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## Body size affects individual winter foraging strategies of thick-billed murrelets in the Bering Sea

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1 **Body size predicts individual winter foraging strategies of thick-billed murre in the Bering Sea**

**Comment [RP1]:** Maybe relates to instead of predicts?  
As many other factors may explain the foraging strategies as commented by reviewers

2  
3 Running Head: Winter foraging strategies of thick-billed murre

4  
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18

19 **Abstract**

- 20 1. Within populations, individual foraging strategies can reduce competition, however seasonal  
21 changes in environmental conditions and subsequent responses of prey populations can alter the  
22 relative effectiveness of strategies. For marine birds that fly and dive, body size constraints  
23 present a trade-off for migratory decisions as smaller bodies reduce flight costs whereas larger  
24 bodies are advantageous for diving deeper.
- 25 2. This study tests the hypothesis that body size influences individual wintering strategies of deep  
26 diving thick-billed murres (*Uria lomvia*)- breeding in three Pacific colonies where birds are  
27 apparently heavier than Atlantic colonies, breeding at St. Paul, St. George, and Bogoslof islands in  
28 the south-eastern Bering Sea.
- 29 3. We used geolocation time-depth recorders and stable isotopes from feathers to examine-determine  
30 differences in foraging behaviour and diet of thick-billed murres breeding at St. Paul, St. George,  
31 and Bogoslof islands in the south-eastern Bering Sea during three non-breeding periods, 2008-11.  
32 Body size was quantified by a principle component analysis (of wing, culmen, head+bill, and  
33 tarsus length) and examined in relation to foraging and diets. A hierarchical cluster analysis  
34 identified w Winter foraging strategies were identified using a hierarchical cluster analysis based  
35 on individual movement, diving behaviour, and diet (stable isotopes).
- 36 4. Structural body size-differed by colony and sex. Larger birds from St Paul had higher wing-  
37 loading than smaller birds from St. George. Larger birds (regardless of colony?, mainly from St.  
38 Paul?)) were found at deeper depths, spent more time in the Bering Sea, and likely consumed  
39 higher trophic prey in the late winter. Of the three winter foraging strategies identified, small  
40 birds from all colonies employed Three winter foraging strategies were identified. The main  
41 strategy, employed by small birds from all colonies in two years, was characterized by high  
42 residency areas south of the Aleutians and nocturnal diving in two years where birds dove largely  
43 at night. In contrast, a subset of large birds from St Paul (31%) remained in the Bering Sea, and  
44 foraged mainly during the day possibly feeding mainly on higher trophic prey. Analysis of throat

**Comment [RP2]:** Maybe “examine the influence of body size on individual ....”

**Comment [RP3]:** Not sure if sex should be included as it does not seem to be a main result and it is not mentioned later

**Comment [RP4]:** Do you know if these birds were larger than the rest of STP birds who did not stay in the Bering Sea?

31% of what, of all birds, only STP birds? I mentioned this before I think. I still have a hard time with this percentage. It does not seem like a strong foraging strategy when related to body size, why not all large birds use this foraging strategy or the other 70% were small birds

45 feather stable isotopes indicates that individuals from this colony exhibit dietary flexibility. The  
46 second-last strategy only occurred in 2010/11, when birds from all colonies? dove more and  
47 deeper was year-dependant, and possibly a response to suggesting limited prey resources in  
48 2010/11. The third strategy was composed of a subset of large birds from St Paul (31%) who  
49 remained in the Bering Sea, foraged mainly during the day and likely consumed higher trophic  
50 prey. Throat feather stable isotopes indicate that individuals exhibit flexibility in the use of this  
51 colony specific foraging strategy.

- 52 5. Foraging strategies were linked to body size and partitioned with respect to annual differences,  
53 presumably in response to shifts in the distribution of prey. The presence of a colony specific  
54 wintering strategy suggests a complex regulation of overwinter survival of birds originating from  
55 St Paul where body size is the largest.

56  
57 **Keywords:** geolocation, foraging strategies, marine habitats, Bering Sea, stable isotopes, body size,  
58 winter migration, local adaptation, *Uria lomvia*

## 60 INTRODUCTION

61 Both migration and niche specialization can evolve in response to resource limitation (Chase & Leibold  
62 2003; Milner-Gulland, Fryxell & Sinclair 2011). Within populations, individual foraging strategies can  
63 reduce competition, however changing environmental conditions and subsequent responses of prey  
64 resources can seasonally alter the effectiveness of strategies. The use of individual foraging strategies,  
65 though widespread across taxa (Bolnick *et al.* 2003), appears to be especially common in diving marine  
66 predators (Hoelzel, Dorsey & Stern 1989; Kato *et al.* 2000; Tremblay & Cherel 2000; Tinker *et al.* 2007;  
67 Woo *et al.* 2008; Weise, Harvey & Costa 2010; Kim *et al.* 2012). Many of these predators also make  
68 extended seasonal migrations (Bost *et al.* 2009; Block *et al.* 2011; Gaston *et al.* 2011). The temporal scale  
69 of studies investigating individual foraging strategies varies widely (breeding season, migration, multiple  
70 years) and influences both the types of strategies observed and how they are quantified. Seasonal changes

**Comment [RP5]:** Not sure what is the importance of this part for the abstract

**Comment [RP6]:** Do you know if these birds were larger than the rest of STP birds who did not stay in the Bering Sea?

I got my answer, 31% of St. Paul birds. Maybe specify in abstract. This is a weak support for influence of body size in STP foraging strategy.

**Comment [RP7]:** It has not been clear that strategies is colony specific above (no mention of the other two colonies, so not sure if this is a good follow up conclusion. And you are not saying before that only 31 % birds from STP uses one strategy? Confusing.

71 in available prey resources, particularly shifts in prey depth, as well as resource utilization of a new  
72 habitat may alter how individuals forage (Sims *et al.* 2005; Harding *et al.* 2013). Long time frames are  
73 necessary to understand how individuals are able to adjust foraging behaviour to changing conditions to  
74 fulfil life history needs, especially in species that appear to employ specialized predatory strategies.

75         Body size is a fundamental characteristic that influences life history traits including animal  
76 movements, reproduction and longevity (Peters 1983; Schmidt-Nielsen 1984). Within a species, body size  
77 differences arise through a number of mechanisms, including ontogeny, sexual selection, and local  
78 adaptations (Bolnick & Doebeli 2003; Millien *et al.* 2006; Fairbairn 2010). In some marine predators  
79 individual foraging strategies are independent of body size (Le Vaillant *et al.* 2012), in others, body size  
80 constrains behaviours as the physiology of diving and flying are strongly related to allometric relationships  
81 (Costa 1991; Costa & Shaffer 2012). Diving-flying seabirds face body size constraints in two modes of  
82 movement. Larger body sizes generally equate to enhanced diving performance where durations are  
83 longer and depths are deeper (Burger 1991; Boyd & Croxall 1996). Additionally, wings with reduced  
84 surface area are better for propulsion underwater (Pennycuik 2008). These large bodies and small wings  
85 are not efficient for flying and result in high wing-loading, fast flight speeds and greater flapping rates to  
86 stay aloft (Pennycuik 2008). Within flying-diving species, differences in body size can facilitate niche  
87 partitioning and diet specialization between size classes (Wanless & Harris 1991; Paredes *et al.* 2008;  
88 Ratcliffe *et al.* 2013) or be the result of local adaptations to environmental conditions around breeding  
89 colonies (e.g. Hilton *et al.* 2000; Cook *et al.* 2013).

