge areas, begging the question of whether  
80 at-sea surveys within the DBO array provide a useful representation of the greater region, or of seabird  
81 communities therein.

82

83 Seabird surveys have been conducted in and near the DBO sites annually from 2007 to 2015,  
84 although not with consistency in space and time. In addition to the DBO sampling stations, we were able  
85 to combine surveys conducted as part of a variety of projects, including industry-based studies, the Arctic  
86 Marine Biodiversity Observing Network (AMBON), and other vessel-based programs. Using these  
87 combined data, we questioned whether the samples collected within the DBO polygons are representative  
88 of the seabird communities in their respective regions, and if they captured areas of high seabird  
89 abundance for the entire study area. In this paper, we describe the distribution and abundance of seabirds  
90 of the Pacific Arctic in the context of the DBO array and surrounding waters. In doing so, we provide a  
91 step towards application of DBO sites to upper trophic levels.

92

## 93 **2. METHODS**

94

### 95 2.1. Study area

96

97 The main study area (Fig. 1) includes the northern Bering, eastern Chukchi, and Beaufort seas, from  
98 60°N to 73°N. The eastern and western boundaries in the northern Bering Sea extend from 179°W, at the  
99 northwestern edge of Bering Sea continental shelf, eastward to 162°W, at Norton Sound. In the Chukchi  
100 and Beaufort seas, the longitude extends from 169°W, at the international dateline, eastward to 126°W, at  
101 the west end of Amundsen Gulf in the Canadian Arctic. We considered three major geographic regions:  
102 the northern Bering (north of 60°N to Bering Strait), which contains DBO sites 1 and 2; the eastern  
103 Chukchi (Bering Strait to Pt. Barrow), containing DBO sites 3, 4, and 5; and the Beaufort (east of Pt.

104 Barrow), containing DBO sites 6, 7, and 8. Hereafter we refer to the regions, respectively, as the Bering,  
105 Chukchi, and Beaufort regions.

106

107 *2.1.1. Physical properties*

108

109 The Pacific Arctic is hydrographically and biologically distinct from the southern Bering Sea, and is  
110 generally defined as beginning at ~60°N, with seasonal variations (Stabeno et al., 2010; Sigler et al.,  
111 2011). The continental shelf ecosystem of the northern Bering and southern Chukchi Sea is influenced by  
112 salinity and temperature characteristics of three major water masses and their associated currents: Anadyr  
113 Water, Bering Shelf Water, and Alaska Coastal Water (Coachman et al., 1975; Weingartner et al., 1999;  
114 Fig. 2). These water masses advect nutrients, heat, and plankton northward from the Bering Sea, resulting  
115 in high productivity in the Bering Strait region, i.e. the Chirikov Basin (between St. Lawrence Island and  
116 Bering Strait; Fig. 2) and Hope Basin (north of Bering Strait), and throughout the Chukchi Sea (Springer  
117 and McRoy, 1993; Grebmeier et al., 2006). Both Anadyr Water and Bering Shelf Water are relatively  
118 cold, saline, and nutrient rich (Coachman and Shigaev, 1992; Weingartner et al., 2013). North of Bering  
119 Strait, Anadyr Water and Bering Shelf Water merge and become Bering Sea Water, which then bifurcates  
120 towards the Arctic Basin and branches around the shallow (40 m depth) plateau known as Hanna Shoal  
121 (Coachman et al., 1975; Dunton et al., 2017; Fig. 2).

122 Alaska Coastal Water, transported in the Alaska Coastal Current (Fig. 2), is heavily influenced by  
123 river input from the Bering Sea coast. It is relatively warm, fresh, and nutrient poor (Springer et al., 1984;  
124 Coachman and Shigaev, 1992) compared to water masses found farther offshore. The Alaska Coastal  
125 Current flows roughly parallel to mainland Alaska, until reaching Pt. Barrow, where it branches to the  
126 west or continues east along the Beaufort coast. The Beaufort and northern Chukchi seas are also  
127 influenced by deep Atlantic water flowing eastward near the shelf edge and the westerly flowing Beaufort  
128 Gyre in the Arctic Basin (Fig. 2). These water masses vary seasonally and interannually in their physical  
129 characteristics, spatial extent, and degree of mixing, due to changes in atmospheric circulation, regional

130 wind patterns, and sea-ice extent and timing of retreat (Weingartner et al., 1999, 2005; Woodgate et al.,  
131 2015; Pickart et al., 2009, 2013).

132       Sea-ice cover changes seasonally and dramatically in the Pacific Arctic, with direct and indirect  
133 consequences for upper trophic level organisms (Grebmeier et al., 2010; Stabeno et al., 2018), including  
134 seabirds (Hunt et al., 2018). Sea ice cover expands southward from the Beaufort and Chukchi seas in late  
135 fall and typically extends into the middle of the Bering Sea by March (Stabeno et al., 2010). Within the  
136 pack ice, open water areas (polynyas) persist throughout winter and spring, providing habitat for those  
137 species of birds and mammals that remain (Stringer and Groves, 1991). Sea ice retreats in spring,  
138 generally reaching Bering Strait by mid-June, although in recent years it has retreated north of the Strait  
139 by early June (NSIDC, 2010; Okkonen et al., 2018). Sea ice continues to retreat in the Arctic throughout  
140 summer and early fall, with minimal ice coverage in late September or early October. Wind direction and  
141 storms affect the extent of winter sea ice (Okkonen et al., 2018) and the timing of sea-ice spring or  
142 summer retreat affects water mass properties and subsequent productivity throughout the open water  
143 period, roughly June through October (Weingartner et al., 2005; Arrigo et al., 2008; Blanchard et al.,  
144 2017; Stabeno et al., 2018), which is the seasonal period of this study.

145

#### 146 *2.1.2. Lower trophic levels*

147

148       During summer, the zooplankton and pelagic fish communities of the northern Bering and eastern  
149 Chukchi seas reflect the underlying hydrography, with strong gradients operating nearshore to offshore,  
150 and from south to north (Sigler et al., 2017). Zooplankton densities are generally highest just north of  
151 Bering Strait, although their distribution and abundance vary seasonally and interannually (Hopcroft et  
152 al., 2010; Eisner et al., 2013). Zooplankton communities tend to be associated with specific water masses,  
153 e.g. large copepods are found primarily in cold, high salinity Anadyr Water and small copepod species in  
154 warmer, low salinity Alaska Coastal Water (Eisner et al., 2013). Species composition of zooplankton  
155 communities also show a latitudinal gradient, ranging from Subarctic species in the northern Bering and

156 southern Chukchi seas, to primarily Arctic species in the northern Chukchi Sea (Piatt and Springer, 2003;  
157 Hopcroft et al., 2010; Eisner et al., 2013). The majority of plankton and particle biomass primarily sinks  
158 to the benthos in the Chukchi, but there is flow from Barrow Canyon eastward along the Beaufort  
159 Shelf and shelf break, and minimal advection off shelf into the Arctic basin (Ashjian et al., 2005). The  
160 zooplankton community in the Beaufort Sea consists primarily of *C. glacialis*, an arctic species with  
161 circumpolar distribution (Daase and Falk-Petersen, 2013).

162 The principal prey of piscivorous seabirds are structured primarily along a latitudinal gradient and  
163 secondarily with water masses (Eisner et al., 2013, Norcross et al., 2013). Capelin (*Mallotus villosus*) are  
164 most abundant in the northern Bering and southern Chukchi seas. Juvenile saffron cod (*Eleginus gracilis*),  
165 juvenile Arctic cod (*Boreogadus saida*), and Pacific sand lance (*Ammodytes hexapterus*) are most  
166 abundant in the central and northern Chukchi Sea, and walleye pollock (*Theragra chalcogramma*) is  
167 common. Both diversity and biomass of fishes decrease with latitude, and high diversity and biomass are  
168 associated with Alaska Coastal Water (Piatt and Springer, 2003; Eisner et al., 2013). The Beaufort Sea  
169 has low fish abundance overall, although less is known about fishes in this region (Rand and Logerwell,  
170 2011, Logerwell et al., 2015). By far the most abundant fish in the Beaufort is Arctic cod (Logerwell et  
171 al., 2015), a species known to be a key prey for Arctic seabirds (Hobson, 1993; Hop and Gjørseter, 2013).  
172 Other common demersal fishes in the Beaufort include eelpouts (*Lycodes* spp), Bering flounder  
173 (*Hippoglossoides robustus*), and walleye Pollock; the latter may be increasing in numbers in the Beaufort  
174 Sea, albeit in much lower densities than in the Chukchi and Bering seas (Rand and Logerwell, 2011).

175

### 176 2.1.3. Seabirds

177

178 The study area supports approximately 60 species of seabirds, including: 1) species that nest along  
179 the study area's coastlines; 2) populations that breed elsewhere in Alaska and use the study area during  
180 other portions of their annual cycle, typically post-breeding; and 3) southern migratory species that forage  
181 in Alaskan waters only during the northern hemisphere summer. The term 'seabirds' typically refers to

182 those species that feed primarily in the marine environment and that nest on coastal cliffs or islands, often  
183 in colonies (e.g. fulmars, shearwaters, gulls, murre, puffins). For this study, we also include other  
184 marine-associated species as ‘seabirds’, including loons, seaducks, and phalaropes (Table 1). These  
185 species-groups spend portions of their lives at sea during which they forage in the marine environment.

186 The coastal bluffs and islands of the Bering and Chukchi seas have some of the largest seabird  
187 breeding populations in the world (Stephensen and Irons, 2003), with large colonies in the northern  
188 Bering Sea and the southern Chukchi Sea (Fig. 1). Approximately 12 million seabirds nest at colonies on  
189 either side of Bering Strait (USFWS, 2014). On the Chukchi Sea coast, the largest colonies are near Cape  
190 Thompson and Cape Lisburne. Farther north, the coast has no habitat suitable for cliff-nesting birds, and  
191 only small scattered colonies or breeding pairs occur there and farther eastward along the Beaufort coast  
192 (Stephensen and Irons, 2003; USFWS, 2014). Seaducks and phalaropes nest in scattered coastal and  
193 inland locations throughout the study area (Johnson and Herter, 1989).

194 Offshore, seabird densities in the study area range from among the highest recorded in the North  
195 Pacific and Atlantic (i.e. Bering Strait) to among the lowest (i.e. the Beaufort) (Humphries and  
196 Huettmann, 2014; Wong et al., 2014; Kuletz et al., 2015). Localized ‘hotspots’ of high seabird density  
197 occur near large seabird colonies (e.g. Chirikov Basin; Piatt and Singer, 2003) but also in offshore waters  
198 far from colonies (e.g. Hanna Shoal; Gall et al., 2013; Kuletz et al., 2015). Areas with high offshore  
199 seabird abundance often include high proportions of migrants from the southern hemisphere, primarily  
200 short-tailed shearwater (*Ardenna tenuirostris*), which at times may equal or exceed the abundance of  
201 locally breeding birds (Gall et al., 2013; Kuletz et al., 2015).

202

## 203 2.2. Data collection

204

205 The seabird survey data came from two sources, the U.S. Fish and Wildlife Service (FWS; 2007-  
206 2015) and ABR, Inc. (ABR; 2008-2015). The FWS surveys were conducted in collaboration with a  
207 variety of vessel-based research projects that operated throughout the study area (Kuletz and Labunski,



208 2017). The ABR surveys focused primarily in oil and gas lease sale areas of the northeastern Chukchi Sea  
209 (DBO 4) but also included transits and surveys in other areas of the eastern Chukchi Sea. The FWS  
210 surveys were conducted during transits between stations or ports. The ABR surveys had dedicated  
211 sampling time and followed parallel lines spaced ~ 4 km apart within three primary study regions of the  
212 eastern Chukchi Sea, approximately 100-230 km offshore of Wainwright, Alaska (see Gall et al., 2013 for  
213 details). For all projects, survey vessels ranged in length from 35 m (115 ft) to 128 m (420 ft). Total  
214 survey effort (Fig. 1) was thus highest in the DBO 4 site and in proximity to Bering Strait, the latter being  
215 the route between the Bering and Chukchi seas.

216 All data were collected following similar protocols for visual observations and modified strip  
217 transects (Tasker et al., 1984; Kuletz et al., 2008) while underway during daylight hours. The observer,  
218 stationed inside the bridge, recorded all seabirds within 300 m and a 90° arc from the center line of travel.  
219 Transect width was occasionally reduced to 200 m or 100 m depending on visibility conditions, and  
220 surveys were discontinued if visibility was <100 m (i.e. due to fog), or if seas were Beaufort scale > 6.  
221 Birds on the water were recorded continuously and flying birds were recorded during quick 'scans' of the  
222 transect window at intervals of approximately 1 min<sup>-1</sup> (depending on vessel speed) to avoid  
223 overestimating the density of flying birds (Tasker et al., 1984; Gould and Forsell, 1989). Birds actively  
224 foraging from the air, such as surface plunging or touching the water surface, were recorded as 'on water'  
225 (i.e. continuously). Birds were counted on first observation and thereafter ignored to avoid double  
226 counting birds following the vessel.

227 Data were entered directly into a laptop computer connected to the ship's Global Positioning System  
228 (GPS) or a Garmin 60CSx handheld GPS unit, using survey software DLog3 (A.G. Ford, Inc., Portland,  
229 OR; FWS, 2007-2015 and ABR, 2008) or TigerObserver (TigerSoft, Las Vegas, NV; ABR 2009-2014).  
230 Each entry was stamped with time and location (latitude and longitude), which were also recorded  
231 automatically at 20 sec intervals to track survey effort. Binoculars (10 x) were used to aid in species  
232 identification, and if necessary, a digital camera was used for later confirmation of identification. A  
233 geometrically marked wooden dowel was used to estimate distance from the line of travel to the bird, and

234 verified when possible with a laser rangefinder. The observer recorded species, number of individuals,  
235 and behavior (on water, on ice, foraging, or in air). Birds were identified to the lowest taxonomic level  
236 possible. For details see Kuletz et al. (2008) and Gall et al. (2013).

237

### 238 2.2.1. Data selection

239

240 We extracted all survey data from 2007-2015 for the months of July through October. We  
241 subdivided transect lines (which varied in length) into continuous ~ 3-km segments ( $n = 34,521$ ) and then  
242 calculated density (birds•km<sup>-2</sup>) for each segment based on transect width (typically 300 m), using the  
243 latitude and longitude of the segment centroid as the location. We did not correct for detection because  
244 our primary goal was to describe distribution and relative abundance, and comparisons among DBO sites  
245 and regions should not be affected by biases from detection probabilities. Survey effort differed between  
246 regions, with 9404, 21,393, and 3724, 3-km segments available in the Bering, Chukchi, and Beaufort  
247 regions, respectively. For community cluster analysis we generated a 30-km hexagonal grid over the  
248 study area and averaged the density values for each species using all 3-km segments within each grid cell.  
249 We retained hexagon grid cells that had five or more 3-km segments, considered a minimum to obtain a  
250 representative sample within each cell while still providing sufficient spatial coverage of all DBO sites;  
251 the minimum 15 km of transects per cell is similar in scale to that used in Kuletz et al. (2015).

252 Our analyses included 11 bird families: Podicipedidae (grebes), Scolopacidae (phalaropes),  
253 Stercorariidae (jaegers), Alcidae (auks), Laridae (gulls, terns), Gaviidae (loons), Diomedidae (albatross),  
254 Procellariidae (fulmars, shearwaters), Hydrobatidae (storm-petrels), Phalacrocoracidae (cormorants), and  
255 marine species of Anatidae (eiders, scoters, other seaducks). From these families, 11 species or species  
256 groups (Table 1) were selected for further analysis, because they together comprised about 95 % of all  
257 recorded birds (for some analyses, the two murre species were combined into a 'total murre' taxa). 'Total  
258 birds' refers to all species combined, including those not identified to the species level (but within the  
259 families above). Where possible, birds identified only to family or genus were incorporated into data

260 analyses. This was accomplished using two separate methods; the first was used in analysis of species  
261 richness and the second was used in analyses and visualizations of species densities (see below).

262

### 263 2.2.2. *Data analysis*

264

265 For each DBO site or region, and for the entire study area, we endeavored to characterize three  
266 aspects of the seabird community; 1) species richness and diversity, 2) distribution and abundance, and 3)  
267 patterns of community composition. To address the issues of unequal sampling among regions, we  
268 compared species richness among locations using rarefaction, a method that facilitates comparisons  
269 among groups with different numbers of samples, and also used an index of diversity to examine  
270 evenness of species. We used a statistical modeling approach to evaluate spatial and temporal variation in  
271 seabird abundance. Finally, we used cluster analysis and data visualizations to examine spatial patterns of  
272 community composition.

273

### 274 2.2.3. *Species richness and diversity*

275

276 To examine seabird species richness for the each region we used rarefaction curves, which depicted  
277 the number of species observed as a function of the number of 3-km segments sampled, generated  
278 through random resampling of the data. This approach addresses the issue of variable sample size and of  
279 uneven distribution of birds, which affects estimates of species richness (Magurran and McGill, 2011).  
280 We assessed species richness using the combined data across years for each region (Bering, Chukchi,  
281 Beaufort), creating rarefaction curves by randomly sampling (with replacement) 3-km segments within  
282 each region. We calculated 95% confidence intervals using quantiles from 2000 random draws for each  
283 sample size along the rarefaction curve. We also determined observed species richness for each DBO site  
284 using combined years of data collected within each site.

285 Not all birds were identified to species level. To address this issue, we incorporated higher-order taxa  
286 into our analyses of species richness by counting them as a unique species if no corresponding lower-  
287 order taxa were present in the sample. In other words, if, and only if, no thick-billed murre or common  
288 murre were present in a sample (i.e. either a random draw of 3-km segments, or all segments within a  
289 DBO site), then an unidentified murre was counted as a species.

290 Finally, we compared seabird diversity among regions and DBO sites using the Shannon Index  
291 (Shannon, 1948; MacArthur and MacArthur, 1961), which incorporates the number of species and the  
292 evenness of abundance values.