90         For flying-diving seabirds, the dual use of specialized locomotion through two mediums has  
91 required functional compromises that may vary in importance during breeding and migration. Migration  
92 necessitates relatively large-scale movements outside of home ranges and appears to be important in  
93 flying-diving seabird life histories (e.g. Gaston *et al.* 2011; Guilford *et al.* 2011); therefore body size also  
94 influences migratory ability and strategies, both in locomotion mode and in how animals fuel migrations  
95 (Milner-Gulland *et al.* 2011). Thick-billed murre (*Uria lomvia*) are at the extreme of this junction,  
96 physiologically adapted to dive to extreme depths for their body size (~210 m, (Croll *et al.* 1992), with

97 lower than predicted costs, but with flight costs that are the highest recorded at 0.83 J/Nm (Elliott *et al.*  
98 2013). Regardless, some birds make foraging trips of up to 70 km when breeding (Harding *et al.* 2013)  
99 and migrate from high Arctic colonies to lower latitudes to winter (Gaston *et al.* 2011; McFarlane  
100 Tranquilla *et al.* 2013; Fort *et al.* 2013). Murres are adaptable predators and adjust their diving behaviour  
101 relative to ocean stratification and prey patch size and distribution (Takahashi *et al.* 2008; Benoit-Bird *et*  
102 *al.* 2011). However, individual learning and experiences are likely important for successful predatory  
103 strategies as these long-lived birds employ extended parental care and can specialize on prey species over  
104 many breeding seasons (Woo *et al.* 2008).

105 In this study, we tracked birds during the non-breeding period from the largest bodied subspecies  
106 of thick-billed murre (*U. l. arra*, Pallas, 1811) breeding at three colonies along a north-south transect in  
107 the south-eastern Bering Sea. We hypothesized that body size differences, between sexes and colonies,  
108 constrain influence individual wintering strategies of thick-billed murres. Metrics of body size, spatial  
109 distributions, diving behaviour and diet data inferred from stable isotopes of feathers were used to identify  
110 migratory foraging strategies and to make linkages to body size. ~~We hypothesized that body size~~  
111 ~~differences, between sexes and colonies, constrain individual wintering strategies of thick-billed murres.~~  
112

## 113 METHODS

114 The Pribilof Islands, with St Paul (57°10'N 170°17'W) to the north and St George (56°34'N 169°36'W)  
115 ~70 km the south, are situated on the edge of the shallow continental shelf in the south-eastern Bering Sea  
116 at the limit of winter sea ice extent, while ~350 km to the south, Bogoslof Island (53°55'N 168°02'W) is  
117 surrounded by deep waters that remain ice free. At these colonies, chick-rearing murres were captured off  
118 ledges using a telescoping noose pole; at recapture some failed breeders were caught with foot snares. A  
119 combined geolocation and time-depth logger (LAT2500, 3.6g, Lotek Wireless Inc., Ontario, CA),  
120 weighing 0.3% of thick-billed murres (hereafter murres) body mass (n = 148, 1058 ± 112 g), was  
121 deployed attached to leg bands during July of 2008-2010, at St Paul (n<sub>LAT2500</sub> = 13/25/19, per year  
122 respectively), St George (n<sub>LAT2500</sub> = 15/16/15) and at Bogoslof in 2008 only (n<sub>LAT2500</sub> = 15). Additional

123 birds used in overwinter survival estimates and for isotope analysis were deployed with a time-depth  
124 logger in 2010/11 (LAT1500, 3.4g, St Paul n=10, St George n=12). Blood samples were taken for  
125 molecular sexing (Fridolfsson & Ellegren 1999). To examine logger effects, 1) body mass of individual  
126 murrelets deployed with loggers at recapture was compared to mass at deployment and 2) body mass was  
127 compared between chick rearing birds retrieved with loggers (2009 and 2010) and birds without.

128 A principal component analysis (PCA) integrated scaled body size metrics measured at  
129 deployment (head+bill, culmen, tarsus, and natural wing chord). The first principle component (PC1)  
130 representing 51.4% of the variance was retained for comparison with foraging strategies as the other  
131 principal components had eigen values less than 1 (Table 1); PC1 was significantly positively correlated  
132 with body mass ( $r^2 = 0.441$ ,  $p < 0.001$ ). In 2011 only, we measured wing area using wing tracings to  
133 calculate wing loading (weight / wing area) (Shaffer, Weimerskirch & Costa 2001; Pennycuik 2008). To  
134 investigate the association of body size with foraging behaviour, PC1 [scores of all birds??](#) was regressed  
135 against the metrics of foraging ([XXX, name them](#)) used to determine migratory strategies.

136

### 137 *Migratory Strategies*

138 To process locations calculated by the geolocation loggers (Ekstrom 2004), we used a generalized  
139 additive model (GAM) with thin plate regression splines to separately smooth both latitude and longitude  
140 over time (Mosbech *et al.* 2011). This allowed for both short and rapid long distance changes in location  
141 and provided tentative estimations during the equinox periods; full tracks are presented, however  
142 residency and associated behaviour analysis was limited to October thru February. We felt that the GAM  
143 approach was warranted, as there was a high degree of error in the tag-derived geolocations, likely due to  
144 periods when the sensor was obscured. For longitude we allowed gamma to remain at the default 1 to  
145 prevent over-smoothing, while the gamma for latitude was adjusted to 1.4 (Mosbech *et al.* 2011). Daily  
146 locations were then predicted using the GAM output.

147 The cumulative amount of time an individual animal spends within a circle of constant radius  
148 around each point, or residency time (Barraquand & Benhamou 2011), was calculated along each track.

149 Ideally this radius is based on a biologically relevant characteristic such as sensory perception, but in our  
150 case we chose a radius (60 km) roughly equivalent to the standard error of the GAM models for latitude  
151 ( $\pm 0.66^\circ$ ) and longitude ( $\pm 0.53^\circ$ ). Because murrelets spent long periods of time in localized areas we used a  
152 temporal step length of one day. Areas of high residency were identified as the upper quartile of each  
153 individual's residency times (Torres *et al.* 2011). The percentage of high residency locations in the Bering  
154 Sea was calculated as a metric of large-scale habitat use. The maximum distance from the colony and the  
155 minimum convex hull area of high residency locations were used to determine individual spatial patterns  
156 and area use.

157         Loggers recorded pressure conditionally every minute below 5 dBar, equivalent to 5 m. Average  
158 dive durations during the breeding season range from 89-120 s (Paredes *et al.* 2008), suggesting our  
159 sampling rate likely provided 1-2 samples per dive, however short shallow dives may be missed. Loggers  
160 independently recorded daily maximum dive depth. Sunrise and set times were determined from  
161 geolocations and matched to dive records to identify dives as day or night ('suncycle', air-sea toolbox 2.0).  
162 Dive bout end criteria were calculated using maximum likelihood estimates from a mixture of 2 random  
163 Poisson processes (DiveMove 1.3.4, (Luque & Guinet 2007)). For the resolution of this dataset, dive bouts  
164 concluded when  $25.7 \pm 3.1$  min ( $n = 80$ ) transpired without a dive.

165         For  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  stable isotope analysis we sampled breast feathers grown in the fall and throat  
166 feathers from breeding plumage grown between February and March (Gaston & Jones 1998). Feathers  
167 were analysed using a Carbo-Elba elemental analyser interfaced with a Finnigan Delta Plus XP mass-  
168 spectrometer (Light Stable Isotope Lab, UCSC). Measurement precision (standard deviation), based on  
169 within-run replicates of the laboratory standard (pugel), was 0.13‰ for  $\delta^{13}\text{C}$  and 0.14‰ for  $\delta^{15}\text{N}$ .

170         Migration foraging strategies were identified on the basis of individual spatial distributions,  
171 diving behaviour, and feather stable isotope values. Standard deviations of diving parameters were  
172 included to account for temporal variation. A PCA was run on the correlation matrix of scaled parameters  
173 (Lê, Josse & Husson 2008). Eight PCs, accounting for 78% of the variance (Table 2), were loaded into a  
174 hierarchical clustering algorithm using Ward's method and Euclidean distances to build the tree. Clusters



175 were determined by minimizing inertia gain between potential clusters (Lê *et al.* 2008). *Post-hoc*, cluster  
176 composition was tested in relationship to body size (PC1), colony, sex, year, and breeding status at  
177 recapture (egg or chick vs. failed). To look at temporal variability in foraging effort within clusters,  
178 percent time diving at night was compared to the fraction of the moon illuminated  
179 (<http://aa.usno.navy.mil/data/docs/MoonFraction.php>). Likewise, stable isotope values from the two  
180 feather tracks and seasonal changes in diving behaviour were assessed within strategies.

181 All data processing and spatial analysis were conducted using MATLAB (The Mathworks,  
182 Natick, MA, USA). All statistical tests were done in R 3.0.0 (R Development Core Team, 2013).  
183 Significance was set to  $p < 0.05$ .

184

## 185 RESULTS

186 Overall, 84% of birds were resighted each year (St George: 2009 = 80%, 2010 = 65%, 2011 = 85%; St  
187 Paul: 2009 = 92%, 2010 = 80%, 2011 = 84%; Bogoslof: 2009 = 93%). Logger recovery rates were 68%  
188 on the Pribilofs and 93% on Bogoslof. Logger failures were common, however 74 tracks and 83 dive  
189 records of various lengths were obtained, resulting in full datasets for 49 individuals (St Paul = 29, St  
190 George = 14, Bogoslof = 6). There was no significant difference in mass between deployment and  
191 recapture for all birds that carried a logger (paired-t = -0.584,  $p = 0.561$ ,  $n = 105$ ), but in 2010, birds  
192 retrieved with loggers, attending chicks, were significantly lighter than control birds ( $F_{1,101} = 7.76$ ,  $p =$   
193  $0.006$ ; Logger =  $1043 \pm 88$ ,  $n = 14$ ; Control =  $1068 \pm 118$ ,  $n = 94$ ); this effect was not different by sex or  
194 colony.

195

### 196 *Body Size*

197 Murres from St Paul had higher mass and wing loading than murres from St George, whereas  
198 measurements of murres from Bogoslof overlapped with both colonies, but St Paul murres were still  
199 heavier (Table 1). Significant sexual size dimorphism was apparent, as males were heavier with larger  
200 structural size (Table 1). Body size (PC1) differed by colony ( $F_{1,47} = 9.97$ ,  $p < 0.001$ ) and sex ( $F_{1,47} =$

201 | 9.71,  $p = 0.003$ ). Body Size had a significant negative relationship to daytime dive depth ( $r^2 = 0.157$ ,  
202 |  $p = 0.003$ ) and bout depth ( $r^2 = 0.200$ ,  $p < 0.001$ ) and a positive relationship to throat feather  $\delta^{15}\text{N}$  ( $r^2 =$   
203 |  $0.121$ ,  $p = 0.011$ ) and  $\delta^{13}\text{C}$  ( $r^2 = 0.229$ ,  $p < 0.001$ ); larger birds were more likely to have high residency  
204 | locations in the Bering Sea than south of the Aleutian Islands (logistic regression,  $z = -16.18$ ,  $p < 0.001$ ;  
205 | Figure 1). Sex differences were found in breast feather  $\delta^{15}\text{N}$  ( $\text{♂} = 16.07 \pm 1.12 \text{‰}$ ,  $\text{♀} = 16.74 \pm 0.59 \text{‰}$ ,  $t =$   
206 |  $2.92$ ,  $p = 0.005$ ), maximum distance of high residency locations ( $\text{♂} = 184 \pm 35$ ,  $\text{♀} = 205 \pm 37$ ,  $t = 2.13$ ,  $p =$   
207 |  $0.038$ ), and percent time diving at night ( $\text{♂} = 6.7 \pm 3.5\%$ ,  $\text{♀} = 10 \pm 6.3\%$ ,  $t = -2.46$ ,  $p = 0.0175$ ).

208

### 209 *Colony Differences in Winter Distributions*

210 | Murres predominantly ( $n =$ ) wintered in the south-eastern Bering Sea and areas south of the Aleutian  
211 | Islands (Figure 2). A few birds travelled away from common wintering areas; three of XX birds from St  
212 | Paul moved into to the western Bering Sea while seven birds from Bogoslof and St George travelled  
213 | eastward into the Gulf of Alaska (Figure 2). Murres from St George and Bogoslof largely left the Bering  
214 | Sea from November through January, while 88% of birds from St Paul ( $n = \text{XX}$ ) spent some of this time  
215 | in the Bering Sea.