293

#### 294 *2.2.4. Abundance and distribution*

295

296 To examine the potential for latitudinal or longitudinal influence on overall distribution across the  
297 entire study area, we first used Generalized Additive Models (GAM) to examine spatial variation in  
298 abundance of seabirds. The GAM used the centroid of each 3-km segment as location, a smooth term  
299 (thin plate regression spline), a maximum basis dimension of 100, and a likelihood defined by the  
300 Tweedie distribution with a log link and estimated scale parameter (Wood, 2017). We examined various  
301 choices of maximum basis dimension to ensure that our choice did not influence the final smooth, based  
302 on an approximation to cross validation (Wood, 2017). Model fit diagnostics were examined and found  
303 reasonable for all but a few extreme high-density observations. The above model was also compared to  
304 alternatives using Poisson, quasi-Poisson, and negative binomial likelihoods. These alternatives had  
305 worse model fit diagnostics than that using the Tweedie likelihood. We compared various basis  
306 specifications for the smooth term (Gaussian process models, a smooth on the sphere, and an adaptive  
307 smooth where the amount of smoothing depends on geographic locations; all documented in the R  
308 package mgcv; Wood, 2017). All models gave similar general patterns, except an adaptive smooth model  
309 where the uncertainty was extreme in areas with sparse data (high latitudes  $>70^{\circ}\text{N}$ ). The model estimates

310 predict seabird density as a function of latitude at 168°W longitude (directly through the Bering Strait)  
311 and as a function of longitude at 71°N latitude (to bisect both the Chukchi and Beaufort regions).

312 Second, we examined spatial variation of seabird density in each region or DBO site using the same  
313 GAM model but with location (DBO site or region) defined as a random effect (bs="re" option of the  
314 mgcv smooth specification), instead of a smooth based directly on latitude and longitude. The modeled  
315 estimated densities were constructed for total birds and the 10 species or species groups (Table 1). We  
316 plotted the estimates in rank order of the DBO site number, which are aligned south (DBO 1) to north  
317 (DBO 4) and west (DBO 4) to east (DBO 8).

318 Finally, to examine the relative influence of spatial (DBO site or region) and temporal (year)  
319 variation in seabird density we fit the model with the location and year factors as random effects. We  
320 report the estimates of the standard error (with 95% confidence intervals) for year and DBO site or region.  
321 We performed each analysis above using total seabirds and for each of the same 10 taxa used for the  
322 GAM model.

323

#### 324 2.2.5. *Community composition and distribution*

325

326 We took two complementary approaches to the community analysis. First, we illustrated community  
327 composition within DBO sites using waffle charts (square pie charts), which depict both species  
328 composition and density values using rectangular grids (Rudis and Gandy, 2017). This allowed  
329 comparisons among DBO sites. Second, to understand how the DBO sites fit into the broader regional  
330 context, we evaluated the major patterns of seabird community composition for the entire study area. We  
331 used K-means cluster analysis (Hartigan and Wong, 1979) to describe patterns of community composition  
332 across the study area (all three regions) by grouping 30-km hexagonal grid cells based on similarity in  
333 densities and species of birds. We included all 30-km grid cells with centroids  $\geq 60^\circ\text{N}$  and  $\leq 74^\circ\text{N}$ , and  
334 log-transformed densities prior to performing the cluster analysis. Clustering was based on species  
335 densities only, not geographic coordinates of the grid cells. The optimal clustering was determined by

336 comparing the inflection point of within-group sums of squares to the number of clusters (Hartigan and  
337 Wong, 1979). We then used waffle charts to compare species composition of each identified cluster type.  
338 We also evaluated spatial patterns of community composition by mapping the identified clusters of cells  
339 back onto the 30-km hexagonal grid.

340 Prior to these analyses, we apportioned all higher-order taxa to species using a two-step approach.  
341 First, we prorated higher-order taxa to species based on the corresponding species ratios within each grid  
342 cell. For example, if higher-order taxon A could be species B or C, we allocated the density of A among  
343 B and C based on their proportional density in that grid cell. In some cases, a higher-order taxon was  
344 present, but there were no corresponding species in a given grid cell. Therefore, in a second step, we  
345 prorated the remaining values to species based on spatial interpolation of species ratios; for this, we used  
346 kriging, with a distance cutoff of 60 km (~ 2 grid cells).

347 All analyses were done using R functions and scripts (R Core Team, 2015). Kriging of species ratios  
348 used function *krige* in package *gstat* (Pebesma, 2004). The General Additive Model used function *gam* in  
349 the package *mgcv* (Wood, 2017). Cluster analysis was performed using the R function *kmeans* (Hartigan  
350 and Wong, 1979). Waffle charts made use of the R package *waffle* (Rudis and Gandy, 2017).

351

### 352 3. RESULTS

353

#### 354 3.1.1 Species richness and diversity

355

356 The estimated species richness was highest for the Bering region (asymptote at ~ 50 species),  
357 followed by the Chukchi region (~ 40 species), and lowest for the Beaufort region (~ 35 species) (Fig. 3).  
358 In most cases, the rarefaction curve indicated that the observed richness within the DBO sites was within  
359 the expected bounds of regional species richness, given the sampling effort. The exception was DBO 4,  
360 which had extremely high sampling (>5500 segments) and an observed 34 species, whereas ~ 40 species  
361 was predicted for the region at that sampling level. For most DBO sites, however, actual sampling effort

362 was not sufficient to reach the asymptote, particularly for the three DBO sites in the Beaufort region (Fig.  
363 3). Among DBO sites, DBO 3 had the highest observed species richness (35 species). The lowest species  
364 richness was recorded in DBO 8, where glaucous gull was the only species recorded on transect.

365 The Shannon Index ( $H'$ ) was 2.47 for the entire study area. Diversity was highest in the Bering  
366 region followed closely by the Chukchi region, and was lowest for the Beaufort region (Table 2). Among  
367 DBO sites, there was little difference in  $H'$ , with most DBO sites ranging from 1.46 to 2.15. Despite high  
368 seabird abundance, two of the Chukchi DBO sites (4 and 5) had lower diversity indices than Beaufort  
369 DBO sites 6 and 7, indicative of the numerical dominance of a few species in the Chukchi. DBO 8 had an  
370 extremely low  $H'$  (near zero) because only one species was recorded on transect there.

371

### 372 3.2. Abundance and distribution

373

374 Seabirds occurred in nearly all surveyed areas, with the exception of a few cells in Norton Sound,  
375 areas of the Beaufort shelf, and most of the Arctic basin (Fig. 4). Seabird abundance was highest along  
376 the outer shelf of the Bering Sea, the Chirikov Basin through Bering Strait and parts of Hope Basin, and  
377 near Pt. Barrow (Fig. 4).

378 For total seabirds, modeled abundance by latitude (with longitude held constant), which highlights  
379 DBO sites 1 – 4, dipped between the shelf edge ( $\sim 60^\circ\text{N}$ ) to  $\sim 61^\circ\text{N}$ , then increased northward and peaked  
380 at  $\sim 65^\circ\text{N}$  (near Bering Strait) and then declined gradually continuing north to  $\sim 70.5^\circ\text{N}$  (Hanna Shoal area)  
381 (Fig. 5, top). Abundance then declined sharply near the Arctic shelf break at  $\sim 72^\circ\text{N}$ , with greater  
382 uncertainty in the estimated values, reflecting low sampling effort in the far north (Fig. 1) as well as low  
383 encounter rates of birds. From the Chukchi to the Beaufort and moving west to east, which highlights  
384 DBO sites 4 – 8, peaks in abundance are evident at  $\sim 172^\circ\text{W}$  (west of Hanna Shoal) and  $\sim 162^\circ\text{W}$  near Pt.  
385 Barrow. Abundance declines farther eastward to  $\sim 140^\circ\text{W}$ , with a slight increase west of DBO 8, but with  
386 higher uncertainty in estimates (Fig. 5, bottom). Overall, expected densities were above 1 bird $\cdot 3\text{-km}$   
387 segment (log zero) with respect to latitude except at the far northern latitudes, where error in estimates

388 were high. In contrast, expected densities fall below 1 bird•3-km segment over a wide range of  
389 longitudes, starting near DBO 7. The highest expected densities were near Pt. Barrow, at ~55 birds•3-km  
390 segment (Fig. 5, bottom) and near Bering Strait, at ~32 birds•3-km segment (Fig. 5, top). There were,  
391 however, a variety of species-specific distribution patterns in modeled abundance with respect to latitude  
392 and longitude (Appendix A).

393 The modeled abundances of total seabirds for the DBO sites were in most cases similar to those of  
394 their respective regions (estimates for regions did not include 3-km segments inside DBO polygons) (Fig.  
395 6). However, abundance in DBO 2 was higher than the greater Bering region, while DBO sites 7 and 8  
396 were much lower than the Beaufort region. Among sites, abundance estimates generally declined moving  
397 north (to DBO 4) and eastward (from DBO 5 to 8). Abundance declined sharply in the Beaufort, with  
398 estimates below 1 bird•3-km segment (below log zero) for DBO sites 7 and 8 (Fig. 6).

399 The patterns in abundance were more complicated for individual taxa (Fig. 7). For species that were  
400 more evenly dispersed (black-legged kittiwakes, glaucous gull) or of low abundance (murrelets),  
401 estimates were similar between DBO sites and regions. Taxa that tended to be more aggregated  
402 (phalaropes, shearwaters) or with large local colonies (crested and least auklets, murrelets, puffins) had  
403 DBO site estimates either higher or lower than the respective region. Overall, for all 30 taxa-site  
404 comparisons, there were 16 equivalent estimates between DBO sites and the respective region, 8 with  
405 lower DBO site estimates and 6 with higher DBO site estimates. Four of 10 taxa (northern fulmars, black-  
406 legged kittiwakes, murrelets, and puffins), showed a roughly linear decline in abundance from south to north  
407 and west to east; these species are all primarily piscivorous. Shearwaters (which are omnivorous) declined  
408 abruptly at DBO sites 7 and 8. Phalaropes, least auklet, and crested auklet (all planktivores) peaked  
409 between DBO sites 2-4, encompassing Bering Strait, Hope Basin, and Hanna Shoal. Glaucous gull and  
410 murrelets (primarily piscivores, but also consume invertebrates and krill) varied little among DBO sites  
411 (Fig. 7), except that murrelets were absent in DBO 8.

412 Total seabird density had higher spatial variance (i.e. among regions or sites) than it did among years  
413 (Fig. 8), indicating that seabird abundance was more consistent among years than among locations. Most



414 of the taxa examined also showed higher variance among sites than years. Among regions, however,  
415 shearwaters, phalaropes, and glaucous gulls had temporal variance that was similar to or higher than  
416 spatial variance (Fig. 8), indicating that their abundance varies more by year than by location. Among  
417 DBO sites, only murrelets had higher temporal variance, although both values were very low for this taxa.  
418

### 419 3.3. Species composition and seabird communities

420

421 The seabird community within the study area clustered into six community types. Of the six  
422 community types identified, five had a species composition predominated by one species that composed >  
423 25% of total seabird density (Fig. 9). Although other species were part of each community type, we  
424 hereafter refer to the community types by their predominate species (Appendix B). The ‘least auklet  
425 community’ had the highest total density (34.9 birds•km<sup>2</sup>), and included short-tailed shearwaters, crested  
426 auklet, black-legged kittiwake, both murre species, northern fulmar, phalaropes, and 34 other species.  
427 Three community types (northern fulmar, short-tailed shearwater, thick-billed murre) had similar total  
428 densities, ranging from 11.7 to 17.3 birds•km<sup>-2</sup> (Fig. 9, Appendix B). The ‘crested auklet community’ had  
429 the lowest total density of the species-identified community types (Fig. 9), with a total of 9.7 birds•km<sup>-2</sup>  
430 (Appendix B). The ‘low density community’ included 52 species, with a total density of 1.6 birds•km<sup>-2</sup>,  
431 and no numerically dominant species.

432 Mapping the community types revealed the distribution of the six primary seabird communities  
433 throughout the study area (Fig. 10), with all six community types occurring in Hope Basin (with DBO 3).  
434 Three communities showed clear geospatial aggregations. The northern fulmar community was found  
435 mostly in the outer Bering Sea shelf, south of DBO 1; the least auklet community occurred in the  
436 Chirikov Basin (with DBO 2) and Bering Strait (between DBO 2 and 3); and the crested auklet  
437 community occurred in the Hanna Shoal area, including most of DBO 4. Three communities were more  
438 spatially dispersed; these included communities dominated by thick-billed murre, short-tailed shearwater,  
439 and the low-density community.

440 The thick-billed murre community type occurred across a large area in the Bering region's central  
441 shelf (with a small number of cells in DBO 1) and in a smaller patch near the Siberian coast (outside of  
442 DBO 2). It also occurred in the Chukchi region near Cape Thompson to Cape Lisburne, with portions in  
443 DBO 3 (Fig. 10). The short-tailed shearwater community type was the most dispersed of the communities  
444 that were dominated by one species; it stretched in a band across the Bering Shelf south of St. Lawrence  
445 Island (DBO 1), and northward along the eastern Bering region (partially captured by DBO 2), through  
446 Bering Strait and northward along the Chukchi coast (partially in DBO 3), with high densities from  
447 Wainwright to the mouth of Barrow Canyon (DBO 5), and into the western Beaufort Sea (partially in  
448 DBO 6; Fig. 10). The low density community was widely dispersed, particularly in the Beaufort (DBO  
449 sites 6, 7, 8) as well as the northernmost waters of the Chukchi and most inshore waters of all regions  
450 (Fig. 10).

451 Within DBO sites, species composition was typically numerically dominated by one or two species,  
452 with shearwaters the most abundant in five of eight DBO sites (Fig. 11), in which they represented 43 –  
453 76 % of total birds in a given DBO site (Appendix C). DBO 1 included high proportions of shearwaters,  
454 thick-billed murre, and northern fulmar. DBO 2 had the highest mean total density (32.5 birds•km<sup>-2</sup>), with  
455 least auklet composing 40% of the total (Fig. 11, Appendix C). DBO 3 had high proportions of  
456 shearwaters, least auklet, and phalaropes. In DBO 4, crested auklet was numerically dominant, composing  
457 58% of total density. DBO 5 had the highest proportion of shearwaters, which composed 78% of total  
458 density. The Beaufort DBO sites had much lower densities than other sites, ranging from 2.5 birds•km<sup>-2</sup>  
459 (DBO 6) to 0.1 birds•km<sup>-2</sup> (DBO 8), with shearwaters still predominate in DBO 6, composing 63% of  
460 total birds. Seaducks (mainly long-tailed ducks and king eiders) composed 54% of total density in DBO  
461 7, but at low density (0.3 birds•km<sup>-2</sup>, combined). (See Appendix D for species-specific distribution maps).

462

#### 463 4. DISCUSSION

464

465 The Distributed Biological Observatory seeks to leverage multiple research campaigns to build and  
466 maintain long-term data sets in the Pacific Arctic, with the goal to address ecological and management  
467 issues in the dynamic regions of the northern Bering, eastern Chukchi, and Beaufort seas. By combining  
468 10 years of at-sea surveys derived from a variety of vessel-based programs, our study is the first to use the  
469 DBO array to describe the seabird communities of these contiguous marine ecoregions. We also put the  
470 DBO sites in context of the broad-scale patterns of seabird distribution, and found that the DBO sites  
471 have captured most, but not all, of the areas of high seabird abundance for the study area.

472

#### 473 4.1. Species richness and diversity

474

475 We found differences in species richness among the three marine regions, with distinctly low values  
476 in the Beaufort region. Although predicted values indicated higher species richness overall in the Bering  
477 than the Chukchi, the highest observed values were in Chukchi DBO sites, perhaps partly due to higher  
478 sampling effort there (Fig. 1). For most DBO sites, observed species richness was consistent with values  
479 predicted by the regional rarefaction curves, given their respective sampling efforts. Two exceptions were  
480 DBO sites 1 and 4, which had lower than predicted species richness; both of these sites are farther  
481 offshore than the others. In DBO 1, seabird abundance was high but species richness was low due to the  
482 predominance of shearwaters (Fig. 11). DBO 4 is far from land or suitable breeding habitat, thus breeding  
483 birds would be less likely to frequent the area, as indicated by the low numbers of coastal species  
484 observed there (Appendix C). Species diversity among DBO sites was similar, but generally lower than  
485 that of their respective regions; this is likely a consequence of the smaller spatial scale and in some cases  
486 (e.g. DBO sites 1, 7, 8), lower survey effort within DBO sites, both of which can reduce measures of  
487 diversity (Willig and Presley, 2017).

488 In the Bering, DBO 2 had relatively high species richness (Fig. 3), consistent with Santora et al.  
489 (2018), which found an increase in seabird species richness with latitude that culminated in the Chirikov  
490 Basin, based on a biogeographic analysis of the entire Bering Sea. As a transitional zone between the

491 southern Bering and Chukchi seas (Sigler et al., 2011, Stabeno et al., this issue), the northern Bering  
492 might be expected to have higher seabird species richness and diversity overall (Table 2), as was  
493 predicted had there been greater sampling effort (Fig. 3). Seabird species that breed in the northern Bering  
494 Sea are joined by post-breeding and non-breeding seabirds from the south. In comparison, smaller  
495 populations of fewer species breed in the Chukchi Sea, and even fewer in the Beaufort Sea (USFWS,  
496 2014).

497

#### 498 4.2. Seabird abundance and species composition in DBO sites

499

500 We found clear evidence of latitudinal and longitudinal gradients on total seabird abundance which  
501 the DBO array, in most cases, appears to represent fairly well. For total seabirds, locations of high seabird  
502 abundance stand out, particularly the south side of Bering Strait and near Pt Barrow at the mouth of  
503 Barrow Canyon. The abundance of birds in the outer Bering shelf, Chirikov Basin, and near Pt. Barrow is  
504 likely a function of high nutrient flow and high zooplankton abundance, concentrated by strong physical  
505 forcing in these areas (Piatt and Springer, 2003; Grebmeier et al, 2006; Ashjian et al., 2010; Danielson et  
506 al., 2017). The high proportion of shearwaters and northern fulmar in DBO 1 partly reflects the proximity  
507 to the shelf break, sites of upwelling and fronts (Springer et al., 1996), where these birds tend to feed  
508 (Schneider et al., 1987, 1990). Species abundant in and around DBO 1, including northern fulmars and  
509 thick-billed murre, nest at large colonies on St. Matthew Island, located between DBO sites 1 and 2 (Fig.  
510 1).

511 The abundance of seabirds within ~ 100 km either side of Bering Strait (Fig. 4), which is captured by  
512 DBO sites 2 and 3, partly reflects the effect of birds moving through a narrow bottleneck connecting two  
513 high-nutrient areas. In addition, the area is in proximity to large seabird breeding colonies on islands in  
514 the northern Bering region, and on the mainland in the Chukchi region (Fig. 1). Within foraging range of  
515 these colonies, strong currents through the ~82 km wide strait advect nutrients and lower trophic  
516 organisms (Sigler et al., 2011) and create predictable prey aggregations (Hunt, 1997; Grebmeier et al.,

517 2006; Eisner et al., 2013). Piscivorous murre, puffins, kittiwakes, and other species also nest on these  
518 islands (Stephensen and Irons, 2003; USFWS, 2004), but the high seabird abundance in DBO 2 was  
519 driven primarily by least auklets (Fig. 11), which often feed near the Anadyr Current (Hunt, 1997;  
520 Sheffield-Guy et al., 2009). The nutrient rich waters of the Anadyr Current, and associated eddies, bring  
521 copepods and euphausiids within foraging range of > 5 million nesting planktivorous auklets (Elphick  
522 and Hunt, 1993; Piatt and Springer, 2003), as well as high numbers of shearwaters pursuing euphausiids  
523 (Nishizawa et al., 2017).