216

### 217 *Migration Strategies*

218 | Overall, 19 variables contributed significantly to the cluster analysis and three migration foraging  
219 | strategies were identified (Table 2). Individuals in the first cluster had low  $\delta^{15}\text{N}$  values from throat  
220 | feathers, spent the most time diving, particularly at night, and had longer and more variable dive bouts  
221 | (Table 2), therefore this cluster was termed high frequency divers (Cluster HF). Spatial distributions of  
222 | Cluster HF were largely outside of the Bering Sea along the southern side of the Aleutian Islands (Figure  
223 | 3a). Individuals in the next cluster had the highest values for throat feather  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  (Table 2). These  
224 | birds spent the majority of their time in the Bering Sea (Figure 3a). They dove the least at night, diving  
225 | deeper, mainly during daytime; therefore this cluster was termed deep day divers (Cluster DD). The final

226 cluster was characterized by low throat feather  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$ , similar to Cluster HF, but birds dove to  
227 shallower depths spending less time diving during the day and during dive bouts; these birds spent the  
228 least amount of time in the Bering Sea (Figure 3a). This cluster was termed shallow night divers (Cluster  
229 SN). Maximum dive depth did not contribute to the clusters, but the deepest dive recorded was 207 m.

230 The three clusters related significantly to year ( $\chi^2_4 = 41.93, p < 0.001$ ) and colony ( $\chi^2_4 = 12.03, p$   
231  $= 0.017$ ), but not sex ( $\chi^2_2 = 1.09, p = 0.579$ ) or post-breeding status ( $\chi^2_2 = 3.77, p = 0.152$ ). Cluster SN  
232 contained birds from all three colonies and the majority of birds from 2008/09 (75%) and 2009/10 (81%).  
233 Cluster HF was composed of both St Paul and St George birds from only 2010/11, constituting 87% of  
234 birds from this year; the others were contained in Cluster DD. Cluster DD was composed entirely of birds  
235 from St Paul from all three study years; 31% of birds from St Paul. Body size, represented by PC1, was  
236 significantly related to Cluster DD and SN, with larger bodied birds comprising Cluster DD and smaller  
237 in Cluster SN (Table 2), however body size of birds in Cluster DD was not significantly different than  
238 birds from St Paul in other clusters ( $F_{2,26} = 1.38, p = 0.27$ ).

239 All clusters showed shifts in diving behaviour throughout the non-breeding period, along with  
240 shifts in isotopic values (Table 2, Figure 3b). For all three clusters, depth utilization was at a minimum in  
241 November, and then rapidly increased with the deepest dive depths occurring January through March  
242 (Figure 2b). Depth utilization showed strong monthly cycles in shallow dive depths for Cluster HF  
243 (Figure 2b). A significant positive relationship was found between percent time diving at night and the  
244 fraction of the moon illuminated for Cluster HF ( $F_{1,82} = 9.74, p = 0.002$ ), but not for the other two  
245 clusters. Overall, time spent diving, was lower for birds in Clusters DD ( $6.3 \pm 2.4\%$ ) and SN ( $6.9 \pm$   
246  $2.1\%$ ), whereas birds in Cluster HF increased time spent diving from  $8.0 \pm 2.3\%$  in the fall (Oct-Nov) to  
247  $17.3 \pm 4.0\%$  in (Feb-Mar; Figure 4). Breast feathers (fall) were not a significant contributor in  
248 determining foraging clusters, however throat feathers (late winter) were (Table 2). Seasonal shifts were  
249 evident as breast feather  $\delta^{15}\text{N}$  was significantly higher than throat feather  $\delta^{15}\text{N}$  for Cluster HF (paired-t =  
250  $3.73, p = 0.002$ ) and Cluster SN (paired t =  $5.71, p < 0.001$ ); however,  $\delta^{15}\text{N}$  was not different for Cluster

**Comment [RP8]:** It is not clear to me how the three clusters were related to colony. Cluster SN have all colonies, and HF has both STP and STG, only DD is colony specific.

Although cluster DD were all from STP, 69% of the birds used a different foraging strategy even if they were similarly large in size than those that stay in the Bering Sea. This suggest body size maybe a factor but not a strong one for explaining winter foraging strategies. Do you know whether most remaining birds from STP were in Cluster HF (year-related). If so it could partially explain shifts of strategies due to environmental conditions.

251 DD (paired-t = -1.04,  $p = 0.3282$ ). Significant shifts in  $\delta^{13}\text{C}$  occurred from fall to winter; decreasing for  
252 Cluster HF (paired-t = 2.32,  $p = 0.039$ ) and Cluster SN (paired t = 2.17,  $p = 0.040$ ), while Cluster DD  
253 increased (paired-t = -3.44,  $p = 0.009$ ).

254 Since isotope values in throat feathers significantly influenced foraging clusters, we analysed  
255 these from all birds sampled throughout the study ( $n = 211$  winter trips) in a hierarchical cluster analysis  
256 to test association of foraging clusters with isotopic based clusters. Murres clustered into three groups  
257 significantly related to colony ( $\chi^2_4 = 52.69$ ,  $p < 0.001$ ) and year ( $\chi^2_4 = 27.63$ ,  $p < 0.001$ ), but not sex ( $\chi^2_4 =$   
258  $0.04$ ,  $p = 0.978$ ; Figure 5). Birds from St Paul dominated Cluster C (94%), characterized by high  $\delta^{15}\text{N}$  and  
259  $\delta^{13}\text{C}$ . All of the tracked birds from Cluster DD, were included in this elevated  $\delta^{15}\text{N}$  group along with two  
260 two birds from St George and two birds from Cluster HF, suggesting that this solely isotopic based cluster  
261 related strongly to the St Paul deep day diving strategy. We then assessed the prevalence of elevated  $\delta^{15}\text{N}$   
262 (Cluster C) and tested fidelity to this strategy between years ( $n = 28$  birds). The proportion of birds in  
263 Cluster C differed by year (2008/09 = 57.7%, 2009/10 = 31.7%, 2010/11 = 46.4%), with 60% of  
264 individuals from St Paul using this foraging strategy in at least one year. Individuals were not always  
265 faithful to this strategy as 64% of birds changed isotopic clusters. The other isotope clusters did not  
266 separate according to foraging cluster (Figure 5).

267

## 268 DISCUSSION

269 Wintering murres maintained a relatively large degree of spatial structure in both horizontal and vertical  
270 distributions relative to their breeding colony, which was associated with body size differences. We found  
271 that metrics of foraging behaviour, specifically dive depth, late winter isotopic values, and residency in  
272 the Bering Sea, correlated significantly with body size and predicted the winter foraging strategies of  
273 individual thick-billed murres. A portion of the birds from the colony with the largest body size, St Paul,  
274 utilized a unique more residential deep day diving foraging strategy. Nonetheless, these birds were able to  
275 switch foraging strategies between years. The majority of the birds in our study, significantly smaller in  
276 body size, travelled south of the Aleutian Islands and employed a shallow night diving strategy. Birds

277 seasonally adjusted foraging behaviour indicating high flexibility in response to environmental changes.