524 The northern gateway to Bering Strait, DBO 3, with the second highest seabird abundance,  
525 encompasses the slopes of Hope Basin and diverging currents flowing northward, and is within foraging  
526 range of birds nesting on the Diomedede islands (as evidenced by high proportions of least and crested  
527 auklets). In the Chukchi, > 600,000 piscivorous seabirds, primarily murre and black-legged kittiwakes,  
528 nest at Cape Thompson and Cape Lisburne (Dragoo et al., 2017). However, these locally nesting species  
529 composed low proportions of the birds observed offshore, with both murre species combined contributing  
530 ~ 12 % and kittiwakes < 4 % of total birds. Rather, the abundant species in DBO 3 were migratory  
531 shearwaters and phalaropes, as well as northern fulmars and least and crested auklets, none of which nest  
532 in the Chukchi region. Notably, our analysis pooled all summer and fall months (July – October), whereas  
533 recent surveys conducted in June 2017 and 2018 found that locally nesting murre, kittiwakes, and puffins  
534 predominated in offshore waters of DBO 3 in early summer (KJK, unpubl. data).

535 Far from large seabird colonies, DBO 4 had lower total densities of seabirds than DBO sites farther  
536 south, but high densities of crested auklets. DBO 4 includes Hanna Shoal, a shallow (~ 40 m) plateau of  
537 high productivity surrounded by nutrient rich Bering Sea Waters (Schonberg et al., 2014; Weingartner et  
538 al., 2017) with high copepod and euphausiid biomass (Grebmeier et al., 2006; Ashjian et al., 2017). Late  
539 season plankton blooms and stratification of the water column make copepods available and aggregated  
540 into late summer (Weingartner et al., 2013; Danielson et al. 2017), which appears to attract non-breeding  
541 or post-breeding crested auklets > 600 km northward from the nearest auklet colonies. In addition, crested  
542 auklets fitted with geolocators at nest sites in the Aleutian Islands also traveled to the Chukchi Sea after

543 breeding (Will et al., 2017). Perhaps because those birds complete chick rearing several weeks earlier  
544 than auklets in the northern Bering Sea, auklets are relatively abundant in the area throughout summer  
545 and fall (Gall et al., 2013; Kuletz et al., 2015), a phenomena clearly represented by DBO 4.

546 The DBO 5 site encompasses the mouth of Barrow Canyon, where easterly-flowing Beaufort Water  
547 and Arctic Basin Water is upwelled onto the Chukchi shelf (Pickart et al., 2013), periodically resulting in  
548 a zone of high nutrients and zooplankton biomass that attract piscivorous belugas (Stafford et al., 2013).  
549 Under certain conditions (i.e. a relaxation of the Alaska Coastal Water and increased influence of the  
550 Beaufort Gyre), large zooplankton are ‘trapped’ near the canyon mouth, drawing foraging aggregations of  
551 feeding whales (Ashjian et al., 2010; Okkonen et al., 2011), along with shearwaters and other seabirds  
552 (Kuletz et al., 2015). This highly dynamic set of conditions may at times extend into the westernmost  
553 Beaufort site, DBO 6, where shearwaters remained the predominate species.

554 Overall, the lack of seabirds we found in the Beaufort region is similar to other accounts of low  
555 seabird abundance in offshore waters of the Beaufort Sea (Sigler et al., 2011; Wong et al., 2014), and is  
556 consistent with observations of low prey availability and smaller prey species there (Sigler et al., 2011).  
557 The extremely low values we found for species richness, diversity, and abundance in the Beaufort region,  
558 particularly in DBO sites 7 and 8, must be considered in the context of low survey effort in that region,  
559 but are also likely an accurate reflection of the region’s coastal and marine habitats. The Beaufort  
560 coastline has no suitable nesting habitat for most seabird species. However, the coastal waters which we  
561 rarely surveyed support a variety of birds, including terns, gulls, loons, seaducks, waterfowl, and  
562 shorebirds (Johnson and Herter, 1989; Fischer and Larned, 2004). Farther offshore, where most of our  
563 surveys occurred, the shelf and slope is dominated by nutrient poor waters of the Beaufort Gyre,  
564 subsurface Atlantic waters, and Alaska Coastal Water (Pickart et al., 2013). Consequently, the Beaufort  
565 has low abundance and diversity of benthic, invertebrate, and fish taxa, compared to the Chukchi and  
566 Bering seas (Rand and Logerwell, 2011; Sigler et al., 2011; Iken et al., 2018). Among the individual taxa,  
567 the gradual decline in piscivorous species from south to north and west to east (Fig. 7), may reflect  
568 gradients in fish abundance as well as absence of nesting habitat. In contrast, planktivorous birds peaked

569 in abundance between DBO sites 2 – 4, indicative of highly aggregated zooplankton in those regions.

570 Thus, while the individual DBO sites may have been established to track changes in benthic hotspots,

571 together they also appear to capture the broad-scale gradients in seabird communities of the regions.

572

#### 573 4.3. Spatial and interannual variance

574

575 For total seabirds and most examined taxa, interannual consistency in abundance was a contrast to  
576 the high regional or DBO site variance (Fig. 8), which indicates both the potential usefulness of the DBO  
577 array for monitoring seabirds (because in general, species tended to go to the same large-scale locations),  
578 and that the entire array is necessary to capture the variety of seabird communities. There was slightly  
579 higher variance among years than among regions for shearwaters, phalaropes, and glaucous gulls, which  
580 can be linked to their life history. Shearwaters and phalaropes are not tied to breeding sites during this  
581 time of year, and can more readily respond to changes in location of prey. For example, the short-tailed  
582 shearwater appears to track euphausiids from the Bering Sea into the Chukchi Sea in late summer and fall,  
583 resulting in strong seasonal shifts in distribution (Suryan et al., 2016; Nishizawa et al., 2018). Phalaropes  
584 (mainly red phalaropes) nest in scattered locations inland and gather at sea following breeding, to  
585 replenish fat reserves prior to migrating south (Taylor et al., 2011). Although individual glaucous gulls  
586 may breed locally in scattered locations, this circumpolar species is wide-ranging, omnivorous, and  
587 forages in a variety of habitats (Petersen et al., 2015).

588 Variance in seabird abundance was even higher at the smaller scale of DBO sites. Among DBO sites,  
589 only murrelets (primarily ancient murrelet, and lower numbers of Kittlitz's murrelet) showed slightly  
590 greater variance among years than among sites. Ancient murrelets breed from British Columbia to the  
591 Aleutian Islands and have only recently been common in the Pacific Arctic (Day et al., 2013). Kittlitz's  
592 murrelets nest on coastal mountains from the northern Gulf of Alaska to the Aleutian Islands, with small  
593 populations in northwestern Alaska (Day et al., 1999). Both of these species have been shown via birds  
594 fitted with satellite tags to migrate to the Chukchi Sea after breeding.

595 While interannual variability in seabird abundance and species composition in this study area has  
596 been shown previously (e.g. in DBO 4; see Gall et al., 2013), our study indicates that within the northern  
597 Bering to Beaufort seas, meso-scale patterns of seabird distribution are generally consistent. Habitat  
598 features (including location of breeding colonies) attracted a distinct community of seabirds that differed  
599 among DBO sites, and was fairly consistent over our time frame of eight years. However, at a greater  
600 temporal scale of decades, seabird communities may exhibit long-term ecosystem changes. Recent  
601 examples include the shift in offshore waters of the northeast Chukchi Sea from primarily piscivorous  
602 seabirds to planktivorous seabirds (Gall et al., 2017), and evidence of southern Bering Sea species shifting  
603 their distribution northwards, including murrelets (Day et al., 2013), northern fulmar (Renner et al., 2013)  
604 and albatrosses (Kuletz et al., 2014).

605

#### 606 4.4. Community Composition

607

608 The six seabird community types that we identified within our study area were sometimes associated  
609 with specific bathymetric or oceanographic characteristics, including currents, shoals, and underwater  
610 canyons. The fulmar-dominated community type, which included other pelagic seabird species that prefer  
611 shelf-edge sites, occupied the northern extent of the ‘green belt’ that stretches along the length of the  
612 Bering Sea outer shelf (Springer et al., 1996), but which was not captured by the nearest DBO site (DBO  
613 1). Northern fulmars nest on St. Matthew Island, south of DBO 1, and although they are far-ranging,  
614 colony location is the key factor influencing their offshore distribution in Alaska (Renner et al., 2013).  
615 The thick-billed murre community type included a high proportion of other species, with distinct but  
616 disjunct patches across the study area south of 70°N. Murres typically forage within 100 km of their  
617 colonies (Coulson, 2002), which is likely why this community type was closely associated with colony  
618 sites. Most of this community type was outside the DBO array, although it had some representation in  
619 DBO sites 1 and 3. In contrast, the least auklet-dominated community type was well represented by DBO  
620 2 and to lesser extent, by DBO 3; it extended from the Chirikov Basin through Bering Strait, and reflected



621 proximity to auklet breeding sites and known forage areas (Hunt 1997, Gall et al., 2006; Sheffield-Guy et  
622 al., 2009).

623 The extent of the shearwater-dominated community type throughout the study area explains how  
624 shearwaters dominated DBO sites 2 - 6. Shearwaters are omnivorous and feed both on and under the  
625 water surface (Weimerskirch and Sagar, 1996; Burger, 2001), and they track changes in prey over large  
626 regions (Nishizawa et al., 2017). Although shearwaters were temporally variable among regions (Fig 8),  
627 this community occurred throughout the study area and thus was well represented by the DBO array. In  
628 contrast, the restricted extent of the spatially well-defined crested auklet community type was only  
629 represented in DBO 4, and was uniquely disconnected from breeding sites. Anecdotal observations during  
630 at sea surveys (AEG, KJK) suggest that at least some of these auklets were undergoing post-breeding  
631 molt in this area, thus access to dependable, high densities of zooplankton would be essential.

632 The low density community type extended throughout the eastern side of most of the study area, and  
633 throughout most of the Beaufort region and Arctic shelf and basin (Fig. 10). The occurrence of this  
634 community type in more inshore waters and northern portions of the Chukchi and Beaufort regions was  
635 coincident with low survey coverage, yet even when accounting for that effect (i.e. GAM models of  
636 abundance), the relative paucity of seabirds in these areas is striking. Furthermore, our results were  
637 consistent over multiple surveys and years in this study, and this pattern has been noted in other studies  
638 (Wong et al., 2014) and in earlier overviews (Piatt and Springer, 2003). The Beaufort DBO sites were  
639 primarily composed of the low density community type, and the near absence of this community in other  
640 DBO sites indicates that Bering and Chukchi DBO sites are located in areas of high seabird abundance,  
641 relative to the entire study area.

642

## 643 **5. Conclusion**

644

645 Overall, we conclude that the DBO sites can be used to characterize the seabird community of the  
646 Pacific Arctic, although only when examined in their entirety, because each site captured a different

647 community type. The unique composition of seabirds among DBO sites reflect the diversity of marine  
648 habitats throughout the DBO array. Although short-tailed shearwaters were numerically dominant  
649 throughout much of the study area, the DBO array also captured areas of high abundance for a variety of  
650 species. In particular, DBO sites 2 and 3, and surveys between, highlight the importance of the northern  
651 Bering Sea seabird colonies, which stand in the path of increased vessel activity and potential pollution  
652 issues as traffic through Bering Strait increases (Humphries and Huettmann, 2014).

653 The DBO array does, however, have limitations. For example, the northern fulmar-dominated  
654 community type was found primarily south of DBO 1, illustrating that the current DBO array does not  
655 capture the ‘green belt’ of seabird activity on the outer Bering shelf. Notably, unlike the planktivorous  
656 auklets, most piscivorous colonial species (murre, puffins, kittiwakes) are not as well covered by the  
657 DBO array. A sampling site west of St. Matthew Island that straddles both the northern fulmar and thick-  
658 billed murre communities could help to address this gap.

659 Our results suggest that most DBO sites are high-use areas for seabirds, albeit of different  
660 community types, and therefore should be useful for integration with other disciplines. For example, in  
661 DBO 2, there should be strong links between planktivorous auklets and zooplankton. Near DBO 3, based  
662 on prey collected from kittiwakes and murre at the Cape Lisburne colony (1975-2015), a wide variety of  
663 fishes and in some years high proportions of invertebrates are consumed, including Gadidae (primarily  
664 Arctic cod), Osmeridae, Ammodytidae, Pleuronectiformes, Cottidae, and others (Drummond, 2016); these  
665 species were also found in regional fish surveys (Rand and Logerwell, 2011; Logerwell et al., 2015),  
666 providing a trophic link within the region.

667 Because seabirds are highly mobile, particularly non-breeding birds, sampling over large areas is  
668 necessary, but in some locations the level of effort required may not be achievable. For example, because  
669 of extremely low seabird abundance, an order of magnitude increase in sampling effort would be  
670 necessary to adequately describe the seabird communities of DBO sites 7 and 8. Effort might be better  
671 spent improving coverage within foraging range of large colonies of piscivorous seabirds. With the  
672 predicted dramatic changes in sea ice, which will alter ocean properties and thereby seabird prey in the

673 Pacific Arctic (Gerbmeier et al., 2010, 2018; Stabeno et al., 2018), it may be necessary to concentrate  
674 efforts where impacts to seabirds could be greatest.

675 To fully realize the potential for understanding seabirds and their trends in these three regions,  
676 several gaps need to be addressed: 1) coverage would need to be spatially expanded to capture the  
677 northern Bering outer shelf, and increased if the goal is to capture the Beaufort coastal areas; 2) broader  
678 seasonal coverage would be needed to capture shifts in seabird communities during early summer in the  
679 Chukchi Sea, particularly now that ice retreats earlier in the year and returns later (Frey et al., 2015;  
680 Stabeno et al., 2018), and; 3) a more equal distribution of effort among DBO sites would strengthen the  
681 spatial comparisons in seabird abundance and species composition. Combining efforts across  
682 organizations and science programs has provided spatial and temporal data on seabirds not otherwise  
683 possible for this large and remote ecosystem. The data acquired are possibly unique, particularly for this  
684 area, and critical at a time when the Arctic is changing so rapidly. We conclude that the DBO array will  
685 be a good tool for monitoring offshore habitat use of seabirds in the Pacific Arctic.

686

## 687 **Acknowledgements**

688

689 This study was the result of multiple research projects and funding entities. The U.S. Fish and Wildlife  
690 Service surveys were funded in part by: 1) the North Pacific Research Board during Projects 637 (2006-  
691 2008) and B64 (2008-2010); 2) an Interagency Agreement with the Bureau of Ocean Energy Management  
692 AK-10-10 (2010-2015; IA No. M10PG00050); and 3) the Arctic Marine Biodiversity Observing Network  
693 (AMBON) via a grant from the National Science Foundation to Dr. Katrin Iken, University of Alaska,  
694 Fairbanks. ABR seabird surveys were supported by Conoco Phillips, Shell, and Statoil USA, and included  
695 programs CSESP (2010–2015) and AKMAP (2011). We thank Dr. Martin Renner of Tern Again  
696 Consulting for processing much of the USFWS data. The seabird survey data were collected by four of  
697 the authors and a number of dedicated observers throughout the years. We are indebted to the crews of  
698 multiple research vessels and chief scientists, too many to list, which made our surveys possible. For the

699 impetus behind the establishment of the Distributed Biological Observatory we thank Dr. Jackie  
700 Grebmeier and the Pacific Arctic Group, and for the drive to include upper trophic level organisms in the  
701 DBO overview, we thank Dr. Sue Moore. The careful appraisals by three anonymous reviewers and the  
702 editors greatly improved the manuscript, and we thank them for their time and efforts.

703

## 704 **References**

705

706 Arrigo, K.R., van Dijken, G., Pabi, S., 2008. Impact of shrinking Arctic ice cover on marine primary  
707 production. *Geophys. Res. Lett.* 35, L19603.

708 Ashjian, C.J., Gallager, S.M., Plourde, S., 2005. Transport of plankton and particles between the Chukchi  
709 and Beaufort Seas during summer 2002, described using a Video Plankton Recorder Deep Sea  
710 Res. Part II 52, 3259-3280. <https://doi.org/10.1016/j.dsr2.2005.10.012>

711 Ashjian, C.J., Braund, S.R., Campbell, R.G., George, J.C., Kruse, J., Maslowski, W., Moore, S.E.,  
712 Nicolson, C.R., Okkonen, S.R., Sherr, B.F., Sherr, E.B., Spitz, Y.H., 2010. Climate variability,  
713 oceanography, bowhead whale distribution and Inupiat subsistence whaling near Barrow, Alaska.  
714 *Arctic* 63, 179-194.

715 Ashjian, C.J., Campbell, R.G., Gelfman, C., Alatalo, P., Elliot, S.M., 2017. Mesozooplankton abundance  
716 and distribution in association with hydrography on Hanna Shoal, NE Chukchi Sea, during  
717 August 2012 and 2013. *Deep-Sea Res. II* 144, 21–36.

718 Benoit-Bird, K.J., Kuletz, K., Heppell, S., Jones, N., Hoover, B., 2011. Active acoustic examination of  
719 the diving behavior of murrelets foraging on patchy prey. *Mar. Ecol. Progr. Ser.* 443, 217–235.

720 Benoit-Bird K.J., Battaile, B.C., Heppell, S.A., Hoover, B., Irons, D., Jones, N., Kuletz, K.J., Nordstrom,  
721 C.A., Paredes, R., Suryan, R.M., Waluk, C.N., Trites, and A.W., 2013. Prey patch patterns predict  
722 habitat use by top marine predators with diverse foraging strategies. *PLoS ONE* 8: e53348.

723 Burger, A.E., 2001. Diving depths of shearwaters. *The Auk* 118, 755–759.

- 724 Coachman, L.K., Aagaard, K., Tripp, R.B., 1975. Bering Strait: The regional and physical oceanography.  
725 University of Washington Press, Seattle, Washington.
- 726 Coachman, L.R., Shigaev, V.V., 1992. Northern Bering-Chukchi Sea ecosystem: The physical basis.  
727 Pages 388-393 in: Nagel, P.A., editor. Results of the Third Joint US-USSR Bering and Chukchi  
728 Seas Expedition (BERPAC), summer 1988. U.S. Fish and Wildlife Service, Washington, D.C.
- 729 Coulson, J.C., 2002. Colonial breeding in seabirds. In: Burger, Schreiber (Eds.), Biology of Marine Birds.  
730 CRC Press, New York, pp 87–113.
- 731 Daase, M., Falk-Petersen, S., 2013. Timing of reproductive events in the marine copepod *Calanus*  
732 *glacialis*: a pan-Arctic perspective. Can. J. of Fish. Aqua. Sci., 70, 871–884.  
733 doi/abs/10.1139/cjfas-2012-0401.
- 734 Danielson, S. L., Eisner, L., Ladd, C., Mordy, C., Sousa, L., & Weingartner, T. J., 2017. A comparison  
735 between late summer 2012 and 2013 water masses, macronutrients, and phytoplankton standing  
736 crops in the northern Bering and Chukchi Seas. Deep-Sea Research Part II: Top. Stud. in  
737 Oceanog. 135, 726. <http://doi.org/10.1016/j.dsr2.2016.05.024>
- 738 Day, R.H., Gall, A.E., Morgan, T.C., Rose, J.R., Plissner, J.H., Sanzenbacher, P.M., Fenneman, J.D.,  
739 Kuletz, K.J., Watts, B.A., 2013. Seabirds new to the Chukchi and Beaufort seas, Alaska: response  
740 to a changing climate? Western Birds 44, 174–182.
- 741 Day, R.H., Kuletz, K.J., Nigro, D.A., 1999. Kittlitz' s Murrelet (*Brachyramphus brevirostris*). In: Poole,  
742 A. (Ed). The birds of North America, No. 435. Philadelphia, PA, & Washington, DC: Academy  
743 of Natural Sciences & American Ornithologists' Union.
- 744 Divoky, G.J., Douglas, D.C., Stenhouse, I.J., 2016. Arctic sea ice a major determinant in Mandt' s black  
745 guillemot movement and distribution during non-breeding season. Biol. Lett. 12. 0160275.  
746 <http://dx.doi.org/10.1098/rsbl.2016.0275>.
- 747 Dragoo, D. E., Thomson, G., Romano, M.D., 2017. Biological monitoring at Cape Lisburne, Alaska in  
748 2017. U. S. Fish and Wildl. Serv. Report AMNWR 2017/15. Homer, Alaska. Available at:

- 749 <https://absilcc.org/science/amnwr/Shared%20Documents/Cape%20Lisburne%202017.pdf>
- 750 Drummond, B.A., 2016, Summary figures of diet data from birds on the Alaska Maritime National  
751 Wildlife Refuge. U.S. Fish and Wildl. Serv. Rep., AMNWR 2016/06. Homer, Alaska. Available  
752 at:<https://absilcc.org/science/amnwr/Shared%20Documents/Seabird%20Diet%20Summary.pdf>
- 753 Dunton, K. H., Grebmeier, J.M., Trefry, J.H., 2017. Hanna Shoal: An Integrative Study of a High Arctic  
754 Marine Ecosystem in the Chukchi Sea. *Deep Sea Res. II*, 144, 1 - 5.  
755 <https://doi.org/10.1016/j.dsr2.2017.09.001>
- 756 Dunton, K.H., Weingartner, T., Carmack, E.C., 2006. The nearshore western Beaufort Sea ecosystem:  
757 Circulation and importance of terrestrial carbon in arctic coastal food webs. *Progress in*  
758 *Oceanography* 71, 362–378.
- 759 Eisner, L., Hillgruber, N., Martinson, E., Maskelo, J., 2013. Pelagic fish and zooplankton species  
760 assemblages in relation to water mass characteristics in the northern Bering and southeast  
761 Chukchi seas. *Polar Biol.* 36, 87–113.
- 762 Elphick, C.S., Hunt Jr., G.L., 1993. Variations in the distributions of seabirds with water mass in the  
763 northern Bering Sea. *Condor* 95, 33–44.
- 764 Fischer, J.B., Larned, W.W., 2004. Summer Distribution of Seabirds in the Western Beaufort Sea. *Arctic*  
765 57(2), 43-159.
- 766 Gall, A.E., Day, R.H., Weingartner, T.J., 2013. Structure and variability of the marine-bird community in  
767 the northeastern Chukchi Sea. *Continental Shelf Res.* 67, 96-115.
- 768 Gall, A.E., Morgan, T.C., Day, R.H., Kuletz K.J., 2017. Ecological shift from piscivorous to  
769 planktivorous seabirds in the Chukchi Sea, 1975-2012. *Polar Biology*, 61-78. 10.1007/s00300-  
770 016-1924-z.
- 771 Gall, A.E., Roby, D.D., Irons, D.B., Rose, I.C., 2006. Inter-annual variation in diet and nest survival of  
772 plankton feeding auklets on St. Lawrence Island, Alaska. *Mar. Ecol. Prog. Ser.* 308, 279–291.

- 773 Grebmeier, J.M., Cooper, L.W., Feder, H. M., Sirenko, B.I., 2006. Ecosystem dynamics of the Pacific-  
774 influenced Northern Bering and Chukchi Seas in the Amerasian Arctic. *Prog. in Oceanog.* 71,  
775 331–361.
- 776 Grebmeier, J.M., Frey, K.E., Cooper, L.W., Kędra, M., 2018. Trends in benthic macrofaunal populations,  
777 seasonal sea ice persistence, and bottom water temperatures in the Bering Strait region.  
778 *Oceanography* 31(2), <https://doi.org/10.5670/oceanog.2018.224>.
- 779 Grebmeier J.M., Moore, S.E., Overland, J.E., Frey, K.E., Gradinger R., 2010. Biological response to  
780 recent Pacific Arctic sea ice retreats. *EOS* 91(18), 161-162.
- 781 Gould, P.J., Forsell, D.J., 1989. Techniques for shipboard surveys of seabirds. U.S. Department of the  
782 Interior, Fish and Wildlife Service, Washington, D.C.
- 783 Hartigan, J. A., Wong, M. A., 1979. A K-means clustering algorithm. *Applied Statistics* 28, 100–108.
- 784 Hobson, K.A., 1993. Trophic relationships among high Arctic seabirds: insights from tissue-dependent  
785 stable-isotope models. *Mar Ecol Prog Ser* 95,7–18
- 786 Humphries, G.W., Huttemann, F., 2014. Putting models to a good use: A rapid assessment of Arctic  
787 seabird biodiversity indicates potential conflicts with shipping lanes and human activity.  
788 *Diversity and Distributions* 2014, 1–13.
- 789 Hunt, G. L. Jr., 1997. Physics, zooplankton, and the distribution of least auklets in the Bering Sea – a  
790 review. *ICES J. Mar. Sci.*, 54, 600–607.
- 791 Hunt Jr., G.L., Renner, M., Kuletz, K.J., Salo, S., Eisner, L., Ressler, P., Ladd, C., Santora, J.A., 2018.  
792 Timing of sea-ice-retreat affects the distribution of seabirds and their prey in the southeastern  
793 Bering Sea. *Mar. Ecol. Prog. Ser.* 593, 209-230.
- 794 Hunt Jr., G.L., Schneider, D.C., 1987. Scale dependent processes in the physical and biological  
795 environment of seabirds. Pages 7-41 in: Croxall J., editor. *Seabirds: feeding biology and role in*  
796 *marine ecosystems*. Cambridge University Press, Cambridge.

- 797 Hop, H., Gjørseter, H., 2013. Polar cod (*Boreogadus saida*) and capelin (*Mallotus villosus*) as key species  
798 in marine food webs of the Arctic and the Barents Sea, *Mar. Biol. Res.* 9(9), 878-894, DOI:  
799 10.1080/17451000.2013.775458
- 800 Hopcroft, R.R., Kosobokova, K.N., Pinchuk, A.I., 2010. Zooplankton community patterns in the Chukchi  
801 Sea during summer 2004. *Deep-Sea Res. II* 57, 27–39.
- 802 Iken, K., Mueter, F., Grebmeier, J.M., Cooper, J.W., Danielson, S.L., Bluhm, B.A. 2018. Developing an  
803 observational design for epibenthos and fish assemblages in the Chukchi Sea. *Deep-Sea Res II*,  
804 <https://doi.org/10.1016/j.dsr2.2018.11.005>.
- 805 Johnson, S.R., Herter, D.R., 1989. *The Birds of the Beaufort Sea*. LGL Limited, Sidney, British  
806 Columbia, Canada, Published by BP Exploration (Alaska) Inc., Anchorage, Alaska.
- 807 Kuletz, K.J., Ferguson, M.C., Hurley, B., Gall, A.E., Labunski, E.A., Morgan, T.C., 2015. Seasonal  
808 spatial patterns in seabird and marine mammal distribution in the eastern Chukchi and western  
809 Beaufort seas: identifying biologically important pelagic areas. *Prog. in Oceanogr.* 136, 175-200.
- 810 Kuletz, K.J., Labunski, E.A., 2017. *Seabird Distribution and Abundance in the Offshore Environment*,  
811 Final Report. US Dept. of the Interior, Bureau of Ocean Energy Management, Alaska OCS  
812 Region. OCS Study BOEM 2017-004. Provided to BOEM by the U.S. Fish and Wildlife Service,  
813 59 pp, plus 400 pages of Appendices. Available at: <https://www.boem.gov/2017-004/>
- 814 Kuletz, K.J., Labunski, E.A., Renner, M., Irons, D., 2008. *The North Pacific pelagic seabird observer*  
815 *program*. NPRB Project 637 Final Report, North Pacific Research Board (NPRB), Anchorage,  
816 Alaska.
- 817 Kuletz, K.J., Renner, M., Labunski, E.A., Hunt, G.L. Jr., 2014. Changes in the distribution and abundance  
818 of eastern Bering Sea albatrosses: 1975–2010. *Deep Sea Res II* 109, 282–292.
- 819 Logerwell, E., Busby, M., Carothers, C., Cotton, S., Duffy-Anderson, J., Farley, E., Goddard, P., Heintz,  
820 R., Holladay, B., Horne, J., Johnson, S., 2015. Fish communities across a spectrum of habitats in  
821 the western Beaufort Sea and Chukchi Sea. *Prog. Oceanogr.* 136, 115 – 132.
- 822 MacArthur, R.H., MacArthur, J.W., 1961. On bird species diversity. *Ecology* 42, 594–598.



- 823 Magurran, A. E., McGill, B. J. (Eds.), 2011. Biological diversity: frontiers in measurement and  
824 assessment. New York, NY: Oxford University Press.
- 825 Moore, S.E., Grebmeier, J.M., 2018. The Distributed Biological Observatory: linking physics to biology  
826 in the Pacific Arctic region. *Arctic. Deep-Sea Res II, in press*
- 827 Moore, S.E., Kuletz, K.J. 2018. Marine birds and mammals as ecosystem sentinels in and near Distributed  
828 Biological Observatory regions: An abbreviated review of published accounts and  
829 recommendations for integration to ocean observatories. *Deep Sea Res II*,  
830 <https://doi.org/10.1016/j.dsr2.2018.09.004>
- 831 Moore, S.E., Logerwell, E., Eisner, L., Farley, E., Harwood, L., Kuletz, K., Lovvorn, J., Murphy, J.,  
832 Quakenbush, L., 2014. Marine fishes, birds and mammals as sentinels of ecosystem variability  
833 and reorganization in the Pacific Arctic region. pp 337-392 In *The Pacific Arctic Region:*  
834 *Ecosystem Status and Trends in a Rapidly Changing Environment.* J. Grebmeier and W.  
835 Maslowski (eds) Springer, Dordrecht.
- 836 Moore, S.E., Stabeno, P.J., Grebmeier, J.M., Okkonen, S., 2018. The Arctic Marine Pulses Model: linking  
837 annual oceanographic processes to contiguous ecological domains in the Pacific Arctic. *Deep-Sea*  
838 *Res. II*, 152, 8 – 21. <http://dx.doi.org/10.1016/j.dsr2.2016.10.1011>.
- 839 National Ice Center and National Snow and Ice Data center. Compiled by Fetterer, F., Savoie, M.,  
840 Helfich, S., Clemente-Colón, P., 2010, updated daily. Multisensor analyzed sea ice extent –  
841 northern hemisphere (MASIE-NH), Version 1. NSDIC: National Snow and Ice Data Center,  
842 Boulder, Colorado, USA. doi: <https://doi.org/10.7265/N5GT5K3K>. Accessed June 13, 2018.
- 843 Nishizawa, B., Matsuno, K., Labunski, E.A., Kuletz, K.J., Yamaguchi, A., Watanuki, Y., 2017. Seasonal  
844 distribution of short-tailed shearwaters and their prey in the Bering and Chukchi Seas.  
845 *Biogeosciences* 14, 1-12, doi:10.5194/bg-14-1-2017.
- 846 Norcross, B.L., Raborn, S.W., Holladay, B.A., Gallaway, B.J., Crawford, S.T., Priest, J.T., Edenfield,  
847 L.E., Meyer, R., 2013. Northeastern Chukchi Sea demersal fishes and associated environmental  
848 characteristics, 2009–2010. *Cont. Shelf Res.* 67, 77–95.

- 849 Okkonen, S., Ashjian, C., Campbell, R.G., Alatalo, P., 2018. The encoding of wind forcing into the  
850 Pacific-Arctic pressure head, Chukchi Sea ice retreat and late-summer Barrow Canyon water  
851 masses. *Deep Sea Res. Part II*, doi.org/10.1016/j.dsr2.2018.05.009.
- 852 Okkonen, S.R., Ashjian, C.J., Campbell, R.G., Clarke, J.T., Moore, S.E., Taylor, K.D., 2011. Satellite  
853 observations of circulation features associated with a bowhead whale 'hotspot' near Barrow,  
854 Alaska. *Remote Sensing of Environment* 115, 2168-2174.
- 855 Pebesma, E.J., 2004. Multivariable geostatistics in S: the gstat package. *Computers and Geosciences* 30,  
856 683-691.
- 857 Petersen, A., Irons, D.B., Gilchrist, H.G., Robertson, G., Boertmann, D., Strøm, H., Gavrilov, M.,  
858 Artukhin, Y., Clausen, D.S., Kuletz, K.J., Mallory, M.L., 2015. The Status of Glaucous Gulls  
859 *Larus hyperboreus* in the Circumpolar Arctic. *Arctic*, 68, 107–120.
- 860 Piatt, J.F., Springer, A.M., 2003. Advection, pelagic food webs and the biogeography of seabirds in  
861 Beringia. *Mar. Ornithol.* 31, 141-154.
- 862 Piatt, J., Sydeman, W., Wiese, F., 2007. Introduction: a modern role for seabirds as indicators. In *Seabirds*  
863 *as Indicators of Marine Ecosystems*. *Mar. Ecol. Prog. Ser.* 353, 199-309.
- 864 Pickart R.S., Moore, G.W.K., Torres, D. J., Fratantoni, P.S., Goldsmith, R.A., Yang, J., 2009. Upwelling  
865 on the continental slope of the Alaskan Beaufort Sea: Storms, ice, and oceanographic response. *J.*  
866 *Geophys. Res.*, 114, C00A13, doi:10.1029/2008JC005009
- 867 Pickart, R.S., Schulze, L.M., Moore, G.W.K., Charette, M.A., Arrigo, K.R., van Dijken, G., Danielson,  
868 S.L., 2013. Long-term trends of upwelling and impacts on primary productivity in the Alaskan  
869 Beaufort Sea. *Deep-Sea Res. I* 79, 106-121.
- 870 R Core Team., 2015. R: A language and environment for statistical computing. R Foundation for  
871 Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- 872 Rand, K.M., Logerwell, E.A., 2011. The first demersal trawl survey of benthic fish and invertebrates in  
873 the Beaufort Sea since the late 1970s. *Polar Biol.* 34, 475-488. DOI 10.1007/s00300-010-0900-2

- 874 Renner, M., Parrish, J.K., Piatt, J.F., Kuletz, K.J., Edwards, A.E., Hunt, G.L. Jr., 2013. Modeled  
875 distribution and abundance of a pelagic seabird reveals trends in relation to fisheries. *Mar Ecol*  
876 *Prog Ser* 484, 259–277.
- 877 Renner, M., Salo, S., Eisner, L., Ressler, P., Ladd, C., Kuletz, K., Santora, J., Piatt, J., Drew, G., Hunt Jr.,  
878 G.L., 2016. Timing of ice retreat alters seabird abundances and distributions in the southeast  
879 Bering Sea. *Biol. Lett.* 12, 20160276. <https://doi.org/10.1098/rsbl.2016.0276>.
- 880 Rudis, B., Gandy, D., 2017. Waffle: Create waffle chart visualizations in R. URL: [https://cran.r-](https://cran.r-project.org/web/packages/waffle/waffle.pdf)  
881 [project.org/web/packages/waffle/waffle.pdf](https://cran.r-project.org/web/packages/waffle/waffle.pdf)
- 882 Santora, J. A., Eisner, L.B., Kuletz, K.J., Ladd, C., Renner, M., Hunt G.L., Jr., 2018. Biogeography of  
883 seabirds within a high-latitude ecosystem: Use of a data assimilative ocean model to assess  
884 impacts of mesoscale oceanography. *J. Mar. Syst.* 178, 38–51,  
885 <https://doi.org/10.1016/j.jmarsys.2017.10.006>
- 886 Schneider, D.C., Harrison, N.M., Hunt Jr., G.L., 1987. Variation in attendance at fronts by seabirds in the  
887 Bering Sea. *Estuar. Coast. Shelf Sci.* 25, 135–141.
- 888 Schneider, D.C., Harrison, N.M., Hunt Jr., G.L., 1990. Seabird diet at a front near the Pribilof Islands,  
889 Alaska. *Studies in Avian Biol.* 14, 61–66.
- 890 Shannon, C., 1948. A mathematical theory of communication. *Bell System Technical Journal* 27, 379–  
891 423.
- 892 Sigler, M.F., Mueter, J., Bodil, A., Bluhm, B., Busby, M.S., Cokelet, E.D., Danielson, S.L., De Robertis,  
893 A., Eisner, L.B., Farley, E.V., Iken, K., Kuletz, K.J., Lauth, R.R., Logerwell, E.A., Pinchuk, A.I.,  
894 2017. Late summer zoogeography of the northern Bering and Chukchi seas, *Deep-Sea Res. II*  
895 35,168–189, ISSN 0967-0645. [doi.org/10.1016/j.dsr2.2016.03.005](https://doi.org/10.1016/j.dsr2.2016.03.005)
- 896 Sigler, M.F., Renner, M., Danielson, S.L., Eisner, L.B., Lauth, R.R., Kuletz, K.J., Logerwell, E.A., Hunt,  
897 G.L., Jr., 2011. Fluxes, fins, and feathers: Relationships among the Bering, Chukchi, and  
898 Beaufort Seas in a time of climate change. *Oceanography* 24, 250–265.