278 Overall, winter foraging strategies appear to relate strongly to both body size and annual changes rather  
279 than a random assortment of individual foraging strategies.

Comment [RP9]: This is much more understandable than the abstract

280

#### 281 *Logger Effects*

282 Attaching instruments to a small diving flying seabird is challenging because attachment location and  
283 buoyancy, size and weight of instruments can all have measurable negative effects (Paredes, Jones &  
284 Boness 2005; Vandenabeele *et al.* 2011; Elliott *et al.* 2012). In our study the majority of birds returned to  
285 breed, mass at recapture was not significantly different than at deployment, however following the winter  
286 of 2009/10 birds carrying geolocators (and raising chicks) were lighter than control birds. However, birds  
287 from 2009/10 clustered with the previous year suggesting that behavioral differences were minimal.  
288 Throat feathers from both instrumented and control birds had elevated  $\delta^{15}\text{N}$  and  $\delta^{13}\text{C}$  suggesting that this  
289 strategy is not an artifact of logger effects.

290

#### 291 *Body Size and Foraging Strategies*

292 Differences in body size of birds from our three study colonies could have evolved due to summer  
293 foraging conditions, similar to blue-eyed shags (*Phalacrocorax verrucosus*) breeding in the Kerguelen  
294 archipelago where there are colony based differences in diets, foraging habitats and distances to foraging  
295 areas (Cook *et al.* 2013). Together, long-term differences in summer diets and recent tracking data  
296 (Sinclair *et al.* 2008; Renner *et al.* 2012)(Harding *et al.* 2013), suggest that St Paul birds are constrained  
297 to shelf habitats and may have specialized to feed locally on benthic prey, while murrelets from St George  
298 and Bogoslof are able to forage over the basin. St George birds commute long distances on over-night  
299 trips that may favour smaller body size whereas Bogoslof birds can access deep waters adjacent to the  
300 colony (Harding *et al.* 2013). Regardless of the mechanistic explanation of body size differences, there  
301 appear to be similarities between summer foraging and those behaviours employed during the winter.

302 Flying is the most expensive foraging activity for murrelets, while dive costs are minimal (Elliott *et*

303 | *al.* 2013). Although wintering murre are not constrained by central-place foraging, The the higher wing-  
304 | loading of mures from St Paul, relative to those breeding at St George, may be a contributing factor  
305 | constrain these birds to fly less, thereby for limited limiting distributions of larger birds. Overall our study  
306 | birds did not travel substantial distances, especially when compared to the smaller mures in the North  
307 | Atlantic (Gaston *et al.* 2011; Fort *et al.* 2013), though birds breeding in the northern Bering sea have the  
308 | potential to travel comparable distances to wintering areas. Allometry predicts that divers of larger body  
309 | size will dive deeper and longer due to lower mass-specific metabolic rates and increased O<sub>2</sub> stores  
310 | (Kleiber, 1961; Boyd & Croxall 1996; Schreer & Kovacs 1997; Halsey, Butler & Blackburn 2006). This  
311 | may apply to murre, which daily maximum dive depths negatively correlated with individual body size.  
312 | Larger mures from Cluster DD did not dive to the deepest depths, but did spend the most time at deeper  
313 | depths and overall. These mures also spent the least amount of time diving, suggesting they were able to  
314 | meet daily energetic needs with fewer dive, similar to cormorants wintering in Greenland (Grémillet *et al.*  
315 | 2001). When compared to mures wintering in the Atlantic these larger birds spent less time diving (Fort  
316 | et al. 2013), further suggesting that these birds were able to reduce energy expenditure, despite the higher  
317 | requirements of their larger bodies (Peters 1983). It appears that wintering murre behaviour followed  
318 | expected predictions for both modes of transport, flight and diving.

319 | Murre fathers accompany their flightless chicks out to sea and related differential distributions  
320 | between the sexes are known to occur in Alaskan populations during the fall (Hatch *et al.* 2000), while  
321 | males tracked from the high Canadian Arctic tend to remain farther north than females (Gaston *et al.*  
322 | 2011). Despite these sex specific behaviours and the sexual size dimorphism of our study populations, we  
323 | did not find differences in foraging strategies related to sex. We did find differences in breast feather  
324 |  $\delta^{15}\text{N}$ , percent time diving at night and maximum distance, but these differences did not drive the cluster  
325 | analysis. It appears that though sex differences in behaviour occurred, in particular breast feathers likely  
326 | represent the autumn, during the winter (Oct-Feb) behaviours grouped birds related to colony, body size,  
327 | and year.

328

**Comment [RP10]:** What is the point here. If in general birds did not fly longer distances (including smaller birds from STG) then it does not support flying constraints.

**Comment [RP11]:** These birds are comparable to smaller birds (STG) so it make sense. I think this is too speculative to discuss energy expenditure. It also contradicts the idea of larger body size being a problem for STP birds

**Comment [RP12]:** it does not follow discussion on body size.

329 *Diets, Foraging, and Distributions*

330 In addition to forage fishes and squid, thick-billed murrens consume euphausiids and amphipods, both  
331 during breeding and the winter (Falk & Durinck 1996; Renner *et al.* 2012). Elevated  $\delta^{15}\text{N}$  values can  
332 result from higher trophic level foraging, spatial changes in the baseline of the food web, and fasting (Post  
333 2002). In the Bering Sea there is a strong baseline gradient of  $\delta^{15}\text{N}$  with lower values occurring in the  
334 basin and increasing on the shelf (Schell, Barnett & Vinette 1998; Jones *et al.* 2014); however  
335 euphausiids in the Alaska Stream are more similar to the south-eastern Bering Sea than the Gulf of Alaska  
336 (pers. comm Pomerleau)(Pomerleau *et al.* 2014). Thus given the location data, the throat feather  $\delta^{15}\text{N}$   
337 values indicate that, Cluster DD are likely foraging on a higher trophic diet than the majority of wintering  
338 murrens. For Cluster DD,  $\delta^{15}\text{N}$  increased from fall to winter while most birds maintained residency in the  
339 Bering Sea. This difference, suggests that these birds could be consuming more fish and squid in the later  
340 winter than during the fall, while those in the other clusters reduced their intake. Thick-billed murrens  
341 wintering off the south-west coast of Greenland also appear to increase reliance on fish during the late  
342 winter (Linnebjerg *et al.* 2013), while birds from the high Arctic showed little seasonal variability in diets  
343 (Karnovsky *et al.* 2008).