- 899 Sheffield-Guy, L.M., Roby, D.D., Gall, A.E., Irons, D.B., Rose, I.C., 2009. The influence of diet and  
900 ocean conditions on productivity of auklets on St. Lawrence Island, Alaska. *Mar. Ornith.* 37,  
901 227–236.
- 902 Stafford, K.M., Okkonen, S.R., Clarke J.T., 2013. Correlation of a strong Alaska Coastal Current with the  
903 presence of beluga whales *Delphinapterus leucas* near Barrow, Alaska. *Mar. Ecol. Progr. Ser.*  
904 474, 287-297.
- 905 Stringer, W.J., Groves, J.E., 1991. Location and areal extent of polynyas in the Bering and Chukchi Seas.  
906 *Arctic* 44, 164–171.
- 907 Stephensen, S.W., Irons, D.B., 2003. A comparison of colonial breeding seabirds in the eastern Bering  
908 Sea and Gulf of Alaska. *Mar. Ornith.* 31,167–173.
- 909 Springer, A.M., Roseneau, D.G., Murphy, E.C., Springer, M.I., 1984. Environmental controls of marine  
910 food webs: Food habits of seabirds in the eastern Chukchi Sea. *Can. J. Fish. Aqua. Sci.* 41, 1202–  
911 1215.
- 912 Springer, A.M., McRoy, C.P., Flint, M.V., 1996. The Bering Sea Green Belt: Shelf-edge processes and  
913 ecosystem production. *Fish. Oceanog.* 5, 205–223.
- 914 Springer, A.M., McRoy, C.P., 1993. The paradox of pelagic food webs in the northern Bering Sea - III.  
915 Patterns of primary production. *Cont. Shelf Res.* 13, 575-599.
- 916 Stabeno, P.J., Bell, S.W., Bond, N.A., Kimmel, D.G., Mordy, C.W., Sullivan, M.E., 2018. Distributed  
917 Biological Observatory Region 1: Physics, chemistry and plankton in the northern Bering Sea.  
918 *Deep-Sea Res II*, <https://doi.org/10.1016/j.dsr2.2018.11.006>
- 919 Stabeno, O., Napp, J., Mordy, C., Whitley, T., 2010. Factors influencing physical structure and lower  
920 trophic levels of the eastern Bering Sea shelf in 2005: Sea ice, tides, and winds. *Prog. in Oceanog.*  
921 85, 180–196.
- 922 Suryan, R.M., Kuletz, K.J., Parker-Stetter, S.L., Ressler, P.H., and others, 2016. Temporal shifts in  
923 seabird populations and spatial coherence with prey in the southeastern Bering Sea. *Mar Ecol*  
924 *Prog Ser* 549, 199–215.

- 925 Tasker, M.L., Jones, P.H., Dixon, T., Blake, B.F., 1984. Counting seabirds at sea from ships: a review of  
926 methods employed and a suggestion for a standardized approach. *The Auk* 101, 567–577.
- 927 Taylor, A.R., Lanctot, R.B., Powell, A.N., Kendall, S.J., Nigro, D.A., 2011. Residence time and  
928 movements of post-breeding shorebirds on the northern coast of Alaska. *Condor* 113, 779–794.
- 929 Weimerskirch, H., Sagar, P.M., 1996. Diving depths of Sooty Shearwaters *Puffinus griseus*. *Ibis* 138,  
930 786–794.
- 931 Weingartner, T., Aagaard, K., Woodgate, R., Danielson, S., Sasaki, Y., Cavalieri, D., 2005. Circulation  
932 on the north central Chukchi Sea shelf. *Deep Sea Res. II* 52, 3150–3174.
- 933 Weingartner, T., Fang, Y.C., Winsor, P., Dobbins, E., Potter, R., Statscewich, H., Mudge, T., Irving, B.,  
934 Soursa, L., Borg, K., 2017. The 2011-2013 summer hydrographic structure of the Hanna Shoal  
935 region on the northeastern Chukchi Sea shelf. *Deep-Sea Res. II* 144, 6–20.
- 936 Weingartner, T.J., Danielson, S., Sasaki, Y., Pavlov, V., Kulakov, M., 1999. The Siberian Coastal  
937 Current: a wind- and buoyancy-forced Arctic coastal current. *J Geophys Res* 104, 29697.  
938 doi:10.1029/1999JC900161.
- 939 Weingartner, T., Dobbins, E., Danielson, S., Winsor, P., Potter, R., Statscewich, H. 2013. Hydrographic  
940 variability over the northeastern Chukchi Sea shelf in summer-fall 2008–2010. *Cont. Shelf Res.*  
941 67, 5–22. <http://doi.org/10.1016/j.csr.2013.03.012>
- 942 Will, A., Thiebot, J., Takahashi, A., Kitaysky, A., 2017. Following Least Auklets (*Aethia pusilla*) into the  
943 winter. Poster presentation at Alaska Marine Science Symposium, January 2017, Anchorage,  
944 Alaska.
- 945 Willig, M.R., Presley, S.J., 2017. *Latitudinal Gradients of Biodiversity*. University of Connecticut, Storrs,  
946 CT. Elsevier Inc. Reference Module in Life Sciences. Doi:10.1016/B978-0-12-809633-8.02174-  
947 9.
- 948 Wood, S.N., 2017. *Generalized additive models: An introduction with R*, Second Ed. CRC Press, Taylor  
949 and Francis Group, New York. 476 pp.

- 950 Woodgate, R.A., Stafford, K.M., Prahl, F.G., 2015. A synthesis of year-round interdisciplinary mooring  
951 measurements in Bering Strait (1990-2014) and the RUSALCA Years (2004-2011).  
952 *Oceanography* 28, 39-59.
- 953 Wong, S.N., Gjerdrum, C., Morgan, K.H., Mallory, M.L., 2014. Hotspots in cold seas: The composition,  
954 distribution, and abundance of seabirds in the North American Arctic. *J. Geophys. Res. Oceans*  
955 119, 1691–1705.
- 956

957 Figure Captions

958

959 Fig. 1. The study area, showing survey effort (km surveyed) in 30-km hexagonal cells. Stars  
960 mark locations of major seabird colonies, with numbered DBO site polygons outlined in black.

961

962 Fig. 2. Major currents and oceanographic features of the northern Bering, Chukchi, and Beaufort  
963 seas. Map is by EAL, based on Dunton et al., 2017.

964

965 Fig. 3. Rarefaction curves of predicted species richness based on a random selection of transects  
966 from seabird surveys in the Bering (red), Chukchi (green), and Beaufort (blue) regions. Solid  
967 lines indicate the mean, with shading representing 95% confidence intervals. Numbers in circles  
968 are the observed species richness and sample size within the DBO site.

969

970 Fig. 4. Total seabird densities for the study area, showing the DBO polygons outlined in black.  
971 Densities (birds•km<sup>-2</sup>) are means of 3-km segments within each 30-km hexagonal cell. White  
972 cells indicate sampling effort but no birds observed. Dark dashed lines indicate boundaries of  
973 shelf slopes in the Bering, Chukchi, and Beaufort regions.

974

975 Fig. 5. Modeled total seabird density (log expected count per 3-km segment  $\pm$  2 SE) by latitude,  
976 holding longitude constant at 168°W (top), and by longitude, holding latitude constant at 71°N  
977 (bottom). Arrows highlight locations of major features along the latitudinal gradient (top;  
978 approximate locations of Bering Strait and DBO sites 1 – 4, south to north) and longitudinal

979 gradient (bottom; showing approximate locations of Point Barrow and DBO sties 4 – 8, west to  
980 east).

981

982 Fig. 6. Modeled density (log expected count per 3-km segment  $\pm$  2 SE) for total seabirds, for  
983 DBO sites (circles) and surrounding region (squares). The X-axis is arranged by DOB site  
984 number and regions aligned with their respective sites. Regions are Bering (red), Chukchi  
985 (green) and Beaufort (blue).

986

987 Fig. 7. Modeled density (log expected count per 3-km segment  $\pm$  2 SE) for selected species and  
988 species groups, for DBO sites (circles) and surrounding region (squares). DBO sites are in  
989 numerical order along the X-axis, and regions aligned with their respective sites. Regions are  
990 Bering (red), Chukchi (green) and Beaufort (blue).

991

992 Fig. 8. Standard deviation of log expected density (estimate  $\pm$  95% CI) for location and year for  
993 total seabirds and for 11 taxa, among three regions (top) and among eight DBO sites (bottom).

994

995 Fig. 9. Species composition and relative abundance of the six communities identified with  
996 cluster analysis, using data from 2007 - 2015. Each cell in the waffle graph represents 0.1  
997 birds•km<sup>-2</sup>. See Appendix B for mean densities of all species within each community type.

998

999 Fig. 10. Mapped results of K-means Cluster Analysis using a 30-km hexagonal grid. The colors  
1000 represent six community types, referred to by their most abundant species, or for Cluster F, by  
1001 low density and lack of a dominant species.



1002

1003 Fig. 11. Species composition and densities for the eight DBO sites, based on surveys from 2007-  
1004 2015. Each cell in the waffle graph represents  $0.1 \text{ birds} \cdot \text{km}^{-2}$ . See Appendix C for mean densities  
1005 of all species within each DBO site.

1006

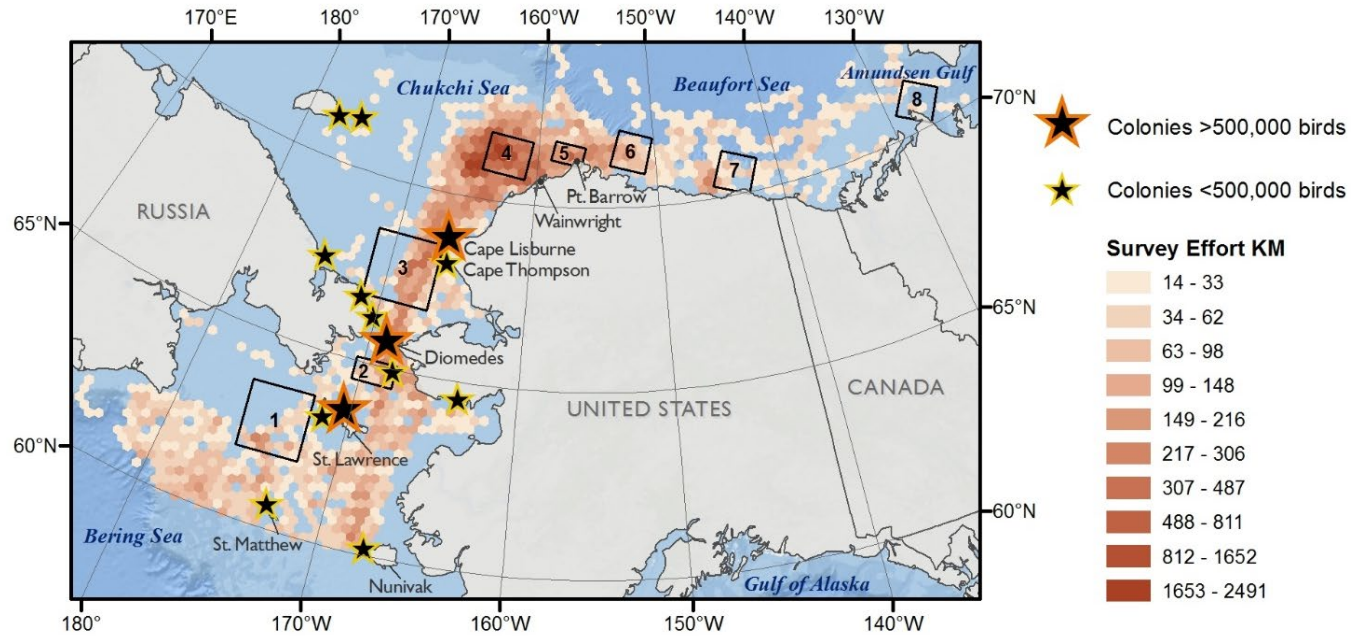


Fig. 1. The study area, showing survey effort (km surveyed) in 30-km hexagonal cells. Stars mark locations of major seabird colonies, with numbered DBO site polygons outlined in black.

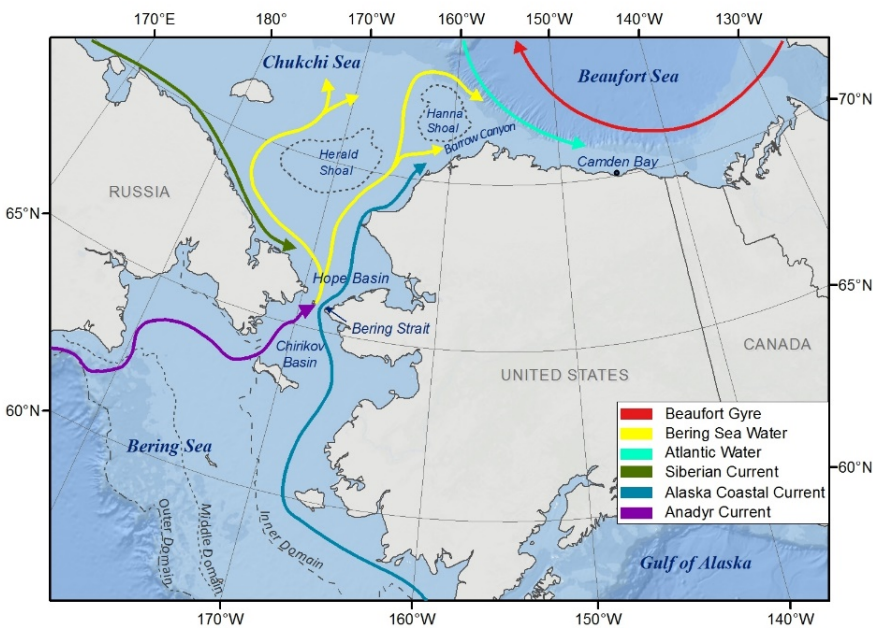


Fig. 2. Major currents and oceanographic features of the northern Bering, Chukchi, and Beaufort seas. Map is by EAL, based on Dunton et al., 2017.

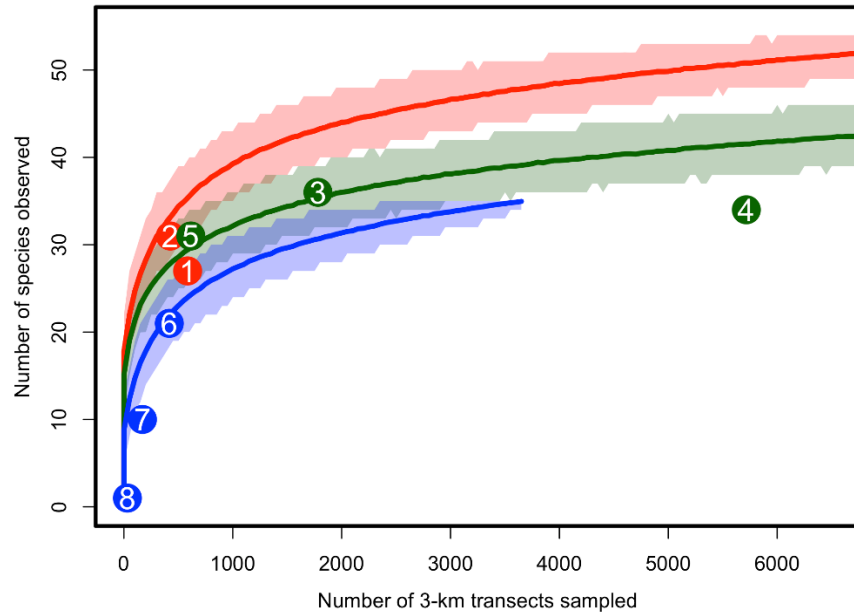


Fig. 3. Rarefaction curves of predicted species richness based on a random selection of transects from seabird surveys in the Bering (red), Chukchi (green), and Beaufort (blue) regions. Solid lines indicate the mean, with shading representing 95% confidence intervals. Numbers in circles are the observed species richness and sample size within the DBO site.

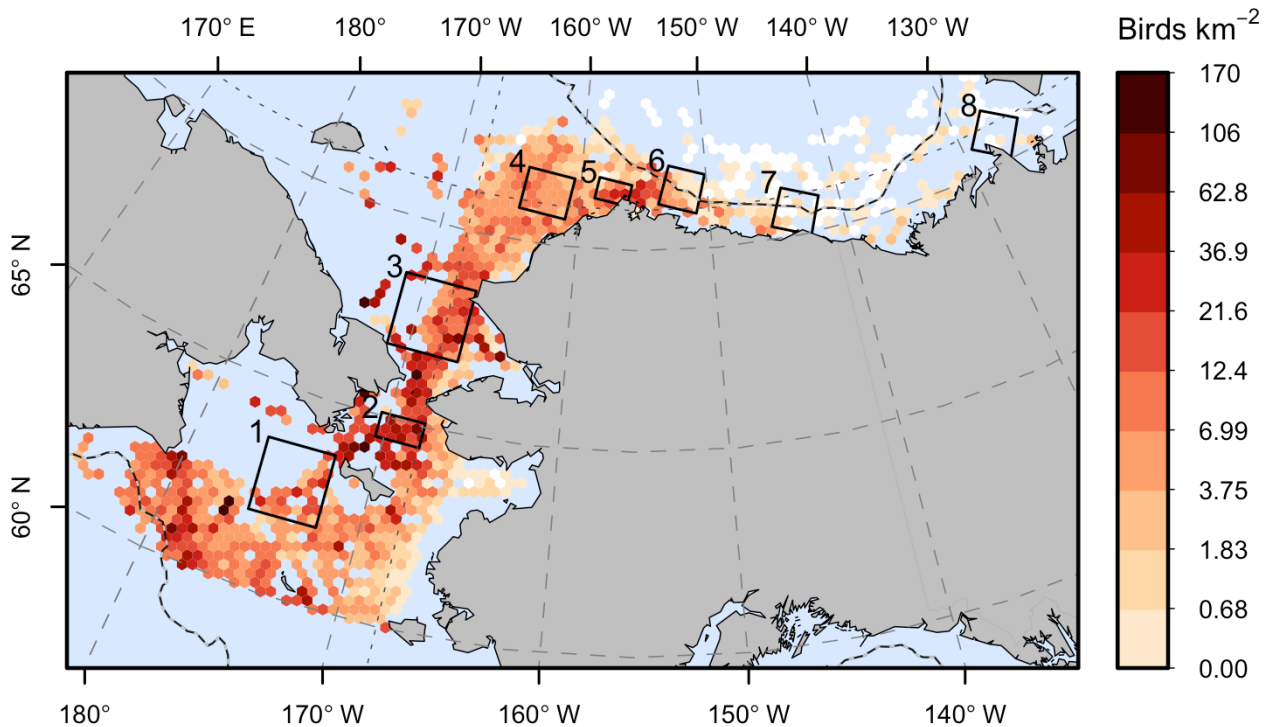


Fig. 4. Total seabird densities for the study area, showing the DBO polygons outlined in black. Densities (birds•km<sup>-2</sup>) are means of 3-km segments within each 30-km hexagonal cell. White cells indicate sampling effort but no birds observed. Dark dashed lines indicate boundaries of shelf slopes in the Bering, Chukchi, and Beaufort regions.

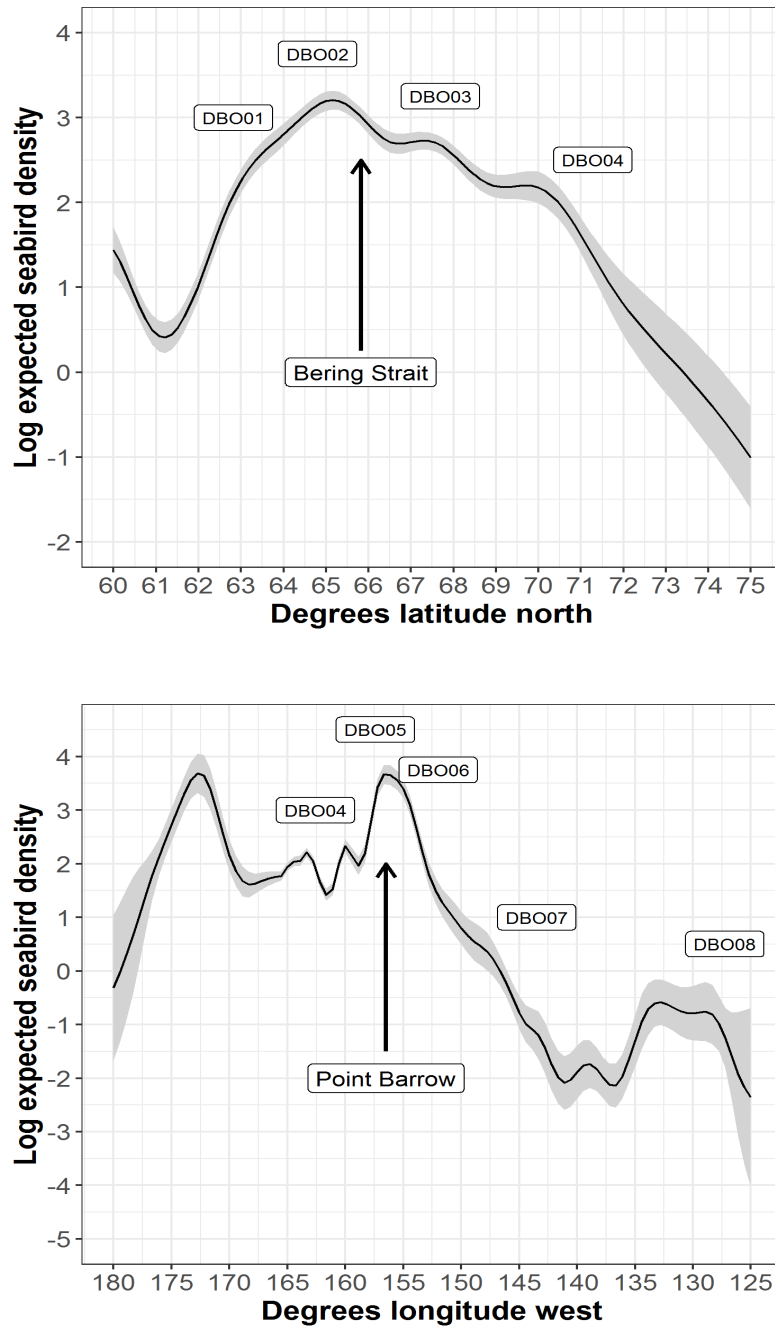


Fig. 5. Modeled total seabird density (log expected count per 3-km segment  $\pm$  2 SE) by latitude, holding longitude constant at 168°W (top), and by longitude, holding latitude constant at 71°N (bottom). Arrows highlight locations of major features along the latitudinal gradient (top; approximate locations of Bering Strait and DBO sites 1 – 4, south to north) and longitudinal gradient (bottom; showing approximate locations of Point Barrow and DBO sites 4 – 8, west to east).

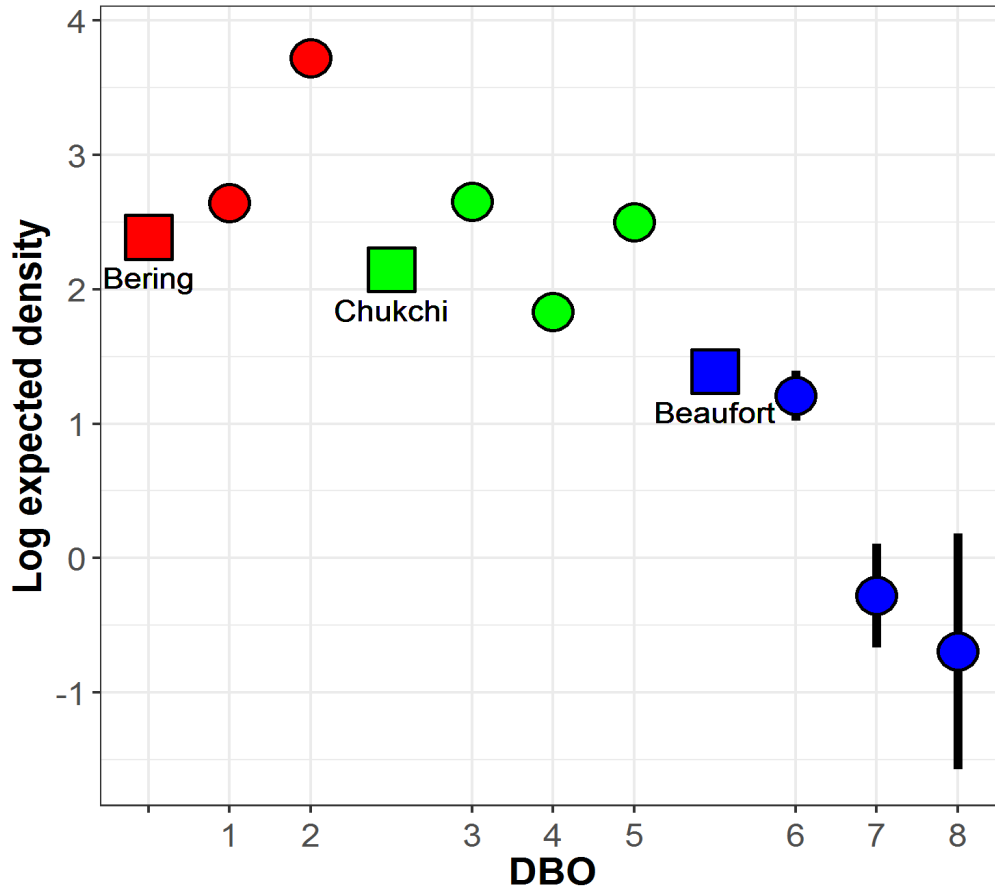


Fig. 6. Modeled density (log expected count per 3-km segment  $\pm$  2 SE) for total seabirds, for DBO sites (circles) and surrounding region (squares). The X-axis is arranged by DBO site number and regions aligned with their respective sites. Regions are Bering (red), Chukchi (green) and Beaufort (blue).

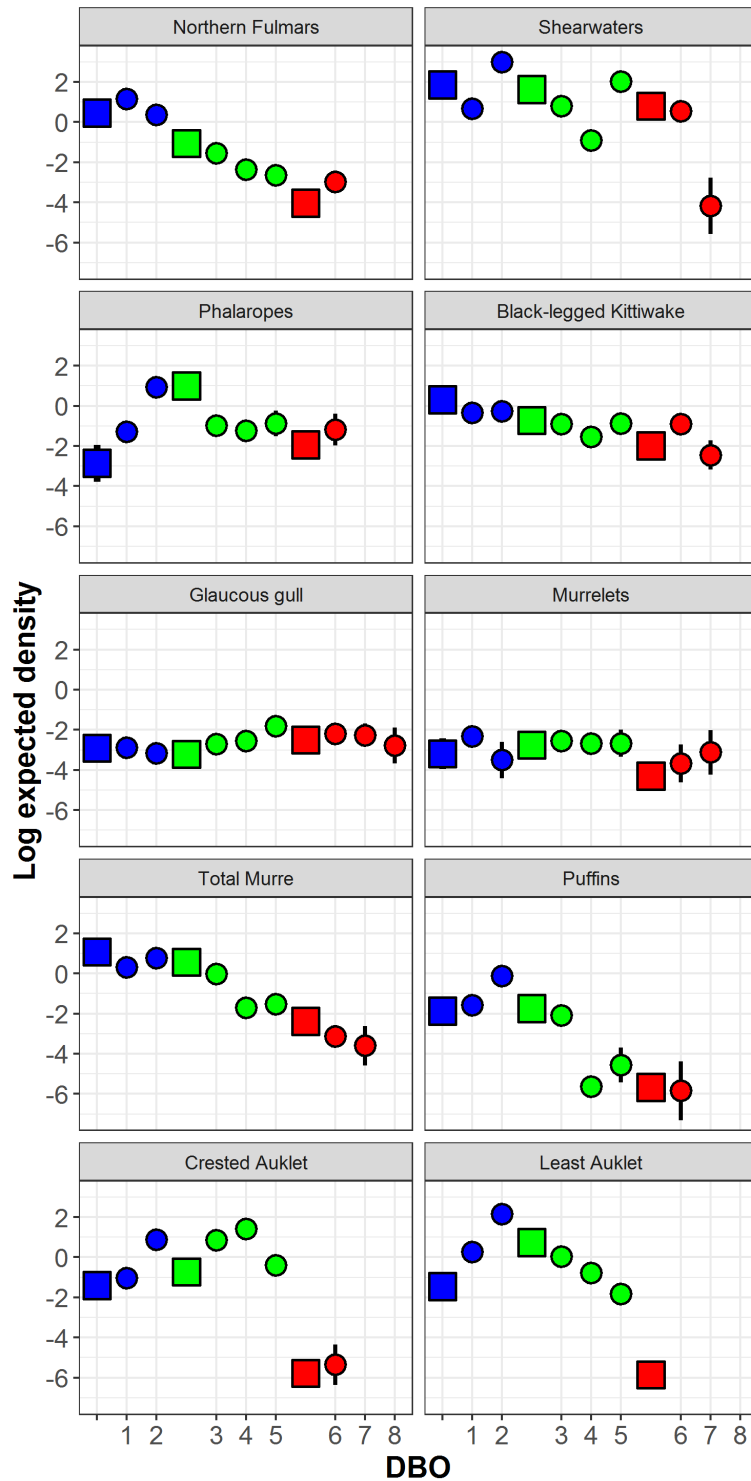


Fig. 7. Modeled density (log expected count per 3-km segment  $\pm$  2 SE) for selected species and species groups, for DBO sites (circles) and surrounding region (squares). DBO sites are in numerical order along the X-axis, and regions aligned with their respective sites. Regions are Bering (red), Chukchi (green) and Beaufort (blue).

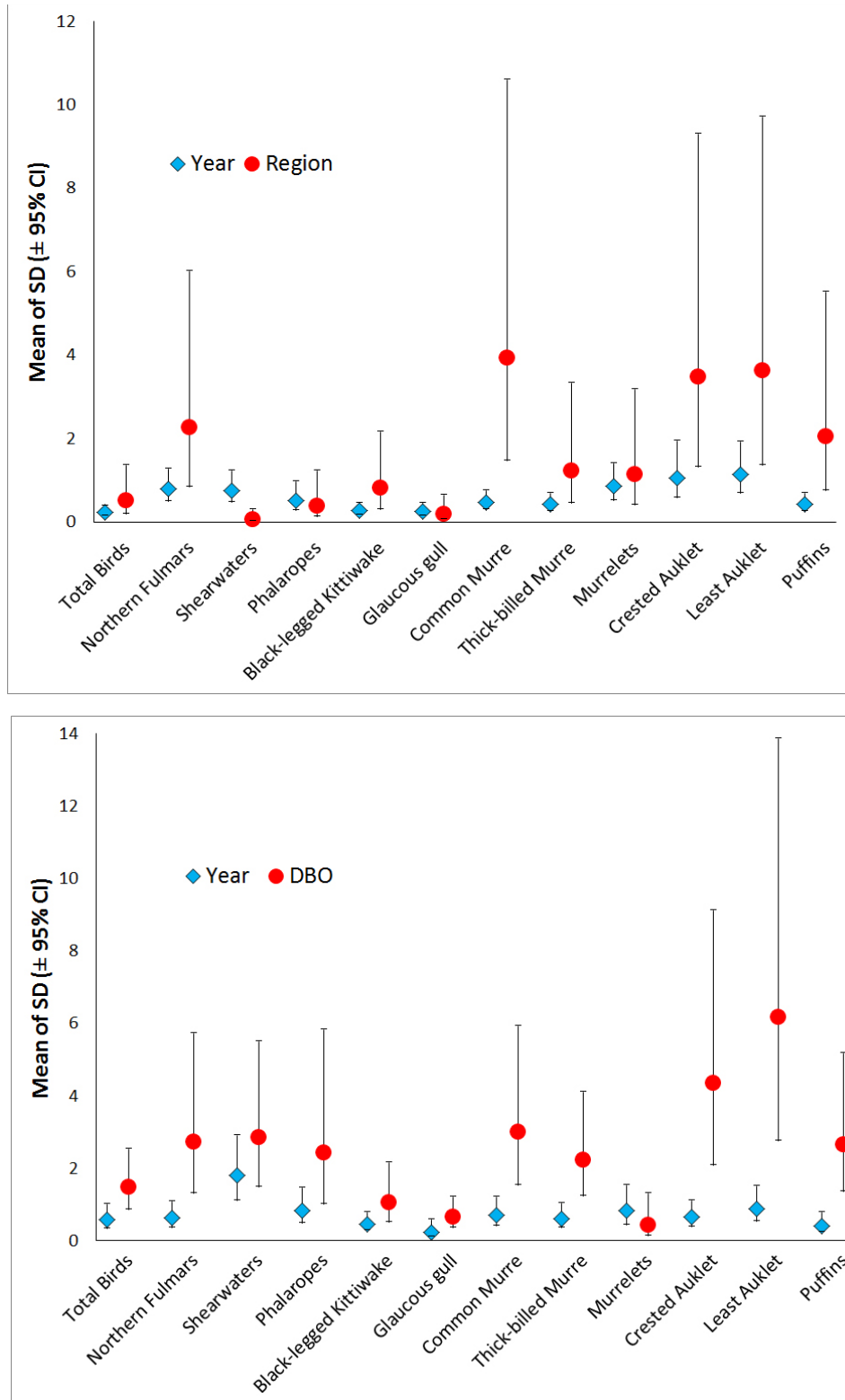


Fig. 8. Standard deviation of log expected density (estimate  $\pm$  95% CI) for location and year for total seabirds and for 11 taxa, among three regions (top) and among eight DBO sites (bottom).

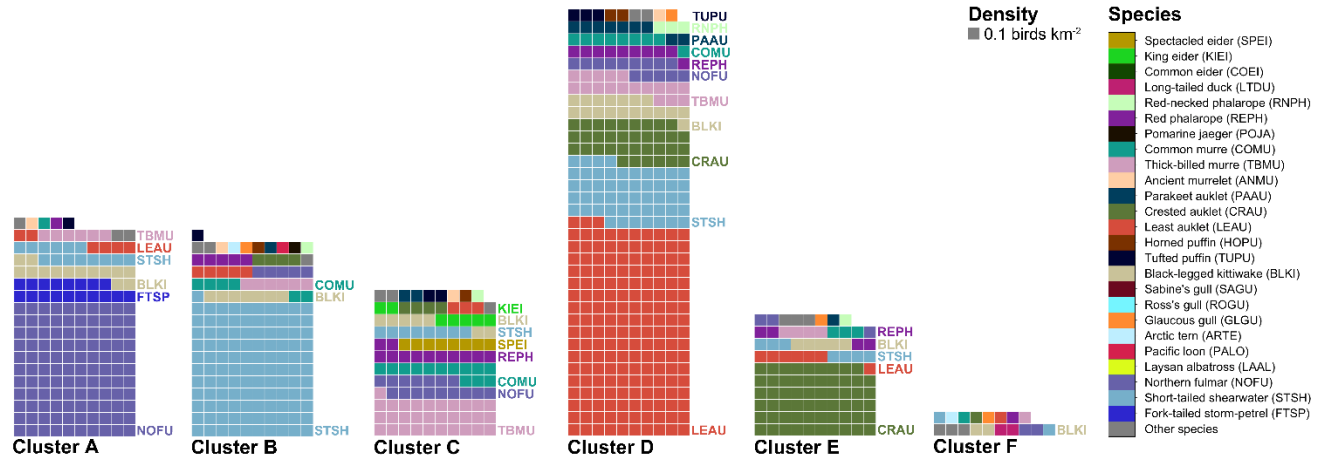


Fig. 9. Species composition and relative abundance of the six communities identified with cluster analysis, using data from 2007 - 2015. Each cell in the waffle graph represents 0.1 birds•km<sup>-2</sup>. See Appendix B for mean densities of all species within each community type.