344 Murrens in both Cluster SN and Cluster HF dived to shallow depths at night, a behaviour  
345 associated with foraging on diel-vertically migrating prey (Benoit-Bird *et al.* 2011; 2013). Birds using  
346 these strategies wintered predominately in oceanic waters south of the Aleutians and along the continental  
347 slope. This off-shore area is influenced by the Alaska Stream and characterized by an oceanic  
348 zooplankton community, including the euphausiid, *Euphausia pacifica* (Coyle 2005). This oceanic  
349 euphausiid may be a predictable prey source for fishes, squids and murrens, as they are omnivorous, can  
350 produce multiple broods in a year, have continuous growth rates and showed little annual variation in  
351 abundance over 5 years in the Gulf of Alaska (Pinchuk, Coyle & Hopcroft 2008). However, despite this  
352 evidence of a predictable prey source, foraging behaviour changed in 2010/11.

353 One of the strongest La Niña years on record occurred during 2010/11 following closely after  
354 central Pacific El Niño conditions (Hu *et al.* 2014). Concomitantly, zooplankton biomass, survival

355 estimates for age-1 pollock, and catch rates of juvenile pink salmon in the Gulf of Alaska were all low  
356 (Orsi *et al.* 2013) Zador (ed.), 2013). During this winter murrens increased their foraging effort; notably  
357 through longer bout durations, moonlight foraging and a ~2-fold increase in time spent foraging,  
358 particularly in the later half of the winter. Murrens from Bogoslof were not tracked in 2010/11, however  
359 the high degree of spatial overlap between St George and Bogoslof birds in 2008/09, suggests that birds  
360 from Bogoslof likely responded similarly to apparent low prey availability.

361         Within each cluster murrens exhibited the capacity to adjust foraging behaviour in response to  
362 environmental changes. On the daily and monthly scales, foraging strategies related to preferences for  
363 foraging during the day or night. Like murrens wintering in the North Atlantic, dives shoaled in the late fall  
364 and then deepened in the mid-winter, probably in response to seasonally driven shifts in prey availability  
365 within the water column (Fort *et al.* 2013). The HF cluster birds dove more with increasing moonlight, a  
366 behaviour observed in common murrens who increased diving efficiency with moonlight versus starlight  
367 (Regular *et al.* 2011). Within the clusters, standard deviations indicate a substantial amount of individual  
368 variation in behaviour. Spatially thick-billed murrens wintering in the northwest Atlantic showed diversity  
369 in core wintering areas (McFarlane Tranquilla *et al.* 2014), similarly in this study individual tracks were  
370 dispersive though the wintering area. Likewise, wintering diets are geographically and seasonally flexible.  
371 Combined, temporal plasticity in foraging behaviour and diversity of behaviours between individuals  
372 shows an impressive capacity to adjust behaviours in response to local conditions.

373

#### 374 *Conclusions*

375 Constrained to relatively small winter ranges thick-billed murrens exhibited remarkable seasonal flexibility  
376 in diving behaviour likely in relationship to seasonal changes in prey distributions. Broadly, foraging  
377 strategies were linked to body size differences associated with the three breeding colonies and partitioned  
378 with respect to annual differences, presumably in relationship to shifts in prey distributions. The  
379 consistent presence of uniquely St. Paul associated wintering strategy indicates a complex regulation of  
380 overwinter survival. As the St. Paul colony is in a continued state of decline (Byrd, Schmutz & Renner



381 2008), the behavioural flexibility exhibited by murre, constrained by body size, may not be enough to  
382 adapt to changing conditions in the Bering Sea.

**Comment [RP13]:** I would end before this paragraph. I am convinced at this point that large body size is a constraint during the winter or move it to discussion but no conclusion

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395

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583 **Table 1.** Morphometric comparison of thick-billed murre (*Uria lomvia algae*) from colonies in the south-eastern Bering Sea. Bold sexual size  
 584 dimorphism (SSD) values indicates sexes are significantly different (SSD = (male-female)/female x 100). Three-way colony comparisons are  
 585 results of t-tests. Sample sizes are indicated in parentheses. Means  $\pm$  SD.

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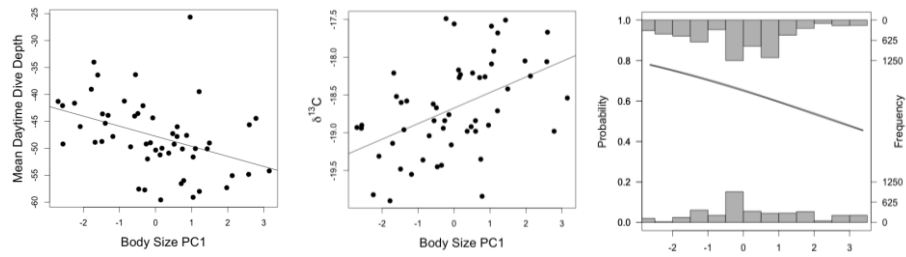
	St Paul (P)			St George (G)			Bogoslof (B)			Colony Comparison
	♂ (39)	♀ (36)	SDD	♂ (53)	♀ (29)	SDD	♂ (17)	♀ (15)	SDD	
Body Mass (g)	1184 $\pm$ 101	1106 $\pm$ 96	<b>7.65</b>	998 $\pm$ 61	960 $\pm$ 65	<b>4.27</b>	1038 $\pm$ 73	1003 $\pm$ 54	<b>3.39</b>	P>B=G
Culmen (mm)	42.8 $\pm$ 2.6	41.6 $\pm$ 2.0	<b>2.88</b>	41.1 $\pm$ 2.1	39.8 $\pm$ 2.0	<b>3.27</b>	42.1 $\pm$ 2.1	40.1 $\pm$ 1.8	<b>5.00</b>	P>G, P=B, G=B
Head+bill (mm)	117.1 $\pm$ 3.2	113.7 $\pm$ 2.4	<b>3.09</b>	112.0 $\pm$ 3.3	109.9 $\pm$ 2.9	<b>1.91</b>	114.9 $\pm$ 2.7	111.1 $\pm$ 3.4	<b>3.42</b>	P>G, P=B, G=B
Tarsus (mm)	40.7 $\pm$ 1.8	39.0 $\pm$ 1.9	<b>4.35</b>	38.9 $\pm$ 1.7	37.8 $\pm$ 1.3	<b>2.91</b>	40.1 $\pm$ 1.4	38.9 $\pm$ 2.5	<b>3.08</b>	P>G, P=B, G=B
Wing (mm)	227 $\pm$ 6	226 $\pm$ 5	0.44	223 $\pm$ 6	222 $\pm$ 4	0.45	223 $\pm$ 7	224 $\pm$ 5	-0.45	P>G, P=B, G=B
Wing Area (cm <sup>2</sup> )*	719.4 $\pm$ 26.2	708.1 $\pm$ 50.0	1.60	679.5 $\pm$ 34.9	647.6 $\pm$ 45.8	4.93	-	-	-	P>G
Wing Loading (Nm <sup>2</sup> )*	163.6 $\pm$ 7.4	165.2 $\pm$ 14.7	-0.96	147.1 $\pm$ 8.1	140.7 $\pm$ 6.0	4.57	-	-	-	P>G

587 \*St Paul ♂ (7), ♀ (8); St George ♂ (12), ♀ (5).