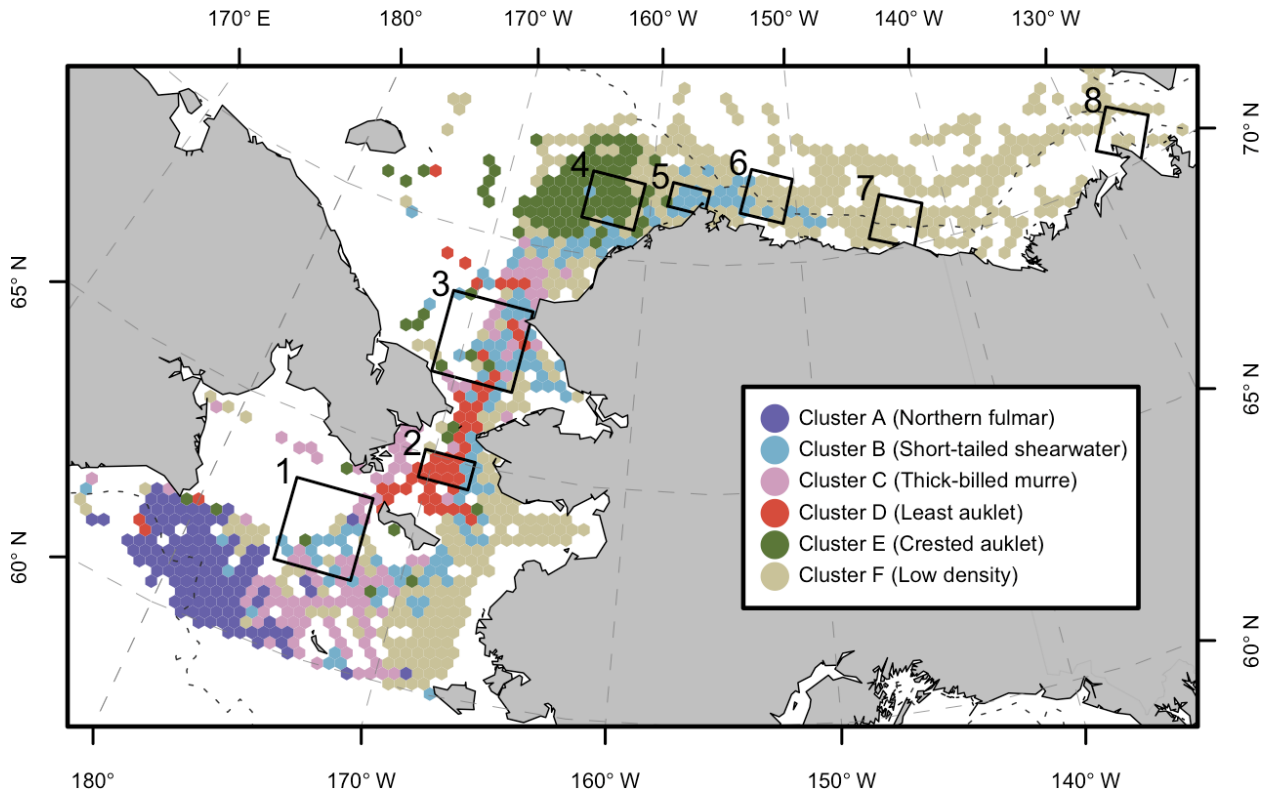


Fig. 10. Mapped results of K-means Cluster Analysis using a 30-km hexagonal grid. The colors represent six community types, referred to by their most abundant species, or for Cluster F, by low density and lack of a dominant species.



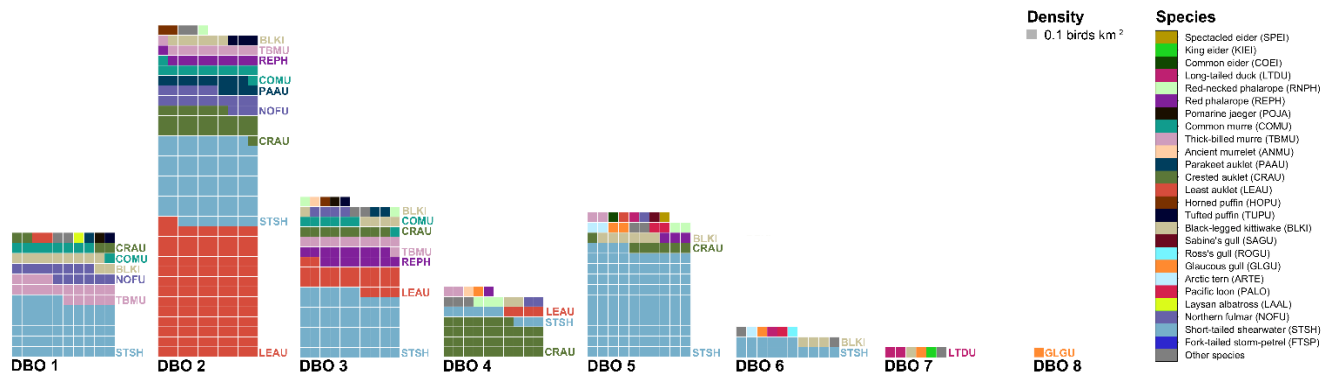


Fig. 11. Species composition and densities for the eight DBO sites, based on surveys from 2007-2015. Each cell in the waffle graph represents 0.1 birds•km<sup>-2</sup>. See Appendix C for mean densities of all species within each DBO site.

Table 1. Species observed in the study area, their foraging mode, primary diet, and nesting or migratory status. Species with names in bold were selected for GAM analyses (see Methods), with some species combined as a single taxa (see footnotes).

Family	Common Name	Latin name	forage mode	primary diet	Colonies in study area	Other nesting areas
Anatidae	Steller's Eider	<i>Polysticta stelleri</i>	benthic	crustacea, molluscs		lagoons & inland
	Spectacled Eider	<i>Somateria fischeri</i>	benthic	crustacea, molluscs		lagoons & inland
	King Eider	<i>Somateria spectabilis</i>	benthic	crustacea, molluscs		lagoons & inland
	Common Eider	<i>Somateria mollissima</i>	benthic	crustacea, molluscs		lagoons & inland
	Harlequin Duck	<i>Histrionicus histrionicus</i>	benthic	crustacea, molluscs		lagoons & inland
	Surf Scoter	<i>Melanitta perspicillata</i>	benthic	crustacea, molluscs		lagoons & inland
	White-winged Scoter	<i>Melanitta fusca</i>	benthic	crustacea, molluscs		lagoons & inland
	Black Scoter	<i>Melanitta americana</i>	benthic	crustacea, molluscs		lagoons & inland
	Long-tailed Duck	<i>Clangula hyemalis</i>	benthic	crustacea, molluscs		lagoons & inland
	Common Merganser	<i>Mergus merganser</i>	diver	fish		lagoons & inland
	Red-breasted Merganser	<i>Mergus serrator</i>	diver	fish		lagoons & inland
Podicipedidae	Red-necked Grebe	<i>Podiceps grisegena</i>	diver	fish		lagoons & inland
Scolopacidae	<b>Red-necked Phalarope<sup>1</sup></b>	<b><i>Phalaropus lobatus</i></b>	surface	zooplankton		lagoons & inland
	<b>Red Phalarope<sup>1</sup></b>	<b><i>Phalaropus fulicarius</i></b>	surface	zooplankton		lagoons & inland
Stercorariidae	Pomarine Jaeger	<i>Stercorarius pomarinus</i>	surface	fish & scavenger		lagoons & inland
	Parasitic Jaeger	<i>Stercorarius parasiticus</i>	surface	fish & scavenger		lagoons & inland
	Long-tailed Jaeger	<i>Stercorarius longicaudus</i>	surface	fish & scavenger		lagoons & inland
Alcidae	Dovekie	<i>Alle alle</i>	diver	zooplankton	yes	mainly Atlantic
	<b>Common Murre<sup>2</sup></b>	<b><i>Uria aalge</i></b>	diver	fish	yes	Bering & GOA
	<b>Thick-billed Murre<sup>2</sup></b>	<b><i>Uria lomvia</i></b>	diver	fish & krill	yes	Bering & GOA
	Black Guillemot	<i>Cepphus grylle</i>	diver	fish	yes	Bering Sea only
	Pigeon Guillemot	<i>Cepphus columba</i>	diver	fish		Bering & GOA
	<b>Marbled Murrelet<sup>3</sup></b>	<b><i>Brachyramphus marmoratus</i></b>	diver	fish		Bering & GOA
	<b>Kittlitz's Murrelet<sup>3</sup></b>	<b><i>Brachyramphus brevirostris</i></b>	diver	fish		Bering & GOA
	<b>Ancient Murrelet<sup>3</sup></b>	<b><i>Synthliboramphus antiquus</i></b>	diver	fish		Bering & GOA
	Cassin's Auklet	<i>Ptychoramphus aleuticus</i>	diver	fish		Bering & GOA
	Parakeet Auklet	<i>Aethia psittacula</i>	diver	fish & zooplankton	yes	Bering & GOA
	<b>Least Auklet<sup>4</sup></b>	<b><i>Aethia pusilla</i></b>	diver	zooplankton	yes	Bering Sea only
	Whiskered Auklet	<i>Aethia pygmaea</i>	diver	fish & zooplankton		Bering Sea only
	<b>Crested Auklet<sup>5</sup></b>	<b><i>Aethia cristatella</i></b>	diver	zooplankton	yes	Bering Sea only
	<b>Horned Puffin<sup>6</sup></b>	<b><i>Fratercula corniculata</i></b>	diver	fish	yes	Bering & GOA
	<b>Tufted Puffin<sup>6</sup></b>	<b><i>Fratercula cirrhata</i></b>	diver	fish	yes	Bering & GOA
	Laridae	<b>Black-legged Kittiwake<sup>7</sup></b>	<b><i>Rissa tridactyla</i></b>	surface	fish	yes
Red-legged Kittiwake		<i>Rissa brevirostris</i>	surface	fish		Bering Sea only
Ivory Gull		<i>Pagophila eburnea</i>	surface	fish & scavenger		Beaufort & Atlantic

Table 1. Species observed in the study area, their foraging mode, primary diet, and nesting or migratory status. Species with names in bold were selected for GAM analyses (see Methods), with some species combined as a single taxa (see footnotes).

Family	Common Name	Latin name	forage mode	primary diet	Colonies in study area	Other nesting areas
	Sabine's Gull	<i>Xema sabini</i>	surface	fish & scavenger		Atlantic/circumpolar
	Black-headed Gull	<i>Chroicocephalus ridibundus</i>	surface	fish & scavenger		Beaufort & Atlantic
	Ross's Gull	<i>Rhodostethia rosea</i>	surface	fish		Atlantic/circumpolar
	Mew Gull	<i>Larus canus</i>	surface	fish & scavenger		Bering & GOA
	Herring Gull	<i>Larus argentatus</i>	surface	fish & scavenger		Bering & GOA
	Iceland Gull	<i>Larus glaucooides</i>	surface	fish & scavenger		Beaufort & Atlantic
	Slaty-backed Gull	<i>Larus schistisagus</i>	surface	fish & scavenger		Western Bering
	Glaucous-winged Gull	<i>Larus glaucescens</i>	surface	fish & scavenger		Bering & GOA
	<b>Glaucous Gull<sup>8</sup></b>	<b><i>Larus hyperboreus</i></b>	surface	fish & scavenger	yes	lagoons & inland
	Aleutian Tern	<i>Onychoprion aleuticus</i>	surface	fish		Bering & GOA
	Arctic Tern	<i>Sterna paradisaea</i>	surface	fish	yes	lagoons & inland
Gaviidae	Red-throated Loon	<i>Gavia stellata</i>	diver	fish		lagoons & inland
	Pacific Loon	<i>Gavia pacifica</i>	diver	fish		lagoons & inland
	Common Loon	<i>Gavia immer</i>	diver	fish		lagoons & inland
	Yellow-billed Loon	<i>Gavia adamsii</i>	diver	fish		lagoons & inland
Diomedidae	Laysan Albatross	<i>Phoebastria immutabilis</i>	surface	squid, fish		central Pacific*
	Short-tailed Albatross	<i>Phoebastria albatrus</i>	surface	squid, fish		central Pacific*
Procellariidae	<b>Northern Fulmar<sup>9</sup></b>	<b><i>Fulmarus glacialis</i></b>	surface	fish, squid		Bering & GOA
	Mottled Petrel	<i>Pterodroma inexpectata</i>	dive & surface	fish, squid, krill		southern hemisphere*
	<b>Short-tailed Shearwater<sup>10</sup></b>	<b><i>Ardenna tenuirostris</i></b>	dive & surface	fish, squid, krill		southern hemisphere*
	<b>Sooty Shearwater<sup>10</sup></b>	<b><i>Ardenna grisea</i></b>	dive & surface	fish, squid, krill		southern hemisphere*
Hydrobatidae	Fork-tailed Storm-Petrel	<i>Oceanodroma furcata</i>	surface	zooplankton		Bering & GOA
Phalacrocoracidae	Red-faced Cormorant	<i>Phalacrocorax urile</i>	diver	fish	yes	Bering & GOA
	Pelagic Cormorant	<i>Phalacrocorax pelagicus</i>	diver	fish	yes	Bering & GOA

\* Indicates species is migratory only, and does not nest in Alaska.

<sup>1</sup> combined as 'Phalarope', with Red Phalarope comprising 80% of this taxa

<sup>2</sup> combined as 'Murre' for some analyses, with 40% Common and 60% Thick-billed murre in this taxa.

<sup>3</sup> combined as 'Murrelets', with 7% Marbled, 25% Kittlitz's, and 68% Ancient murrelets in this taxa

<sup>4</sup> a single species taxa, Least Auklet

<sup>5</sup> a single species taxa, Crested Auklet

<sup>6</sup> combined as 'Puffins', with 34% Horned and 66% Tufted puffins in this taxa.

<sup>7</sup> a single species taxa, Black-legged Kittiwake

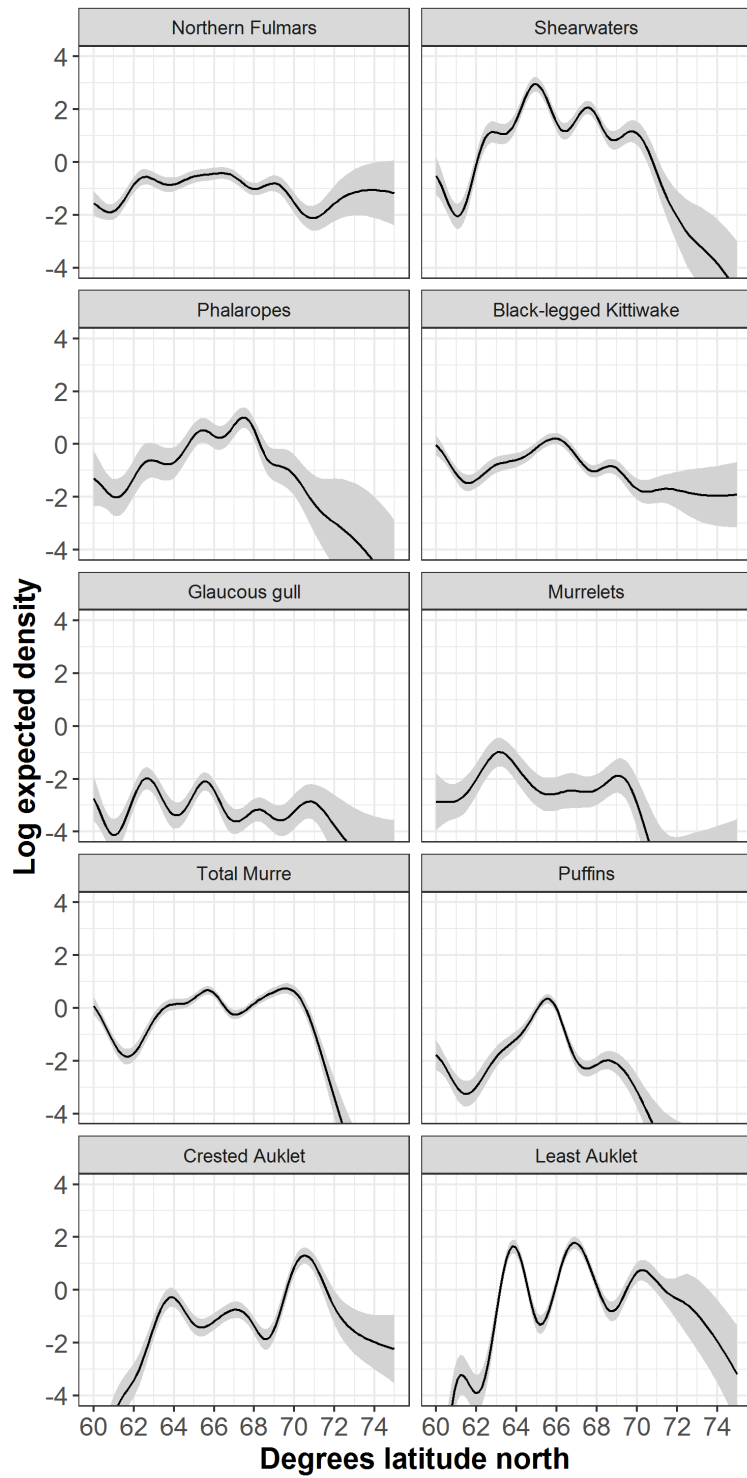
<sup>8</sup> a single species taxa, Glaucous Gull

<sup>9</sup> a single species taxa, Northern Fulmar

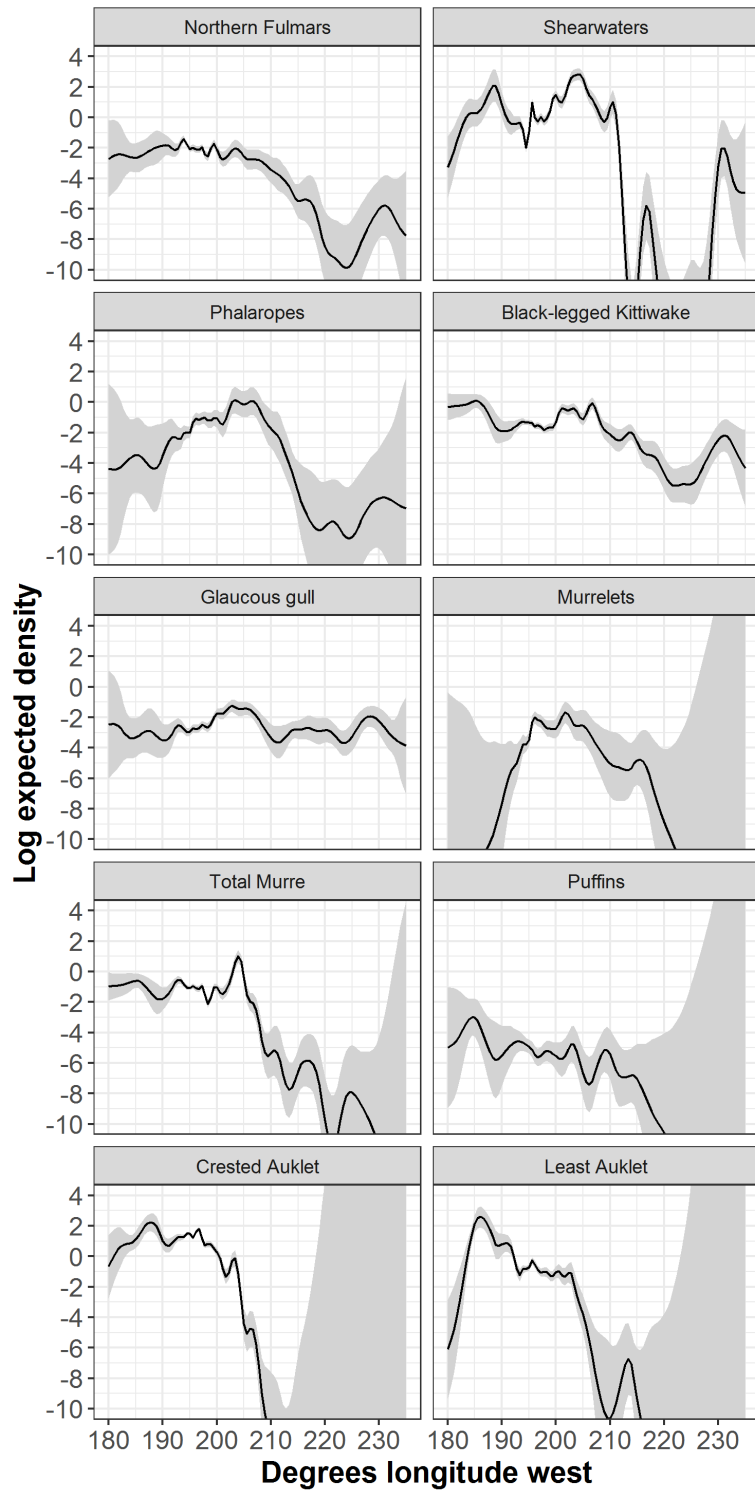
<sup>10</sup> combined as 'Shearwaters', with Short-tailed Shearwater being >99% of this taxa

Table 2. Shannon Diversity Indices ( $H'$ ) for each region (excluding DBO sites) and within each DBO site. Sample units were 3-km transect segments from surveys conducted July – October, 2007 – 2015.