588 **Table 2.** Behavioural parameters ( $\pm$  SD) used to determine wintering foraging clusters of thick-  
589 billed murre. The importance of each variable in determining clusters was tested via an F-test  
590 and variables that significantly contribute to each cluster ( $p < 0.05$ ) are shown in bold.  $\eta^2$  is  
591 presented as an index of the proportion of variance explained by each of the factors, bold  $\eta^2$   
592 indicate a significant contribution to the overall model. Sex, colony, year, and body size PC1  
593 were not included as variables in the cluster analysis.  
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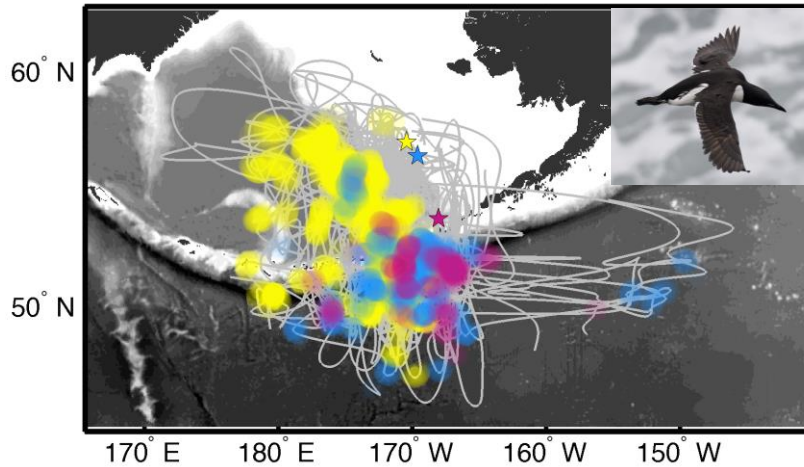
	$\eta^2$	High Frequency	Deep Day	Shallow Night
n		13	9	27
Sex ( $\delta/\text{♀}$ )	-	6/7	6/3	13/14
Colony (P/G/B)	-	7/6/0	9/0/0	13/8/6
Year (2008/2009/2010)	-	0/0/13	3/4/2	9/18/0
Body Size PCI	-	-0.02 ± 1.52	<b>1.20 ± 0.94</b>	<b>-0.42 ± 0.89</b>
<b>Diet</b>				
Throat $\delta^{15}\text{N}$ (‰)	<b>0.41</b>	14.82 ± 1.52	<b>17.05 ± 0.78</b>	<b>14.78 ± 0.89</b>
Throat $\delta^{13}\text{C}$ (‰)	<b>0.41</b>	-18.63 ± 0.31	<b>-17.89 ± 0.31</b>	<b>-18.96 ± 0.49</b>
Breast $\delta^{15}\text{N}$ (‰)	0.10	16.71 ± 1.04	16.69 ± 0.65	<b>16.09 ± 0.96</b>
Breast $\delta^{13}\text{C}$ (‰)	0.12	<b>-18.11 ± 0.48</b>	-18.60 ± 0.60	-18.60 ± 0.66
<b>Spatial</b>				
% HR in Bering Sea convex hull area (Mm <sup>2</sup> )	<b>0.28</b>	27 ± 50	<b>82 ± 32</b>	<b>23 ± 35</b>
Max. distance (km)	0.00	43.2 ± 45.8	52.3 ± 74.7	50.4 ± 62.3
	0.03	189 ± 27	207 ± 31	190 ± 43
<b>Temporal</b>				
date of maximum depth	0.08	Jan 20 ± 26	Jan 13 ± 44	Jan 31 ± 29
date at maximum distance	<b>0.21</b>	<b>Nov 18 ± 42</b>	Nov 11 ± 42	<b>Jan 1 ± 45</b>
<b>Dive</b>				
maximum dive depth (m)	0.13	<b>161.8 ± 22.7</b>	143.6 ± 14.2	152.3 ± 13.7
% 24 hr day diving	<b>0.37</b>	<b>10.2 ± 3.6</b>	7.4 ± 2.5	<b>5.7 ± 2.0</b>
day mean depth (m)	<b>0.35</b>	50.5 ± 6.0	<b>54.1 ± 3.6</b>	<b>44.1 ± 6.3</b>
SD % 24 hr day diving	<b>0.56</b>	<b>7.1 ± 1.2</b>	4.6 ± 2.1	<b>3.6 ± 1.1</b>
SD day depth (m)	<b>0.65</b>	<b>20.5 ± 2.8</b>	<b>11.1 ± 1.9</b>	<b>13.1 ± 2.8</b>
% 24 hr night diving	<b>0.31</b>	<b>13.0 ± 6.8</b>	<b>4.5 ± 2.3</b>	7.9 ± 3.7
night mean depth (m)	0.02	32.3 ± 4.1	33.6 ± 7.3	31.4 ± 6.5
SD % 24 hr night diving	<b>0.47</b>	<b>15.1 ± 6.7</b>	<b>4.1 ± 1.8</b>	<b>7.2 ± 3.5</b>
SD night depth (m)	<b>0.16</b>	<b>13.9 ± 3.2</b>	12.9 ± 2.9	<b>11.2 ± 2.6</b>
<b>Dive Bouts</b>				
bout duration (min)	<b>0.13</b>	<b>80.5 ± 23.3</b>	65.4 ± 10.3	67.9 ± 12.3
bout depth (m)	<b>0.39</b>	40.0 ± 4.1	<b>47.0 ± 4.3</b>	<b>39.6 ± 5.1</b>
% of bout diving	<b>0.64</b>	<b>59.1 ± 3.7</b>	41.4 ± 11.8	<b>39.0 ± 5.6</b>
post bout interval (min)	0.12	333 ± 224	622 ± 651	310 ± 194
# of bouts / day	0.02	4.0 ± 0.5	3.9 ± 0.5	4.1 ± 0.7
SD bout duration (min)	<b>0.42</b>	<b>105.4 ± 26.5</b>	68.0 ± 13.6	<b>68.1 ± 18.0</b>
SD bout depth	<b>0.39</b>	<b>21.4 ± 3.6</b>	16.8 ± 1.7	<b>16.9 ± 2.3</b>
SD % of bout diving	<b>0.31</b>	<b>30.1 ± 4.3</b>	<b>20.9 ± 5.2</b>	23.9 ± 5.3
SD # bouts / day	<b>0.21</b>	<b>1.72 ± 0.35</b>	<b>1.34 ± 0.26</b>	1.48 ± 0.24



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600 Figure 1 Relationship between body size (PC1 of culmen, head+bill, tarsus and wing length) and  
601 a) mean daytime diving depth, b) throat feather  $\delta^{13}\text{C}$  (‰), and c) logistic regression of locations  
602 in the Bering Sea (0) versus locations in the North Pacific south of the Aleutians (1).