Region	$H'$	DBO Site	$H'$
Bering	2.44	1	1.82
		2	1.74
Chukchi	2.30	3	2.15
		4	1.46
		5	1.53
Beaufort	1.74	6	1.72
		7	2.13
		8	0



Appendix A. Modeled total seabird density (log expected count per 3-km segment  $\pm$  2 SE) for 10 taxa, by latitude, holding longitude constant at 168°W. The large error estimates (shading) in the far north are indicative of both low sampling effort and low encounter rates of birds in those areas.



Appendix A. Modeled total seabird density (log expected count per 3-km segment  $\pm$  2 SE) for 10 taxa, by longitude, holding latitude constant at 71°N. The very large error estimates (shading) are indicative of low sampling effort and low encounter rates of birds in those areas.

Appendix B. Mean densities for each community identified by cluster analysis. Data is from 2007-2015, July-Oct. Densities within communities used average density of 30-km grid cells. Species not identified to species were prorated within grid cells using ratio of identified birds. The numerically dominate species for each community is given in parentheses, and color coded headings match communities in Figure 13.

Common Name	Latin name	Cluster A (N. Fulmar)	Cluster B (Shearwater)	Cluster C (TB Murre)	Cluster D (L. Auklet)	Cluster E (C. Auklet)	Cluster F (Low Density)
Steller's Eider	<i>Polysticta stelleri</i>	0.000	< 0.001	< 0.001	0.004	0.000	0.002
Spectacled Eider	<i>Somateria fischeri</i>	0.000	0.008	0.775	0.001	0.002	0.008
King Eider	<i>Somateria spectabilis</i>	0.000	0.025	0.732	0.003	0.007	0.022
Common Eider	<i>Somateria mollissima</i>	0.000	0.048	0.015	0.005	0.001	0.020
Harlequin Duck	<i>Histrionicus histrionicus</i>	0.001	0.000	0.009	0.000	0.000	0.001
Surf Scoter	<i>Melanitta perspicillata</i>	0.000	< 0.001	0.000	0.000	0.000	< 0.001
White-winged Scoter	<i>Melanitta fusca</i>	0.001	0.001	0.004	0.009	< 0.001	0.003
Black Scoter	<i>Melanitta americana</i>	0.000	< 0.001	0.000	0.000	0.000	< 0.001
Long-tailed Duck	<i>Clangula hyemalis</i>	0.000	0.037	0.006	0.001	0.025	0.161
Common Merganser	<i>Mergus merganser</i>	0.000	< 0.001	0.000	0.001	0.000	0.000
Red-breasted Merganser	<i>Mergus serrator</i>	0.000	0.000	0.000	0.000	0.000	< 0.001
Red-necked Grebe	<i>Podiceps grisegena</i>	0.000	< 0.001	< 0.001	0.000	0.000	< 0.001
Red-necked Phalarope	<i>Phalaropus lobatus</i>	0.003	0.078	0.052	0.269	0.109	0.044
Red Phalarope	<i>Phalaropus fulicarius</i>	0.063	0.454	1.221	1.016	0.364	0.081
Pomarine Jaeger	<i>Stercorarius pomarinus</i>	0.040	0.059	0.035	0.035	0.023	0.013
Parasitic Jaeger	<i>Stercorarius parasiticus</i>	0.013	0.023	0.008	0.008	0.005	0.004
Long-tailed Jaeger	<i>Stercorarius longicaudus</i>	0.010	0.004	0.002	0.003	0.002	0.004
Dovekie	<i>Alle alle</i>	0.000	0.002	0.000	0.002	0.001	< 0.001
Common Murre	<i>Uria aalge</i>	0.131	0.635	1.292	0.894	0.259	0.106
Thick-billed Murre	<i>Uria lomvia</i>	0.568	0.623	3.087	1.815	0.441	0.091
Black Guillemot	<i>Cephus grylle</i>	0.000	0.013	< 0.001	0.001	0.005	0.010
Pigeon Guillemot	<i>Cephus columba</i>	0.002	0.001	0.028	0.017	< 0.001	< 0.001
Marbled Murrelet	<i>Brachyramphus marmoratus</i>	0.000	< 0.001	0.005	0.001	0.000	0.001
Kittlitz's Murrelet	<i>Brachyramphus brevirostris</i>	0.000	0.020	0.010	0.002	0.011	0.008
Ancient Murrelet	<i>Synthliboramphus antiquus</i>	0.053	0.116	0.084	0.051	0.032	0.036
Cassin's Auklet	<i>Ptychoramphus aleuticus</i>	0.000	0.000	0.002	0.001	0.000	< 0.001
Parakeet Auklet	<i>Aethia psittacula</i>	0.041	0.143	0.155	0.895	0.050	0.035

Least Auklet	<i>Aethia pusilla</i>	0.581	0.537	0.327	17.316	0.725	0.051
Whiskered Auklet	<i>Aethia pygmaea</i>	0.000	0.000	0.001	0.000	0.000	0.000
Crested Auklet	<i>Aethia cristatella</i>	0.030	0.427	0.403	3.540	5.940	0.081
Horned Puffin	<i>Fratercula corniculata</i>	0.019	0.086	0.148	0.154	0.019	0.011
Tufted Puffin	<i>Fratercula cirrhata</i>	0.129	0.094	0.157	0.348	0.030	0.018
Black-legged Kittiwake	<i>Rissa tridactyla</i>	1.387	0.720	0.698	1.822	0.459	0.235
Red-legged Kittiwake	<i>Rissa brevirostris</i>	0.005	0.004	0.010	0.001	0.000	0.001
Ivory Gull	<i>Pagophila eburnea</i>	0.000	0.000	0.000	0.000	0.001	< 0.001
Sabine's Gull	<i>Xema sabini</i>	< 0.001	0.027	0.004	0.008	0.010	0.020
Ross's Gull	<i>Rhodostethia rosea</i>	0.000	0.010	0.000	0.000	0.024	0.019
Mew Gull	<i>Larus canus</i>	0.000	0.000	0.000	< 0.001	0.000	0.000
Herring Gull	<i>Larus argentatus</i>	0.042	0.004	0.026	0.018	0.006	0.005
Iceland Gull	<i>Larus glaucoides</i>	0.000	0.000	< 0.001	0.000	0.000	< 0.001
Slaty-backed Gull	<i>Larus schistisagus</i>	0.047	< 0.001	0.003	0.017	0.001	< 0.001
Glaucous-winged Gull	<i>Larus glaucescens</i>	0.010	0.013	0.008	0.009	0.002	0.009
Glaucous Gull	<i>Larus hyperboreus</i>	0.031	0.076	0.035	0.087	0.057	0.062
Aleutian Tern	<i>Onychoprion aleuticus</i>	0.000	0.000	0.000	0.000	0.000	< 0.001
Arctic Tern	<i>Sterna paradisaea</i>	0.002	0.075	0.002	0.006	0.007	0.059
Red-throated Loon	<i>Gavia stellata</i>	0.000	0.002	0.002	< 0.001	0.001	0.003
Pacific Loon	<i>Gavia pacifica</i>	0.000	0.076	0.013	0.005	0.030	0.023
Common Loon	<i>Gavia immer</i>	0.000	0.001	0.000	0.000	0.000	0.001
Yellow-billed Loon	<i>Gavia adamsii</i>	0.000	0.001	< 0.001	0.002	0.001	0.002
Laysan Albatross	<i>Phoebastria immutabilis</i>	0.012	0.008	0.012	0.000	0.001	< 0.001
Short-tailed Albatross	<i>Phoebastria albatrus</i>	0.001	0.000	0.000	0.000	0.000	0.000
Northern Fulmar	<i>Fulmarus glacialis</i>	10.962	0.549	1.578	1.374	0.324	0.162
Mottled Petrel	<i>Pterodroma inexpectata</i>	0.002	0.000	< 0.001	0.000	0.000	0.000
Short-tailed Shearwater	<i>Ardenna tenuirostri</i>	1.356	11.072	0.754	5.127	0.718	0.191
Sooty Shearwater	<i>Ardenna grisea</i>	< 0.001	< 0.001	0.001	0.000	0.000	< 0.001
Fork-tailed Storm-Petrel	<i>Oceanodroma furcata</i>	1.799	0.022	0.012	0.020	0.000	0.007
Red-faced Cormorant	<i>Phalacrocorax urile</i>	0.000	0.007	< 0.001	0.000	0.000	< 0.001
Pelagic Cormorant	<i>Phalacrocorax pelagicus</i>	0.001	0.006	0.005	0.003	0.012	0.002
<b>Total Birds</b>		<b>17.340</b>	<b>16.106</b>	<b>11.719</b>	<b>34.892</b>	<b>9.705</b>	<b>1.611</b>



Appendix C. Mean densities (birds•km<sup>-2</sup>) for each DBO site, using data from 2007-2015, July-Oct. Birds not identified to species were prorated based on identified birds within 30-km hexagonal cells, and grid cell densities were averaged to obtain DBO mean densities.

Common Name	Latin name	DBO 1	DBO 2	DBO 3	DBO 4	DBO 5	DBO 6	DBO 7	DBO 8
Steller's Eider	<i>Polysticta stelleri</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.009	0.000
Spectacled Eider	<i>Somateria fischeri</i>	0.000	0.000	0.004	< 0.001	0.092	0.000	0.000	0.000
King Eider	<i>Somateria spectabilis</i>	0.000	0.000	0.016	0.031	0.046	0.039	0.062	0.000
Common Eider	<i>Somateria mollissima</i>	0.000	0.010	0.030	0.001	0.106	0.004	0.000	0.000
Harlequin Duck	<i>Histrionicus histrionicus</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Surf Scoter	<i>Melanitta perspicillata</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
White-winged Scoter	<i>Melanitta fusca</i>	0.000	0.022	0.003	0.001	0.000	0.000	0.000	0.000
Black Scoter	<i>Melanitta americana</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Long-tailed Duck	<i>Clangula hyemalis</i>	0.000	0.000	0.034	0.042	0.118	0.065	0.193	0.000
Common Merganser	<i>Mergus merganser</i>	0.000	0.003	0.001	0.000	0.000	0.000	0.000	0.000
Red-breasted Merganser	<i>Mergus serrator</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Red-necked Grebe	<i>Podiceps grisegena</i>	< 0.001	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Red-necked Phalarope	<i>Phalaropus lobatus</i>	0.000	0.094	0.163	0.320	0.249	0.012	0.000	0.000
Red Phalarope	<i>Phalaropus fulicarius</i>	0.027	0.970	1.654	0.084	0.307	0.028	0.000	0.000
Pomarine Jaeger	<i>Stercorarius pomarinus</i>	0.093	0.031	0.078	0.010	0.021	0.012	0.000	0.000
Parasitic Jaeger	<i>Stercorarius parasiticus</i>	0.011	0.009	0.019	0.004	0.003	0.008	0.006	0.000
Long-tailed Jaeger	<i>Stercorarius longicaudus</i>	0.000	0.000	0.005	0.001	0.003	0.002	0.005	0.000
Dovekie	<i>Alle alle</i>	0.000	0.005	0.000	0.001	0.000	0.000	0.000	0.000
Common Murre	<i>Uria aalge</i>	0.948	1.249	0.696	0.042	0.019	0.011	0.000	0.000
Thick-billed Murre	<i>Uria lomvia</i>	1.918	1.005	1.109	0.173	0.154	0.026	0.002	0.000
Black Guillemot	<i>Cepphus grylle</i>	0.000	0.000	0.001	0.004	0.012	0.000	0.000	0.000
Pigeon Guillemot	<i>Cepphus columba</i>	0.001	0.000	0.001	< 0.001	0.000	0.000	0.000	0.000
Marbled Murrelet	<i>Brachyramphus marmoratus</i>	0.020	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Kittlitz's Murrelet	<i>Brachyramphus brevirostris</i>	0.000	0.000	0.003	0.012	0.043	0.014	0.000	0.000
Ancient Murrelet	<i>Synthliboramphus antiquus</i>	0.033	0.020	0.054	0.066	0.027	0.000	0.000	0.000
Cassin's Auklet	<i>Ptychoramphus aleuticus</i>	0.000	0.005	0.000	0.000	0.000	0.000	0.000	0.000
Parakeet Auklet	<i>Aethia psittacula</i>	0.053	1.258	0.185	0.018	0.004	0.000	0.000	0.000
Least Auklet	<i>Aethia pusilla</i>	0.169	13.231	2.603	0.442	0.063	0.000	0.000	0.000
Whiskered Auklet	<i>Aethia pygmaea</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Crested Auklet	<i>Aethia cristatella</i>	0.373	2.755	0.882	3.733	0.661	0.003	0.000	0.000
Horned Puffin	<i>Fratercula corniculata</i>	0.021	0.153	0.090	0.005	0.000	0.000	0.000	0.000
Tufted Puffin	<i>Fratercula cirrhata</i>	0.139	0.313	0.083	0.001	0.004	0.000	0.000	0.000

Black-legged Kittiwake	<i>Rissa tridactyla</i>	1.120	0.629	0.543	0.247	0.578	0.321	0.070	0.000
Red-legged Kittiwake	<i>Rissa brevirostris</i>	0.004	0.000	< 0.001	0.000	0.000	0.000	0.000	0.000
Ivory Gull	<i>Pagophila eburnea</i>	0.000	0.000	0.000	< 0.001	0.000	0.000	0.000	0.000
Sabine's Gull	<i>Xema sabini</i>	0.005	0.011	0.002	0.008	0.074	0.002	0.000	0.000
Black-headed Gull	<i>Chroicocephalus ridibundus</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Ross's Gull	<i>Rhodostethia rosea</i>	0.000	0.000	0.000	0.031	0.032	0.078	0.000	0.000
Mew Gull	<i>Larus canus</i>	0.000	0.000	< 0.001	0.000	0.000	0.000	0.000	0.000
Herring Gull	<i>Larus argentatus</i>	0.033	0.000	0.003	0.000	0.000	0.000	0.000	0.000
Iceland Gull	<i>Larus glaucoides</i>	0.000	0.000	< 0.001	0.000	0.000	0.000	0.000	0.000
Slaty-backed Gull	<i>Larus schistisagus</i>	0.003	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Glaucous-winged Gull	<i>Larus glaucescens</i>	0.002	0.002	0.000	0.001	0.000	0.003	0.006	0.000
Glaucous Gull	<i>Larus hyperboreus</i>	0.029	0.012	0.040	0.069	0.159	0.126	0.085	0.056
Aleutian Tern	<i>Onychoprion aleuticus</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Arctic Tern	<i>Sterna paradisaea</i>	0.009	0.001	0.003	0.003	0.156	0.113	0.000	0.000
Red-throated Loon	<i>Gavia stellata</i>	0.000	0.001	0.004	0.002	0.012	0.000	0.000	0.000
Pacific Loon	<i>Gavia pacifica</i>	0.000	0.036	0.028	0.049	0.229	0.053	0.044	0.000
Common Loon	<i>Gavia immer</i>	0.000	0.000	0.000	0.000	0.008	0.000	0.000	0.000
Yellow-billed Loon	<i>Gavia adamsii</i>	0.001	0.000	0.000	0.004	0.016	0.000	0.000	0.000
Laysan Albatross	<i>Phoebastria immutabilis</i>	0.051	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Short-tailed Albatross	<i>Phoebastria albatrus</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Northern Fulmar	<i>Fulmarus glacialis</i>	1.445	1.856	0.362	0.180	0.052	0.034	0.000	0.000
Mottled Petrel	<i>Pterodroma inexpectata</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Short-tailed Shearwater	<i>Ardenna tenuirostris</i>	5.495	8.746	6.569	0.861	10.362	1.591	0.006	0.000
Sooty Shearwater	<i>Ardenna grisea</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Fork-tailed Storm-Petrel	<i>Oceanodroma furcata</i>	0.031	0.022	0.001	0.002	0.000	0.000	0.000	0.000
Red-faced Cormorant	<i>Phalacrocorax urile</i>	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Pelagic Cormorant	<i>Phalacrocorax pelagicus</i>	0.000	0.002	0.000	0.000	0.000	0.000	0.000	0.000
Total for DBO		12.033	32.451	15.271	6.449	13.612	2.546	0.488	0.056

Appendix D. Distribution for species groups maps using data from July - October, 2007 – 2015 in the northern Bering, Chukchi and Beaufort seas.