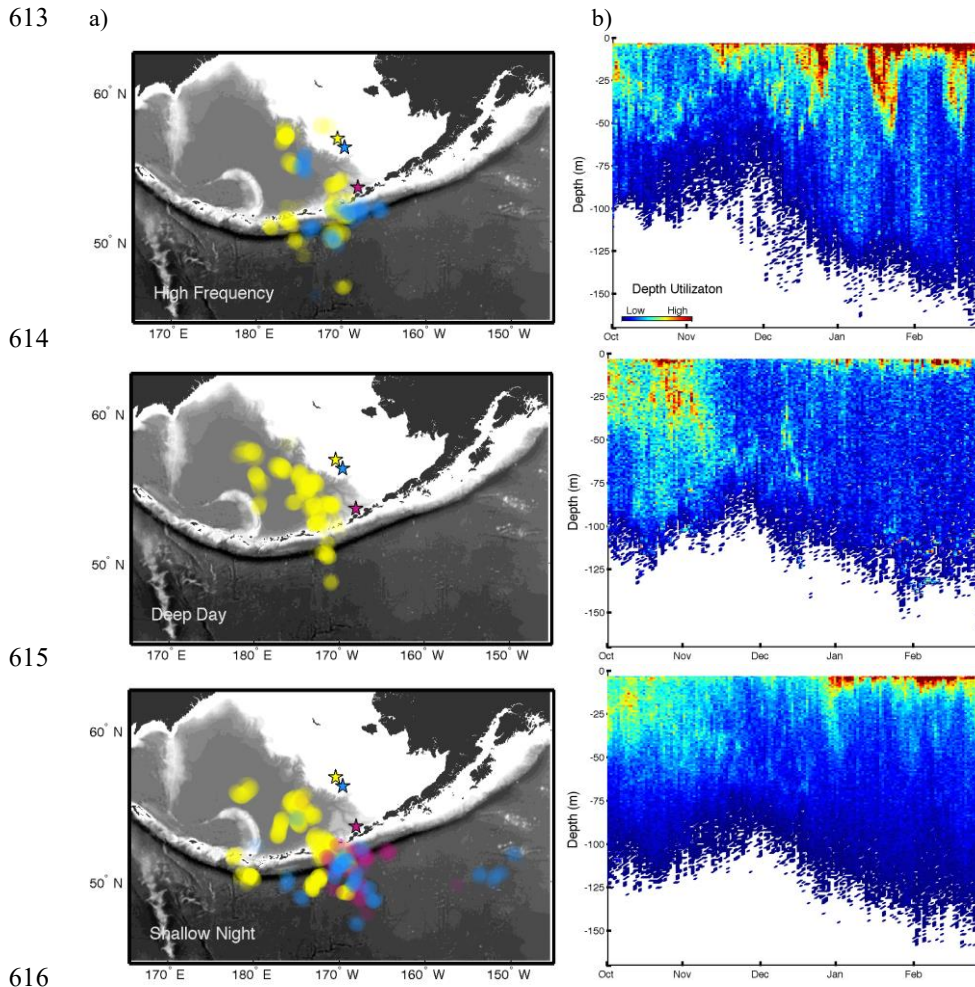
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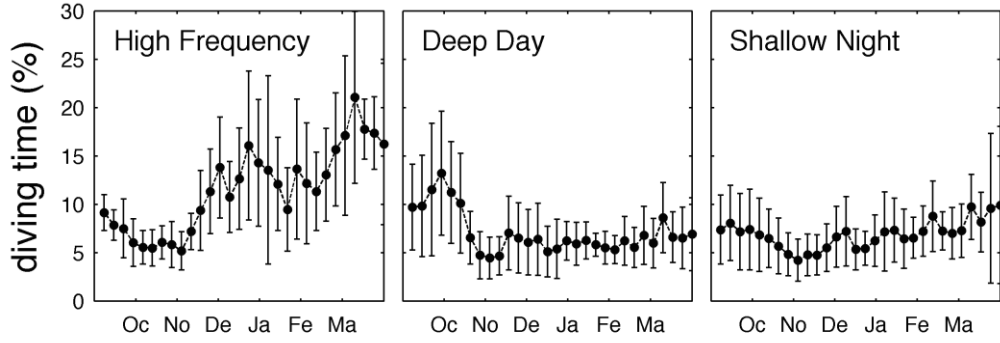
606 Figure 2. Winter distributions of thick-billed murres in the Bering Sea and North Pacific. High  
607 residency locations of birds from St Paul (yellow, n = 40), St George (blue, n = 23) and Bogoslof  
608 (pink, n = 11), are shown from October thru February with complete tracks in grey, the radius of  
609 the circles is scaled to the search area of residency time (60 km). Stars of corresponding colours  
610 label the colonies. Inset: A thick-billed murre in flight at St Paul Island, Alaska (photo: Dan  
611 Cushing).

612



618 Figure 3. Winter distributions and depth utilization of thick-billed murres, October thru February,  
 619 by foraging cluster with a) spatial extent, (high residency locations; St Paul [yellow], St George  
 620 [blue] and Bogoslof [pink]) and b) depth utilization of the three foraging clusters. Depth  
 621 utilization is normalized by the number of birds tracked daily.

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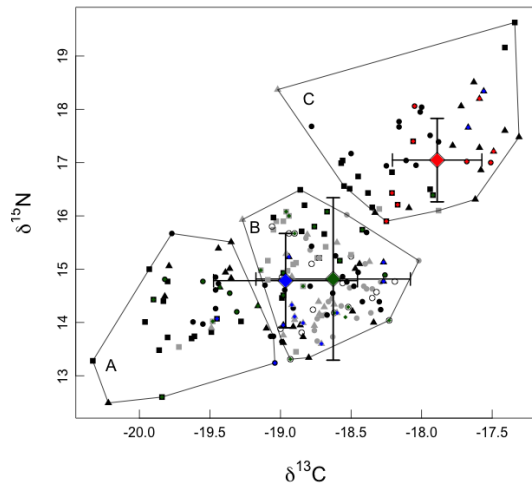
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625 Figure 4. Weekly proportion of time (24 hrs) spent diving ± standard deviation for thick-billed murres

626 from the three winter foraging clusters.

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631 Figure 5. Isotopic Clusters A, B, & C from throat feathers (n = 211), overlaid with isotopic values from  
632 foraging clusters HF, DD, & SN (cross plot  $\pm$  SD). Sampling years (summer) are indicated by circles  
633 (2009), squares (2010), and triangles (2011), while colonies are shown by black (St Paul), grey (St  
634 George), and white (Bogoslof). Points corresponding to individuals included in the foraging cluster  
635 analysis are overlaid with a circle, coloured according to cluster (HF = blue, DD = red, and SN = green).

636